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DOCTOR OF PHILOSOPHY  
In the Faculty of Humanities

**The Effects of Acute Stress on Retrieval of Visual and Spatial Material**

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### **Declaration**

I hereby declare that this submission is my own work, both in concept and execution, and that to the best of my knowledge and belief it contains no material written by another person nor material that has been accepted for the award of any other degree or diploma of the university or other institute of higher learning, except where due acknowledgment has been made in the text.

This thesis contains previously published material. However, the research on which the paper was based is entirely my own, and as first author, I wrote all draft versions of the paper.

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Christopher du Plooy

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Date

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## Abbreviations

The following table describes the significance of various abbreviations used throughout the dissertation.

Abbreviation	Meaning
ACSENT	Applied Cognitive Science and Experimental Neuropsychology Team
ART	Arena Reconstitution Task
BDI-II	Beck Depression Inventory - Second Edition
BLA	basolateral amygdala
$\chi^2$	chi-square
$d$	Cohen's $d$
CG	Computer Generated
CPT	Cold Pressor Test
$d'$	$d$ prime
ECG	electrocardiogram
$\varepsilon$	epsilon
FFST	Fear-Factor Stress Test
fMRI	functional magnetic resonance imaging
GC	glucocorticoid
GSR	galvanic skin response
HPA	hypothalamic-pituitary-adrenal
Hot+	Hot Appetitive
Hot-	Hot Defensive
HR	heart rate
IAPS	International Affective Picture System
ICG	impedance cardiogram
LTP	long-term potentiation
MAST	Maastricht Acute Stress Test
MWM	Morris Water Maze
MTT	Multiple Trace Theory
nmol/L	nanomoles per litre
ORT	Object Recognition Task
$\eta_p^2$	partial eta squared
PET	positron emission tomography
SAM	Self-Assessment Manikin
SCT	Standard Consolidation Theory
SECPT	Socially Evaluated Cold Pressor Test
SRPP	Student Research Participation Program
STAI	State-Trait Anxiety Inventory
TSST	Trier Social Stress Test
UCT	University of Cape Town
VE	virtual environment
VPA	Verbal Paired Associates test
VU-AMS	Vrije Universiteit Ambulatory Monitoring System

## Table of Contents

Declaration .....	2
Acknowledgements .....	3
List of Abbreviations .....	4
Table of Contents .....	5
List of Figures .....	10
List of Tables .....	12
<b>ABSTRACT</b> .....	13
<b>CHAPTER ONE: GENERAL INTRODUCTION</b> .....	14
The Stress Response .....	15
Stress and Memory .....	17
Emotional memory .....	18
Acute Stress and Episodic Memory .....	20
Memory encoding .....	20
Memory consolidation .....	22
Memory retrieval .....	23
Reconsolidation .....	25
Theoretical Explanations for the Effects of Stress on Memory .....	26
State-dependent learning hypothesis .....	27
Inverted-U hypothesis .....	27
Hot-cool theory .....	29
The vertical and horizontal perspective theory .....	30
The Hippocampus and Episodic Memory .....	34
Standard Consolidation Theory .....	35
Multiple Trace Theory .....	36
Hippocampus and Spatial Memory .....	37
Summary .....	40
Aims and Rationale .....	41
<b>CHAPTER TWO: STUDY A – VALIDATION OF THE SPATIAL ENVIRONMENTS</b> .....	43
Cognitive Maps .....	43
Route-, survey-, and landmark-based information .....	44
Landmarks in cognitive maps .....	45
Sex Differences in Spatial Memory .....	47
The Use of Virtual Environments in Cognitive Neuroscience Research .....	48
The Computer-Generated Arena .....	49
Aims, Rationale, and Hypotheses .....	50
<b>Methods</b> .....	51
Participants .....	51
Stimulus Selection .....	52
Apparatus: The CG Arena .....	53
Movement in the CG Arena .....	54
The waiting room .....	54
The CG Arena experimental rooms .....	55
Other Apparatus .....	60
Object Recognition Task (ORT) .....	60
Arena Reconstitution Task (ART) .....	60
Procedure .....	61
Data Analysis .....	62

The CG Arena .....	62
ORT score .....	62
ART score .....	62
<b>Results</b> .....	63
Sample Characteristics .....	63
Training Trials .....	63
Hot and Cool rooms: Effects of counterbalancing .....	65
Invisible Target Trials .....	65
Object Recognition Task .....	67
Arena Reconstitution Task .....	68
Sex Differences .....	69
Between-sex comparisons .....	69
Within-sex comparisons .....	71
<b>Discussion</b> .....	73
Conclusion .....	75
<b>CHAPTER THREE: STUDY B – VALIDATION OF THE STRESSOR</b> .....	76
Laboratory Stressors .....	76
Aims and Hypotheses .....	78
<b>Methods</b> .....	78
Participants .....	78
Experimental Manipulations .....	78
Materials .....	80
Physiological measures .....	80
Self-report measures .....	82
Procedure .....	83
Data Analysis .....	84
<b>Results</b> .....	85
Subjective Anxiety .....	85
Heart Rate .....	86
Cortisol Responses .....	87
Cortisol Responders .....	89
<b>Discussion</b> .....	90
Limitations .....	92
Conclusion .....	94
<b>CHAPTER FOUR: STUDY 1 - THE EFFECTS OF ACUTE STRESS ON RETRIEVAL OF VISUAL AND SPATIAL MATERIAL</b> .....	95
The Effects of Stress on Visual and Spatial Memory .....	95
The effects of stress on visual and spatial retrieval memory in humans .....	96
The Functional Perspective of Memory .....	99
Summary .....	102
Aims, Rationale, and Hypotheses .....	103
<b>Methods</b> .....	105
Participants .....	105
Materials .....	106
Physiological measures .....	106
Self-report measurements .....	107
Apparatus .....	107
The Computer-Generated Arena .....	107
Object Recognition Task (ORT) .....	108
Verbal Paired Associates Test (VPA) .....	108

Procedure .....	110
Day 1 .....	110
Day 2 .....	111
Data Analysis .....	112
<b>Results</b> .....	113
Sample Characteristics .....	113
Age .....	113
BMI .....	113
BDI-II scores .....	114
STAI-Trait scores .....	114
Experimental Manipulation .....	114
Self-report anxiety measure: STAI – State .....	115
Salivary cortisol .....	117
Heart rate .....	119
Galvanic skin response .....	121
CG Arena .....	123
Training Phase: Visible-target training trials .....	123
Acquisition Phase: Invisible-target acquisition trials .....	124
Recall Phase .....	128
Verbal Paired Associates Test .....	134
Day 1: Immediate recall trials .....	135
Day 2: Recall trial .....	136
Cortisol Responders vs. Control Participants .....	138
<b>Discussion</b> .....	140
Summary of Results .....	141
Conclusion .....	148
<b>CHAPTER 5: EFFECTS OF CORTISOL ADMINISTRATION ON RETRIEVAL OF VISUAL AND SPATIAL MATERIAL</b> .....	149
Effects of Cortisol on Memory Retrieval .....	149
Aims, Rationale, and Hypotheses .....	151
<b>Methods</b> .....	152
Participants .....	152
Materials and Apparatus .....	153
Prednisone .....	153
Procedure .....	154
Data Analysis .....	155
<b>Results</b> .....	156
Sample Characteristics .....	156
Age .....	156
BDI-II scores .....	156
STAI-Trait scores .....	157
Experimental Manipulation .....	157
Salivary cortisol levels .....	158
STAI-State .....	160
CG Arena .....	161
Training phase: Visible-target trials .....	161
Acquisition phase: Invisible-target trials .....	162
Recall phase .....	167
Verbal Paired Associates Test .....	173
Day 1: Immediate recall trials .....	173

Day 2: Delayed recall .....	175
<b>Discussion</b> .....	177
Summary of Results .....	178
Summary of results in relation to tested hypotheses .....	180
Conclusion .....	183
<b>CHAPTER SIX: GENERAL DISCUSSION</b> .....	184
Summary of Previous Chapters .....	184
Hypothesis 1: Stress and cortisol administration will impair memory retrieval ....	191
Ceiling/floor effects .....	193
Encoding differences .....	194
Congruent learning/testing context or relaxed testing conditions .....	195
Hypothesis 2: Memory for the different CG Arena rooms will be influenced by the arousal content of the pictures used as landmarks in the rooms .....	197
Findings in Relation to Theoretical Explanations .....	199
Verbal memory .....	200
Visual and spatial memory .....	202
Findings in Relation to the Functional Perspective of Memory .....	203
Hypothesis 3: Women will display inferior spatial memory in comparison to men .....	206
Limitations .....	210
Sample used in the current studies .....	210
Time of day .....	211
Change in apparatus and loss of data in Study 2 .....	211
Spatial environments .....	211
Inter-individual variation on wayfinding task .....	212
Non-emotional verbal task .....	213
Cortisol responders versus non-responders .....	213
Conclusions and Future Research Directions .....	214
<b>REFERENCES</b> .....	217
<b>APPENDIX A: Validation of Visual Stimuli</b> .....	250
Defensive Motivation .....	251
Appetitive Motivation .....	253
Differences in activation of the defensive and appetitive systems .....	253
Sex Differences in Picture Viewing .....	254
Rationale and Hypotheses for the Pilot Study .....	256
<b>Methods</b> .....	257
Participants .....	257
Stimulus Selection .....	257
Apparatus .....	258
Procedure .....	259
<b>Results</b> .....	260
Reliability .....	260
Dimensions of Emotion .....	260
Ratings of Valence, Arousal and Dominance .....	262
Sex Differences in Picture Evaluation .....	264
Dimensions of emotion .....	264
Ratings of valence, arousal and dominance of picture groups between the sexes .....	266
Ratings of valence, arousal and dominance of picture groups within the sexes .....	267

<b>Discussion</b> .....	268
<b>APPENDIX B: Images in the Cool, Hot Appetitive and Hot Defensive CG Arena Rooms</b> .....	283
<b>APPENDIX C: Dimensions and Parameters for the CG Arena Rooms used in Study A, Study 1 and Study 2</b> .....	286
<b>APPENDIX D: Start and Target Locations in The CG Arena for Study A, Study 1 and Study 2</b> .....	288
<b>APPENDIX E: Cool, Hot Appetitive and Hot Defensive Distractor Images in the Object Recognition Task (ORT)</b> .....	290
<b>APPENDIX F: Example of Arena Reconstitution Task Score Sheet</b> .....	293
<b>APPENDIX G: Informed Consent Form for Study A</b> .....	295
<b>APPENDIX H: Demographic Questionnaire</b> .....	299
<b>APPENDIX I: Informed Consent Form for Study B and Study 1</b> .....	301
<b>APPENDIX J: Cortisol Responders versus Control Participant Analyses</b> .....	305
Cortisol Responders vs. Control Participants .....	305
Physiological stress measures .....	305
CG Arena .....	307
Verbal Paired Associates Test .....	314
<b>APPENDIX K: Informed Consent Form for Study 2</b> .....	319

## List of Figures

<i>Figure 1.</i> The layout the waiting room. ....	54
<i>Figure 2.</i> The layout the training room. ....	57
<i>Figure 3.</i> The layout the Cool CG Arena experimental room. ....	58
<i>Figure 4.</i> The layout the Hot Defensive CG Arena experimental room. ....	59
<i>Figure 5.</i> The layout the Hot Appetitive CG Arena experimental room. ....	59
<i>Figure 6.</i> Average path lengths to find the target in four CG Arena rooms. ....	64
<i>Figure 7.</i> Box and whisker plot showing the deviations from optimal path length across the four trials in the CG Arena training room. ....	64
<i>Figure 8.</i> Deviations from the optimal path length across the 7 trials in the Cool, Hot Appetitive and Hot Defensive rooms. ....	67
<i>Figure 9.</i> Object Recognition Task (ORT) accuracy scores for the three CG Arena experimental rooms. ....	68
<i>Figure 10.</i> Arena Reconstitution Task (ART) scores for the three CG Arena experimental rooms. ....	69
<i>Figure 11.</i> Deviations from the optimal path length across the 7 acquisition trials in the Cool, Hot Appetitive, and Hot Defensive rooms for men and women. ....	70
<i>Figure 12.</i> Object Recognition Test (ORT) accuracy scores for men and women in the three CG Arena experimental rooms. ....	72
<i>Figure 13.</i> Sequence of tasks for the Fear-Factor Stress Test (FFST), Trier Social Stress Test (TSST) and Control experimental procedure. ....	79
<i>Figure 14.</i> Timeline of events, from 0 minutes to 80 minutes, during the experimental procedures. ....	84
<i>Figure 15.</i> Salivary cortisol in nanomoles per liter (nmol/l; mean + standard error) at two measurement points in the study. ....	88
<i>Figure 16.</i> Timeline of events, from 0 minutes to 80 minutes, during the experimental procedures on Day 2. ....	112
<i>Figure 17.</i> Changes in self-reported state anxiety (STAI) levels on Day 2 for the combined Stress and combined Control groups. ....	116
<i>Figure 18.</i> Changes in cortisol (CORT) levels on Day 2 for the combined Stress and combined Control groups. ....	118
<i>Figure 19.</i> Changes in heart rate (HR) levels on Day 2 for the combined Stress and combined Control groups. ....	120
<i>Figure 20.</i> Changes in galvanic skin response (GSR) levels on Day 2 for the combined Stress and combined Control groups. ....	122
<i>Figure 21.</i> Mean deviation from the optimal path length for all experimental groups across the training trials. ....	124
<i>Figure 22.</i> Mean deviation from the optimal path length for the acquisition trials in the Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. ....	125
<i>Figure 23.</i> Mean deviation from the optimal path length for recall trials in the Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. ....	129
<i>Figure 24.</i> Mean proportion of dwell time in the target (SW) quadrant on the probe trial in the Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. ...	131
<i>Figure 25.</i> Mean ORT $d'$ scores for the Cool, Hot Appetitive (Hot+), and Hot Defensive (Hot-) CG Arena rooms. ....	132
<i>Figure 26.</i> Mean ART displacement scores for the Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. ....	134
<i>Figure 27.</i> Mean number of words recalled on each trial of the Verbal Paired Associates Test (VPA). Error bars indicate standard error of means. ....	136

<i>Figure 28.</i> Mean percentage retained scores for the delayed recall trial of the Verbal Paired Associates Test. Error bars indicate standard error of means. ....	137
<i>Figure 29.</i> Timeline of events, from 0 minutes to 110 minutes, depicting the experimental procedures on Day 2. ....	155
<i>Figure 30.</i> Changes in cortisol (CORT) levels on Day 2 for the combined Stress and combined Control groups. ....	159
<i>Figure 31.</i> Changes in self-reported state anxiety (STAI) levels on Day 2 for the combined Stress and combined Control groups. ....	161
<i>Figure 32.</i> Mean deviation from the optimal path length across the acquisition trials in the Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. ....	163
<i>Figure 33.</i> Mean deviation from the optimal path length on Trial 6 in the Cool, Hot Appetitive (Hot+), and Hot Defensive (Hot-) CG Arena rooms. ....	165
<i>Figure 34.</i> Mean deviation from the optimal path length for recall trial in the Cool, Hot Appetitive (Hot+), and Hot Defensive (Hot-) CG Arena rooms. ....	168
<i>Figure 35.</i> Mean proportion of dwell time in the Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. ....	169
<i>Figure 36.</i> Mean ORT $d'$ scores for the Cool, Hot Appetitive (Hot+), and Hot Defensive (Hot-) CG Arena rooms. ....	171
<i>Figure 37.</i> Mean ART displacement scores for the Cool, Hot Appetitive (Hot+), and Hot (Hot-) Defensive CG Arena rooms. ....	172
<i>Figure 38.</i> Mean number of words recalled on each trial of the Verbal Paired Associates Test (VPA). ....	174
<i>Figure 39.</i> Mean percentage retained scores for the delayed recall trial of the Verbal Paired Associates Test. ....	177

### List of Tables

Table 1. <i>CG Arena Trial Parameters for the Acquisition Phase</i> .....	56
Table 2. <i>Possible Sequence of Training and Experimental CG Arena Rooms</i> .....	61
Table 3. <i>Demographic frequencies for the entire participant sample (N = 24)</i> .....	63
Table 4. <i>Performance in the Three CG Arena experimental rooms (N = 24)</i> .....	66
Table 5. <i>Between-sex Comparisons: CG Arena performance, ORT score, and ART score (N = 24)</i> .....	70
Table 6. <i>Male Participants: Performance on outcome variables (n = 12)</i> .....	71
Table 7. <i>Female Participants: Performance on outcome variables (n = 12)</i> .....	72
Table 8. <i>Subjective anxiety, heart rate, and cortisol descriptive data (N = 90)</i> .....	85
Table 9. <i>CG Arena Trial Parameters for the Learning Phase</i> .....	109
Table 10. <i>CG Arena Trial Parameters for the Recall Phase</i> .....	109
Table 11. <i>Counterbalanced Sequences of CG Arena Rooms in the Acquisition Phase</i> .....	111
Table 12. <i>Counterbalanced Sequences of CG Arena Rooms in the Recall Phase</i> .....	112
Table 13. <i>Descriptive Statistics for Sample Characteristics (N = 60)</i> .....	113
Table 14. <i>Descriptive Statistics for Self-Report and Physiological Measures (N = 60)</i> .....	115
Table 15. <i>Descriptive Statistics for Performance on Trial 6 in Each CG Arena Room (N = 60)</i> .....	127
Table 16. <i>Descriptive Statistics for Recall Performance in each of the CG Arena rooms (N = 60)</i> .....	129
Table 17. <i>Descriptive Statistics for Verbal Paired Associates Test Recall and Percentage Retained scores (N = 60)</i> .....	135
Table 18. <i>Descriptive Statistics for Sample Characteristics (N = 60)</i> .....	156
Table 19. <i>Descriptive Statistics for Salivary Cortisol and STAI-State Data (N = 60)</i> .....	158
Table 20. <i>Descriptive Statistics for Trial 6 in each CG Arena room (N = 60)</i> .....	165
Table 21. <i>Descriptive Statistics for Recall Performance in each of the CG Arena rooms (N = 60)</i> .....	167
Table 22. <i>Descriptive Statistics for Verbal Paired Associates Test Recall and Percentage Retained scores (N = 60)</i> .....	174

## ABSTRACT

Previously published studies, using human and non-human animal samples, suggest that stress impairs memory retrieval. However, most human studies that report these impairing effects explore verbal memory only. The aim of the studies reported in this dissertation was to explore the effects of an acute stressor (Study 1), and of administration of prednisone (Study 2), on retrieval of visual-spatial material (both emotional and neutral), and to compare the findings against three theories that attempt to account for the effects of stress on memory: the inverted-U hypothesis (de Kloet et al., 1999), hot-cool theory (Jacobs & Metcalfe, 1998), and the integrated vertical and horizontal perspective theory (Schwabe et al., 2012). To explore the research question, I aimed to systematically replicate, in humans, the pioneering study of de Quervain et al. (1998). They demonstrated that both stress (in the form of foot-shocks) and glucocorticoid treatment impaired memory retrieval, as demonstrated by water maze performance, in rodents. To replicate their design for use in humans, I needed to make several apparatus substitutions. Hence, before embarking on the major studies that constitute the dissertation, I undertook two pilot/preparation studies. Study A verified that a novel visual and spatial task (a virtual environment (VE) water maze task) was a suitable human analog for the Morris Water Maze. Twenty-four participants learned the location of a target in three different VE rooms. Landmarks in the first room were neutral non-arousing pictures; in the second, pleasant arousing pictures; and in the third, unpleasant arousing pictures. Emotional content of landmarks did not affect place learning, although the women demonstrated better recognition for arousing than neutral landmarks. Study B verified that a novel laboratory-based stressor was a suitable substitute for the foot-shock stressor. This novel stressor combines the Cold Pressor Test with the Trier Social Stress Test (TSST) into a single procedure: the Fear Factor Stress Test (FFST). Ninety participants completed one of three conditions: FFST-Stress, FFST-Control, or TSST. The FFST-Stress induced a more robust and sustained cortisol response than the TSST (without increasing participant discomfort), while the FFST-Control condition did not provoke a cortisol response. Following these validation studies, Study 1 explored the effects of the FFST on memory retrieval for the VE rooms created in Study A. Sixty participants learned the location of an invisible target in the VE rooms and, 24 hours later, after undergoing either the FFST-Stress or -Control conditions, completed a set of navigational, recall, and recognition memory tests. In Study 2, the FFST conditions were substituted by a 25mg prednisone dose and a placebo. Following ingestion of the prednisone/placebo, 60 participants completed the same set of navigational and memory tests. Results revealed that neither acute stress nor prednisone administration impaired visual and spatial memory. However, exposure to the acute stressor appeared to enhance verbal memory in women, and prednisone administration appeared to impair verbal memory in both men and women. Relating the current findings to theory revealed that only the inverted-U hypothesis was capable of accounting for the observed pattern of data with regard to verbal memory. Specifically, congruent with predictions derived from that theory, a combination of low levels of endogenous cortisol due to the time of day when procedures were performed, along with the dose-dependent effects of cortisol, might account for the contrasting verbal memory findings seen across Studies 1 and 2. However, none of the three theories were capable of explaining the absence of stress effects on visual and spatial memory. Findings from Studies 1 and 2 therefore suggest that being exposed to an acute stressor or being administered prednisone might have had varying effects across memory domains, which is consistent with a functional perspective on memory. These findings indicate that further investigation into domain-specific effects of stress on memory might be a rewarding area of inquiry.

## **CHAPTER ONE: GENERAL INTRODUCTION**

The term “stress” was originally used by engineers with reference to the forces that put strain or pressure on a structure. This strain, if severe enough, can cause the structure to fracture and break. In the mid-1930s, the term “stress” was adopted by Hans Selye and used to refer to a non-specific experience indicative of a sequence of symptoms produced by a broad range of independent noxious agents. For several years, Selye tested the effects of various conditions (e.g., extreme cold, fasting, operative injuries) that produced physiological changes representative of the stress response in both humans and animals. These changes included enlargement of the adrenal glands, atrophy of the thymus, and gastric ulceration. Selye concluded that many non-specific conditions can put strain on an organism, similar to forces that put strain on a structure described by engineers (Selye, 1936).

Due in large part to Selye’s work, the term ‘stress’ has become increasingly fashionable in modern society. In turn, the precise definition of the term has become progressively unclear. The lay definition of the term ‘stress’ in popular culture often refers to time pressure in peoples’ everyday lives (Lupien, Maheu, Tu, Fiocco, & Schramek, 2007). In a similar way to the destructive force first described by engineers and later by Selye, time pressure has also been equated to a destructive force on people. Time constraints in our everyday lives place strain on us and, if the strain is idiosyncratically severe enough, can trigger a set of physiological reactions that are detrimental to our well-being.

However, from a scientific perspective, the term “stress” is not synonymous with time pressure. Instead, general scientific consensus has the term referring to a state or situation in which an individual perceives a real or anticipated threat to his/her homeostasis. This threat could either be psychological or physiological in nature, stimulating an adaptive response from the individual (De Kloet, Joels, & Holsboer, 2005; McEwen, 1998, 2000; Wolf, 2008). It is this latter definition of the term ‘stress’, and its effects on visual and spatial memory performance, that I focus on in this dissertation.

In the following literature review, I discuss the body’s stress response, along with its consequential effects on memory. In doing so, I discuss critical brain regions (the medial temporal lobe and specifically the hippocampus) that are affected by the stress. These brain regions are, by no degree of coincidence, fundamentally involved in certain types of memory (i.e., declarative memory, including episodic visual and spatial memory).

## The Stress Response

Levine (2005) defined stress as a composite, multidimensional construct in which three main subclass components interact. These components are: (i) input, when the stressful stimuli are perceived and appraised, (ii) processing and subjective experience of the stressful stimuli and, (iii) output, or *stress response*. These three component subclasses interact through a complex system of feedback and control loops in order to restore the desired homeostatic state through behavioral and physiological adjustments (Levine, 2005).

A stressor is any specific event that can cause a stress response in an individual. This event can be either absolute or relative to the individual (Lupien et al., 2006). An absolute threat is a threatening real-life situation; it can include anything from experiencing an earthquake or being involved in an accident, to experiencing extreme cold or heat. Absolute stressors are therefore usually physical stressors that necessitate an adaptive response from the body. Extreme or dangerous situations pose a threat to the survival of an individual and thus, due to their aversive nature, they elicit a stress response in order to ensure the individual's survival (Lupien et al., 2007). Relative stressors, on the other hand, are an implied threat to the individual. That is, the situation or event is deemed threatening only through cognitive interpretation by the individual (Lupien et al., 2006). Cognitive interpretation of a situation might seem like an unspecific stressor; however, if the situation is interpreted as being: (i) novel (Rose, 1980), or (ii) unpredictable (Mason, 1968), or (iii) uncontrollable (Henry & Grim, 1990; Sapolsky, 1993), or (iv) has the presence of a social evaluative threat (Dickenson & Kemeny, 2002), then it is most likely to provoke a stress response. However, due to large inter-individual differences in cognitive interpretation of the situation, relative stressors sometimes only elicit a stress response from certain individuals. This response is also highly variable between individuals (Lupien, et al., 2006). For instance, some people find a situation that involves public speaking extremely stressful, whereas others do not. An individual's subjective evaluation of the situation, as well as the coping resources that are available, are important determinants of cognitive interpretation and the impact of the stressful situation (Lazarus, 1993; Mason, 1968; Ursin & Eriksen, 2004).

Although arguably to a different degree, both absolute and relative stressors elicit a common stress response. The stress response is the body's reaction to the threatening event; in other words, the body's adaptive response to the threatening event. This response is characterized by the release of stress hormones that facilitate the adaptation to the threatening situation (De Kloet et al., 2005; Herbert et al., 2006; McEwen, 1998). Two separate but interacting response systems are initiated within the organism. The first is a rapid response of

the noradrenergic system that is orchestrated, for the most part, by the sympathetic nervous system and, to a lesser extent, by the hypothalamic-pituitary-adrenal (HPA) axis (Roozendaal, Barsegyan, & Lee, 2008; Roozendaal, McEwen, & Chattarji, 2009; Roozendaal, Okuda, de Quervain, & McGaugh, 2006). Activation of the hypothalamus stimulates neurons in the spinal cord to signal the release of epinephrine and norepinephrine (a group of hormones known as catecholamines) from the adrenal medulla. Epinephrine and norepinephrine are hormones that stimulate rapid physiological changes in preparation for the stressful event. These changes include increases in heart rate, sweating, breathing frequency, and blood pressure (de Kloet et al., 2005). From a cognitive perspective, epinephrine and norepinephrine only have minimal influence on brain function directly, as they cannot easily cross the blood-brain barrier (Harley, 1991). They can, however, exert some influence on neural structures by stimulating the vagus nerve in the brain stem. Information is then transmitted from the vagus nerve to the brain via the nucleus of solitary tract and the locus coeruleus. These pathways stimulate several brain regions, of which the basolateral amygdala (BLA) is the most relevant. The BLA consists of the lateral, basal, and accessory basal nuclei of the amygdala (Roozendaal et al., 2006).

Glucocorticoids (GCs) released through activation of the HPA axis affect the fast noradrenergic system presynaptically in the brainstem through noradrenergic cell groups projecting to the BLA. In addition, GCs interact with the  $\beta$ -adrenergic system in the BLA postsynaptically through interaction with  $\alpha$ -adrenoceptors (Schwabe, Joëls, Roozendaal, Wolf, & Oitzl, 2012). Recent research indicates that the rapid effects of GCs on the noradrenergic system might be mediated by membrane-bound receptors. These receptors activate a non-genomic signaling surge that leads to alterations in neuronal excitability in the BLA (Barsegyan, Mackenzie, Kurose, McGaugh, & Roozendaal, 2010; Karst, Berger, Erdmann, Schütz, & Joëls, 2010; Karst et al., 2005; Roozendaal et al., 2010).

The second stress-response system is slower and is initiated solely by activation of the HPA axis. Neurons in the hypothalamus release corticotrophin-releasing hormone, which in turn results in the release of adrenocorticotropin from the pituitary gland.

Adrenocorticotropin travels via blood to the adrenal glands and results in the release of GCs (known as corticosterone in animals and cortisol in humans) from the adrenal cortex.

Glucocorticoids, in contrast to catecholamines, can cross the blood-brain barrier easily. They then bind to receptors in various brain regions (de Kloet et al., 2005; Herbert et al., 2006; McEwen, 1998).

Glucocorticoids bind to two different receptor subtypes, namely mineralocorticoid (or Type I) receptors and glucocorticoid (or Type II) receptors. Both Type I and II receptors are crucially involved in mediating the feedback effects of GCs in the brain; however, there are two distinct differences between the two types of receptors (Lupien et al., 2007). First, Type I receptors bind GCs with a greater affinity than Type II receptors, as they have a 10-fold higher affinity for GCs ( $K_d$ : 0.5 nM) than Type II receptors ( $K_d$ : 5 nM). This greater affinity renders target tissues more responsive to changes in GC levels (van der Laan & Meijer, 2008). Thus, Type I receptors are more likely than Type II receptors to become occupied, and consequently, saturated with GCs. Second, the distribution of Type I and Type II receptors differs within the brain. Type I receptors are restrictively distributed in the limbic system and are found chiefly in the hippocampus, parahippocampal gyrus, and the insular and entorhinal cortices. In contrast, Type II receptors are distributed in both subcortical and cortical structures. Subcortically, they are also found in the same limbic structures such as the hippocampus and parahippocampal gyrus, as well as in the paraventricular nucleus and the hypothalamic nuclei. Cortically, Type II receptors are preferentially distributed in the prefrontal cortex (Herbert et al., 2006; Lupien et al., 2007). In addition to distribution and affinity, the functions of these two receptor types are also believed to differ. Type I receptors are thought to be important in determining the threshold for activation of the HPA axis (Cornelisse, Joel, & Smeets, 2011), whereas Type II receptors are thought to have a role in normalizing stress-induced effects and in promoting consolidation (Oitzl et al., 2001; Roozendaal, 2003; Sandi, 1998).

In summary, the body's stress response features both a rapid and a slow reaction to a threatening stimulus. The acutely secreted stress hormones (that is, glucocorticoids and catecholamines) represent the principal mediators in the chain of hormonal events triggered in response to stress. These stress hormones activate the body's fight-or-flight response and promote an adaptive cognitive response to overcome threatening situations. Despite the physiological aspects of the stress response having been well documented, the cognitive consequences of the response still require further understanding.

### **Stress and Memory**

The impact of stress on memory has long been a contentious issue. Although it is generally accepted that stress has an effect on memory, it is the nature of the effect that is the bone of contention (for historical reviews, please see Lupien et al., 2007, and Wolf, 2009). From the onset of the first rat and human studies, conflicting reports of both enhancing and

impairing effects of GCs on memory emerged (Arbel, Kadar, Silbermann, & Levy, 1994; Beckwith, Petros, Scaglione, & Nelson, 1986; Bohus & Lissák, 1968; Flood et al., 1978; Luine, Spencer, & McEwen, 1993). Subsequent research has shown that factors such as acute versus chronic effects of GCs, phase of memory, and level of emotional arousal, all have an important part to play in the inconsistent actions of stress on memory (Lupien et al., 2007; Wolf, 2009).

Conditions that result in chronic elevations of GC levels are typically associated with a general impairment in memory performance (McEwen, 2001; Sapolsky, 2000).<sup>1</sup> On the other hand, acutely elevated GC levels have been reported to have varying effects depending on the phase of memory; that is, at the level of encoding, consolidation, retrieval, or reconsolidation (de Quervain, Aerni, Schelling, & Roozendaal, 2009; Roozendaal et al., 2009; Schwabe et al., 2012; Wolf, 2009). In addition, acutely elevated GC levels are also associated with impaired working memory (Baddeley, 1992; Luethi, Meier, & Sandi, 2009; Lupien, Gillin, & Hauger, 1999; Roozendaal, McReynolds, & McGaugh, 2004; Schoofs, Preuss, & Wolf, 2008; Taverniers, Smeets, van Ruyssevelt, Syroit, & von Grumbkow, 2011; Young, Sahakian, Robbins, & Cowen, 1999). Thus, in order to narrow the scope of this literature review, I will focus primarily on the acute effects of stress on episodic memory.

Episodic memory can be defined simply as explicit and voluntary storage and retrieval of specific events (La Bar & Cabeza, 2006; Wolf, 2008). Before delving into the affects of acute stress on episodic memory, however, another important influencing factor on memory needs to be introduced: emotional arousal.

**Emotional memory.** Both humans and animals process emotional information differently from neutral information. These differences can be seen in the domains of perception, attention, working memory and episodic memory (Dolan, 2002; La Bar & Cabeza, 2006; Packard & Goodman, 2012; Phelps, 2004; Reisberg & Heuer, 2004). Theories behind these processing differences point to the fact that certain information, which is critical for survival, needs processing precedence over less vital information (La Bar & Cabeza, 2006; Wolf, 2008). Due to the continuous bombardment of sensory information, both humans and animals need to filter information quickly not only for sources of threats to homeostasis, but also for sites of nutrition and reproduction as well. It therefore makes sense that we have a tendency to remember emotional experiences far more vividly than we do neutral ones

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<sup>1</sup>Although, memory deficits due to acute (and reversible) elevations in glucocorticoid levels can also occur in chronically elevated conditions (Coluccia, et al., 2008).

(Wolf, 2008). In line with the rest of this review, I will focus on the role of emotional arousal on episodic memory.

Memory for emotional experiences is more robust than memory for neutral experiences. That is, we tend to remember emotional stimuli or events more vividly than we do neutral ones (Heuer & Reisberg, 1990; La Bar & Cabeza, 2006; McGaugh, 2003; Wolf, 2008). Not only are our memories for emotional events more vivid, they are also more accurate (Schmidt, Patnaik, & Kensinger, 2011). Interestingly, it is also generally believed that the valence of a stimulus or event (whether positive or negative) is an inconsequential characteristic with respect to whether or not it is remembered; rather, memory for the stimulus or event depends on the level of emotional arousal of the stimulus (Schmidt et al., 2011; Smeets, Jelicic, & Merckelbach, 2006; Wolf, 2009). From a biological perspective, a possible explanation for the memory benefits seen for emotional stimuli (irrespective of valence) is that the amygdala, and its interaction with the medial temporal lobes, is crucial in the processing of emotional material. The interaction between these two brain regions is correlated with enhanced memory for emotional stimuli (La Bar & Cabeza, 2006; Roozendaal et al., 2004, 2009; Schwabe et al., 2012; Wolf, 2008, 2009). The valence of a stimulus, on the other hand, is believed to be processed predominantly by the frontal lobes (Kensinger, 2004). Thus, the emotionality of a stimulus, not the valence, ensures activation of the amygdala, and the subsequent enhancement of memory. However, regardless of this biological perspective, some studies have reported memory differences that are related directly to the valence of the stimuli (for example, see Domes, Heinrichs, Rimmele, Reichwald, & Hautzinger, 2004; Luethi, Meier & Sandi, 2009; Tops et al., 2003). Discrepancies in the findings regarding valence of the arousing stimulus and memory performance indicates a need for further research.

As previously introduced, emotional arousal can also influence memory performance under stressful conditions. Arousal can be differentiated from stress on a physiological/neurobiological level. In contrast to stress, arousal fails to activate the HPA axis and thus arousal, unlike stress, does not result in the release of GCs (Lovallo & Thomas, 2000). The effects of emotional arousal are therefore attributed to rapid stress response without the concomitant non-genomic effects of GCs (that is, emotional arousal results in the adrenergic activation of the BLA). Both human and animal studies have shown that the noradrenergic activation of the BLA is fundamental for the beneficial modulation of a memory trace, which is stored in other areas of the brain (La Bar & Cabeza, 2006). Patient studies have shown that the BLA is essential for the facilitation of memory for emotional

material (Adolphs, Tranel, & Buchanan, 2005; Cahill, Babinsky, Markowitsch, & McGaugh, 1995). In addition, pharmacological studies have also shown that blockade of the beta-adrenergic system impairs memory for emotional material (Cahill, Prins, Weber, & McGaugh, 1994), whereas artificial stimulation of the central noradrenergic system, either by pharmacological agents or by stimulation of the vagus nerve, results in enhanced memory for emotional material (Clark, Naritoku, Smith, Browning, & Jensen, 1999; Ghacibeh, Shenker, Shenal, Uthman, & Heilman, 2006; Southwick et al., 2002).

Imaging studies using either functional magnetic resonance imaging (fMRI) or positron emission tomography (PET) have also shown strong activation of the amygdala associated with memory consolidation for emotional stimuli (Cahill et al., 1996; Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000). Furthermore, blocking of the beta-adrenergic system leads to a reduced amygdala response to emotional arousing stimuli and, in turn, is associated with poorer memory for the same material (Strange & Dolan, 2004; van Stegeren et al., 2005).

In summary, there is a strong line of research suggesting that activation of the BLA, in conjunction with its interaction with other brain regions (especially the medial temporal lobes), results in enhanced memory for emotionally arousing information (LaBar & Cabeza, 2006; Packard & Goodman, 2012; Phelps, 2004; Wolf, 2008).

### **Acute Stress and Episodic Memory**

Episodic memory comprises of several dynamic stages. First, an experienced episode or event is *encoded*. The encoding of the event results in a new and fragile memory trace that is subsequently stabilized during the *consolidation* stage. The memory can then be reactivated during the *retrieval* phase (Tulving, 1985). Once the memory has been retrieved, the memory trace is believed to resume a fragile state, which needs to be *reconsolidated* in order to again become stable (Dudai, 2006). Stress is reported to have differential effects on each stage of episodic memory- encoding, consolidation, retrieval, and reconsolidation (de Quervain et al., 2009; Roozendaal et al., 2009; Schwabe & Wolf, 2013; Wolf, 2008, 2009). Thus, how stress or GCs effect episodic memory depends on *when* an individual is stressed (Schwabe et al., 2012).

**Memory encoding.** The literature on the effects of stress and GCs on the encoding phase of memory is inconsistent. Some studies that administered stress or GC treatment before learning have reported enhancing effects (Cornelisse, van Stegeren, & Joels, 2011; Domes, Heinrichs, Reichwald, & Hautzinger, 2002; Luethi et al., 2011; Nater et al., 2007; Schwabe, Bohringer, Chatterjee, & Schachinger, 2008; Smeets, Giesbrecht, Jelicic, &

Merckelbach, 2007; Taverniers et al., 2011a; Weymar, Schwabe, Löw, & Hamm, 2012). Other studies have reported impairing effects (Diamond et al., 2006; Elzinga, Bakker, & Bremner, 2005; Kim, Lee, Han, & Packard, 2001; Kirschbaum, Wolf, May, Wippich, & Hellhammer, 1996; Lupien et al., 1997; Richardson & VanderKaay Tomasulo, 2011; Thomas, Lurance, Nadel, & Jacobs, 2010; Schwabe & Wolf, 2010a; Taverniers et al., 2011b).

A possible reason for these inconsistent findings is that studies testing the effects of stress on encoding face the insurmountable task of trying to isolate the encoding phase from the other memory phases. That is, if stress or GC treatment is administered before learning, then the encoding, consolidation and possibly retrieval phases will all be affected by the treatment. Thus, effects on encoding are confounded by effects on consolidation and retrieval (Schwabe et al., 2012). For instance, if stress or GC treatment is administered before learning, and retrieval is tested shortly thereafter, confounding effects of the treatment on encoding will be influenced by retrieval. If, however, retrieval is tested following a long delay, then the confounding effects of stress on consolidation might influence the effects on encoding (Schwabe, Wolf, & Oitzl, 2010; Schwabe et al., 2012). Thus, the difficulty in isolating the encoding phase from the other memory phases may result in inconsistent findings when learning follows stress or GC treatment.

It also appears that effects on encoding may be influenced by the level of emotional arousal induced by the learning material. Some studies have shown that the recall of emotional information is preserved or enhanced by stress or GC treatment before learning, while the recall of neutral material is impaired (Payne et al., 2006, 2007; Tops et al., 2003). In addition, stressor intensity and dose level of GCs also seem to play a role in the effects of stress on encoding. Studies that have used more intense stressors or higher GC doses before learning have found memory impairments (e.g., Abercrombie, Kalin, Thurow, Rosenkranz, & Davidson, 2003; Diamond, Bennett, Fleshner, & Rose, 1992).

An additional factor believed to affect memory performance is the time gap between the stressor and the learning task (Joëls et al., 2006). If the learning task immediately follows the stressor (when adrenergic levels are highest and GCs levels are low) then the influence of the rapid noradrenergic system may have an enhancing influence on memory performance. If, however, there is a delay between the stressor and the learning task (when adrenergic levels have returned to near baseline levels and cortisol levels are elevated) then the slow HPA axis hormones may have an impairing effect on memory performance (Diamond et al., 2007; Joëls et al., 2006).

In summary, several factors have been proposed as explanations for inconsistent effects of stress or GC treatment on the encoding phase of memory. These factors include the interval between learning and the testing of material, the level of arousal of the testing material, the intensity of stress or the GC treatment, and the time delay between the stressor and the learning task.

**Memory consolidation.** In contrast to the inconsistent findings regarding stress and GCs on the encoding phase, reports on the effects of stress and GCs on the consolidation phase are relatively consistent. The beneficial effects of increased GCs on memory consolidation were first reported in animal studies (De Kloet, Oitzl, & Joels, 1999; Roozendaal, 2000). Subsequent studies in humans have reported similar findings. Studies that have applied stress or GC treatment during learning (Buchanan & Lovallo, 2001; Kuhlmann & Wolf, 2006a), or immediately post-learning (Beckner, Tucker, Delville, & Mohr, 2006; Cahill, Gorski, & Le, 2003; Elzinga et al., 2005; Human et al., 2013; Sandi, Loscertales, & Guaza, 1997; Smeets et al., 2007, 2009; Smeets, Otgaar, Candel, & Wolf, 2008; Smeets, Otgaar, Raymaekers, Peters, & Merckelbach, 2012), have reported positive effects on memory consolidation, confirmed by enhanced recall of learned material days to weeks after learning took place.

Some studies have shown the beneficial effect on consolidation to occur across all learned material (Abercrombie et al., 2003; Beckner et al., 2006; Elzinga et al., 2005), whereas others have reported that the positive effect is only seen for emotionally arousing stimuli (Buchanan & Lovallo, 2001; Cahill et al., 2003; Kuhlmann & Wolf, 2006a) or, at least, a greater beneficial effect for emotional material (Smeets et al., 2008, 2009).<sup>2</sup>

It appears that the beneficial effects of stress or GCs on consolidation for emotional information are not only isolated to the testing material. Abercrombie, Speck and Monticelli (2006) reported that their participants' only showed enhanced consolidation when they displayed elevated cortisol levels (due to psychosocial stress) and increased self-report arousal. Similar to arousal, the underlying neural mechanisms responsible for the beneficial effects of GCs on consolidation can be linked to the amygdala (specifically the BLA) and its interaction with the medial temporal lobes (LaBar & Cabeza, 2006; Roozendaal et al., 2006; Wolf, 2009). As highlighted above, activation of the BLA is believed to occur through both noradrenergic activation and non-genomic GC effects. Studies involving patients with BLA

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<sup>2</sup>However, it must also be noted that other studies have failed to find beneficial effects of glucocorticoids on consolidation (e.g., Rimmele, Domes, Mathiak, & Hautzinger, 2003; Wolf, Schommer, Hellhammer, Reischies, & Kirschbaum, 2002).

lesions and pharmacological studies involving beta blockade have shown that noradrenergic activation in the BLA is necessary for the positive effects of GC agonists on memory consolidation (Roosendaal et al., 2006).

In turn, an increase in GC levels might also increase an individual's sensitivity to becoming emotionally aroused. Functional imaging studies have shown that participants with higher endogenous cortisol levels display significantly stronger amygdala activation when viewing emotional slides in comparison to participants with lower cortisol levels (van Stegeren et al., 2007; van Stegeren, Wolf, Everaerd, & Rombouts, 2008). Consequently, simultaneous operation of GCs in conjunction with noradrenergic activation of the BLA are believed to be behind the beneficial effects of GCs on consolidation, especially for emotional material (LaBar & Cabeza, 2006; Rozendaal et al., 2009; Wolf, 2008).

In summary, increased stress or GC levels during or immediately after learning generally lead to enhanced memory consolidation, and result in enhanced retrieval of the learned material (for more in-depth reviews, see de Quervain et al., 2009; Wolf, 2008, 2009; Roosendaal et al., 2009; Schwabe et al., 2012). In addition, this positive effect seems to be more pronounced for consolidation of emotionally arousing material.

**Memory retrieval.** Whereas an acute rise in GCs during or immediately following learning is associated with enhanced memory consolidation, the opposite effect is generally seen during memory retrieval. That is, stress and GCs generally have an impairing effect on memory retrieval.

The negative effect of stress on memory retrieval was first reported in rodent studies. de Quervain, Roosendaal, and McGaugh (1998) reported that both stress and corticosteroids impaired performance on a previously learned spatial maze task. Rats were trained to find the location of a target in a Morris Water Maze (MWM; Morris, 1984) 24 hours before retention testing. Prior to retrieval, the rats were administered foot shocks. A shock administered 30 minutes prior to testing impaired performance, whereas a shock delivered 2 minutes before and 4 hours before, did not. The time-dependent effect on retrieval performance negatively correlated with circulating GC levels at the time of testing. The authors subsequently isolated GCs as the mediator of the effect by, first, neutralizing the impairing effect through administering metyrapone (in order to suppress corticosterone synthesis), and second, by replicating the impairing effect by administering corticosteroids to non-stressed rats. These findings have since been replicated in other rodent studies (e.g., Diamond et al., 2006).

Human studies have replicated the negative effects of stress on retrieval for previously learned material. Studies that have administered GCs have shown retrieval deficits for word

lists (de Quervain, Aerni, & Roozendaal, 2007; de Quervain, Roozendaal, Nitsch, McGaugh, & Hock, 2000; Kuhlmann, Kirschbaum, & Wolf, 2005; Kuhlmann & Wolf, 2005; Tollenaar, Elzinga, Spinhoven, & Everaerd, 2009; Wolf et al., 2001), autobiographical material (Buss, Wolf, Witt, & Hellhammer, 2004), and the recall of contextual pain (Schwegler et al., 2010). In addition, studies employing laboratory stressors have also shown similar retrieval deficits for word lists (Buchanan, Tranel, & Adolphs, 2006; Dome et al., 2004; Kuhlmann, Piel, & Wolf, 2005, Smeets, 2011; Smeets et al., 2008), paired associate word lists (Tollenaar, Elzinga, Spinhoven, & Everaerd, 2008), pictures (Buchanan & Tranel, 2008; Schönfeld, Ackermann, & Schwabe, 2014), socially relevant information (Merz, Wolf, & Hennig, 2010), as well as spatial memory (Guenzel, Wolf, & Schwabe, 2013; Quesada, Wiemers, Schoofs, & Wolf, 2012).

However, some studies have reported no effects on retrieval (Schoofs & Wolf, 2009; Wolf et al., 2002), while other studies have reported enhancing effects on retrieval (Lupien et al., 2002; Schilling et al., 2013, Schwabe et al., 2009).<sup>3</sup> A proposed explanation for these inconsistent findings is that the effects of stress and GCs on memory follow an inverted-U relationship. This theoretical explanation is discussed below under *the inverted-U hypothesis*.

As with consolidation, emotional arousal seems to amplify the negative effects of GCs on retrieval. Several studies have shown greater retrieval impairments for emotionally arousing material in comparison to neutral material (Buchanan et al., 2006; de Quervain et al., 2007; Kuhlmann et al., 2005a; Schönfeld et al., 2014; Kuhlmann et al., 2005b; Smeets et al., 2008; Tollenaar et al., 2008). In general, it seems that the level of arousal of the stimuli seems to be more important than its valence level (Buchanan et al., 2006; Kuhlman et al., 2005a), although valence has been shown to be an important factor in some studies (e.g., Domes et al., 2004).

The exaggerated effects of GCs on retrieval of arousing material again seem to suggest the importance of adrenergic activation in the BLA and its interaction with the medial temporal lobes. Animal studies have shown that, similar to the enhancing effects seen in consolidation, retrieval deficits require noradrenergic activation in both the BLA and the hippocampus, and can be neutralized by the administration of beta-blockers or by BLA lesions (Roozendaal, de Quervain, Schelling, & McGaugh, 2004; Roozendaal, Griffith, Buranday, de Quervain, & McGaugh, 2003; Roozendaal, Hahn, Nathan, de Quervain, &

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<sup>3</sup> Although it must be noted that Schoofs & Wolf (2009) only tested female participants in the luteal phase of their menstrual cycle. The luteal phase is characterized by elevated gonadal steroids, which is associated with reduced glucocorticoid sensitivity in women.

McGaugh, 2004). In humans, de Quervain et al. (2007) demonstrated through pharmacological administration of propranolol (a beta blocker), that the negative effects of GCs on memory retrieval for emotional material can be prevented. Consistent with that finding, Kuhlmann and Wolf (2006b) demonstrated that a relaxing (that is, non-arousing) testing environment also prevents GC effects on memory retrieval. Thus, it seems that arousal, either through emotionally arousing stimuli or an arousing testing environment, exacerbates the negative effects of GCs on memory retrieval.

Imaging studies have demonstrated differences in neural activity during retrieval under high and low GC concentrations. A PET study noted that after GC treatment, reduced blood flow was observed in the medial temporal lobes and was associated with inferior memory retrieval performance (de Quervain et al., 2003). A later event-related fMRI study observed reduced activation in the hippocampus and superior frontal gyrus during successful memory retrieval in participants who had received GCs versus those who had received a placebo (Oei et al., 2007). Thus, converging evidence from these imaging studies indicates that the effects of GCs are, to a large extent, mediated by the medial temporal and frontal lobes.

In summary, an acute increase in cortisol, associated with a stressful experience, has an impairing effect on memory retrieval. Both animal and human studies have shown stress or GC treatment to have a negative effect on retrieval, which is intensified by emotional arousal. Interactions between the BLA and the medial temporal lobes appear to be, for the most part, the neural anatomical sites responsible for the aggravated effects of cortisol and arousal on memory retrieval.

**Reconsolidation.** Although most studies in this area of research have focused on the effects of stress or GCs on the encoding, consolidation, or retrieval phases, several recent studies have shown that effects can extend to the reconsolidation and/or extinction phase of memory too. Evidence from animal studies shows that stress or GC treatment following the retrieval of memory results in impaired later recall (Cai, Blundell, Han, Greene, & Powell, 2006; Maroun & Akirav, 2008; Wang, Zhao, Ghitza, Li, & Lu, 2008). Consistent with results from animal studies, recent human studies have also shown that stress can impair the reconsolidation process (Schwabe & Wolf, 2010b; Zhao, Zhang, Shi, Epstein, & Lu, 2009). However, emotional arousal (in the absence of stress) following memory retrieval has been shown to enhance subsequent retrieval (Finn & Roediger, 2011). Interestingly, the enhancing effect of emotional arousal appears to be valence-specific, as only negative arousal (as

opposed to positive or neutral) enhances subsequent recall (Finn, Roediger, & Rosenzweig, 2012).

Thus, although it is not completely clear why stress or GC treatment impairs memory reconsolidation, findings indicate that the effects are opposite to those on the consolidation phase (Schwabe & Wolf, 2010b). Emotional arousal also seems to influence reconsolidation, which is consistent with the effects on the other memory phases.

In summary, the direction of the effects stress and GCs have on episodic memory depends on *when* an individual is stressed. Despite the effects on encoding being difficult to differentiate, the effects on consolidation are generally positive, while the effects on retrieval and reconsolidation are generally negative. In addition, emotion arousal is consistently reported as an important intensifying factor on the effects of stress and GCs.

Due to the varying directional effects of stress and GC treatment on the various memory phases, the current series of studies primarily aims to examine the effects of stress on the retrieval phase of memory. As noted previously, although stress and GCs generally have a negative effect on memory retrieval, several studies have failed to confirm this impairing effect (Lupien et al., 2002; Schilling et al., 2013; Schoofs & Wolf, 2009; Schwabe et al., 2009; Wolf et al., 2002). Thus, the effects of stress and GCs on memory retrieval still remain relatively unclear, especially on visual and spatial memory domains. The following section focuses on the theoretical explanations for the effects of stress on memory.

### **Theoretical Explanations for the Effects of Stress on Memory**

The idea that stress has an effect on memory has existed for a long time in the disciplines of psychology and psychiatry. Over the last two centuries, theories have been constructed on the workings of stress on memory. For instance, the concept of memory repression was originally suggested by Herbart (1824), and reinforced by Freud's (1915) hypothesis of trauma-associated memory suppression. The past few decades have seen a shift in theoretical formulation due to advances in knowledge of the effects of stress on memory. Two significant findings were integral to the shift in theoretical construction. First, a discovery by McEwen and colleagues (1968) showed that GCs bind to specific receptors in the hippocampus (McEwen, Weiss, & Schwartz, 1968). This finding indicated that GCs target a certain region or location in the brain, thus entailing possible localized effects on cognition. The second, earlier, discovery was that the hippocampus is a critical brain region in terms of declarative or episodic memory (Scoville & Milner, 1958). In conjunction, the two findings

linked GCs and possible effects on episodic memory, and thus paved the way for theories regarding the effects of stress on the hippocampus.

The following section will introduce four of the more recent theories regarding the effects and workings of stress on episodic memory. These theories are: state dependent learning hypothesis; the inverted-U hypothesis; hot-cool theory; and the vertical and horizontal perspective theory.

**State-dependent learning hypothesis.** An early explanation proposed to account for the negative effects of stress or GCs on memory is that of a state-dependent learning effect (e.g., Clark, Milberg, & Ross, 1983; Schramke & Bauer, 1997). State-dependent learning happens when material is learned in one mental or physical state and then the same material is recalled in a different mental or physical state. In the case of testing memory retrieval, material is learned in a relaxed state and then recall is tested shortly after stress or GC treatment (i.e., during a stressful state). Thus, the impairing effect may in fact be due to an altered state, generally, rather than the effects of cortisol on cognition, specifically.

Although this theory is not totally implausible, two reasons suggest that state-dependent learning cannot completely explain the effects of stress on memory. First, although state-dependent learning could account for the predominately negative effects of stress or GCs on retrieval (and reconsolidation) memory, it cannot explain the positive or beneficial effects on memory consolidation, and, in some cases, on encoding (de Quervain et al., 2009; Diamond et al., 2007; Joels, 2010; Joels et al., 2006; Roozendaal et al., 2006; Wolf, 2008, 2009). Second, studies that have examined the state-dependent learning hypothesis by administering stress or GC treatment, both before learning and retrieval, have reported no evidence confirming the hypothesis (Coluccia et al., 2008; Wolf et al., 2002). For instance, Coluccia et al. (2008) showed that retrieval of a word list following treatment with prednisone (cortisol) was still impaired in participants who had learned the list under prednisone. Thus, even though participants were in a similar state during learning and retrieval, GC treatment still had negative effects on retrieval of memory.

In summary, state-dependent learning theories cannot explain the complex effects of stress and GCs on memory. These theories fail to take into account the biological effects of stress on the brain (that is, effects on the hippocampus and BLA) and, therefore, make no predictions concerning the workings of GCs and emotional arousal on memory.

**Inverted-U hypothesis.** The inverted-U function was originally proposed by Yerkes and Dodson (1908) in order to explain the relationship between stimulus strength and rapidity of habit formation. According to the Yerkes-Dodson Law, cognitive performance on a

difficult task will be best when an individual is under optimal stress conditions. Performance on the same task will be impaired if stress levels are above or below optimal conditions (Yerkes & Dodson, 1908; Broadbent, 1965; Mendl, 1999).

In a review, de Kloet et al. (1999) hypothesized that the effects of GCs on memory followed an inverted-U pattern. This hypothesis is based on the affinity of GCs to bind with Type I and II receptors. As mentioned above, GCs bind to Type I receptors with an affinity of 6- to 10-times higher than that of Type II receptors (Reul & De Kloet, 1985). De Kloet and colleagues hypothesized, based on previous research, that the ratio of occupation between Type I and II receptors determines the effect on memory. When the ratio is high (that is, when most of Type I and only a part of Type II receptors are occupied), memory is enhanced, but when the ratio is low (that is, when both Type I and II receptors are either saturated or only partly occupied), then memory is impaired.

Lupien et al. (2002) provided evidence supporting this theory when they demonstrated that artificially lowering GC levels in a human sample also resulted in memory impairment. In addition, the same study showed that the administration of GC treatment to participants in the afternoon (during the circadian trough, when natural cortisol levels are lowest) did not result in memory impairments in the participants. However, it must be noted that in Lupien et al.'s (2002) study, encoding, consolidation and retrieval all took place within an hour of each other, therefore making it difficult to separate the effects of GCs on the various memory phases.

A major criticism of the Yerkes-Dodson Law is that it does not adequately explain the relationship between arousal and performance, but merely proposes a description of the relationship (Landers, 2007). Although de Kloet et al. (1999) do provide an explanation, their inverted-U hypothesis groups memory as a single entity, and fails to distinguish between the effects of stress and GCs on the different episodic memory phases. Even though stress might, in fact, show an inverted-U relationship for the encoding, consolidation, retrieval and reconsolidation phases, the general pattern in the literature shows that stress or GCs have an enhancing effect on memory consolidation and an impairing effect on retrieval and reconsolidation. Thus, the pattern indicates that if stress or GCs display an inverted-U relationship with memory, the intensity of the interaction seems to be different for the various memory phases.

One memory phase in which the inverted-U hypothesis could possibly explain the inconsistent findings is on encoding (Baldi & Bucherelli, 2005).<sup>4</sup> The positive and negative effects of stress on encoding might easily be explained by optimal or sub-/post-optimal levels of circulating GCs at the time of learning. Consistent with this proposal, Salehi, Cordero, and Sandi (2010) demonstrated that rats learned the location of a target in a water maze best under moderate stress conditions, in comparison to high- and low-stress conditions. Thus, an inverted-U relationship might account for inconsistent findings of stress and GCs on the encoding phase (see review).

In summary, an inverted-U relationship has been frequently reported in pharmacological and non-pharmacological treatments pertaining to cognitive functions and memory (Baldi & Bucherelli, 2005). Although this relationship might be able to explain inconsistent findings regarding the encoding phase, it fails to explain the general patterns seen with the consolidation, retrieval, and reconsolidation phases.<sup>5</sup> In addition, as with state-dependent learning theories, the inverted-U hypothesis fails to take into account the prominent effects of emotional arousal (and the BLA-hippocampus interaction) on memory.

**Hot-cool theory.** In what could be considered an expansion on the inverted-U hypothesis, Jacobs and Metcalfe (1998) described two fundamental cognitive subsystems that are important to understanding how human memory function operates under stress: the ‘cool’ memory system and the ‘hot’ emotional fear system. The ‘cool’ system is hippocampally based and records information about events with no emotional overlay. Events recorded in the cool system are well-elaborated (complete with their spatial-temporal context) autobiographical events. The ‘hot’ system, on the other hand, is amygdala-based, and responds to unintegrated fragmentary fear-provoking features of an event. These fear-provoking features become linked directly to fear responses; thus, the hot system is direct, quick, highly emotional, inflexible and fragmentary.

These ‘cool’ and ‘hot’ systems respond differently to increasing stress or GCs. At low levels of stress, the ‘cool’ system is highly responsive. The neurobiological mechanism underlying this response is the differential occupation of Type I and II receptors, as described in the inverted-U hypothesis above. That is, at low levels of stress only Type I receptors in the hippocampus and prefrontal cortex are occupied. The solitary occupation of these receptors in the hippocampus results in the optimal responsiveness of that structure. A rise in

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<sup>4</sup>Although, as noted above, an inverted-U relationship of stress and GCs on memory retrieval has also been reported in several studies (e.g., Lupien et al., 2002; Schilling et al., 2013, Schwabe et al., 2009).

<sup>5</sup>In fairness to the theory, the inverted-U hypothesis was developed before the relatively recent effects of stress and GCs on various phases of memory were established.

stress levels brings with it an increase in cortisol levels, which results in the additional occupation of Type II receptors in conjunction with the Type I receptors. Occupation of these two receptor sites leads the hippocampus to become progressively less responsive until eventually, at extremely high levels of stress, it becomes dysfunctional (de Kloet, et al., 1999; Jacobs & Metcalfe, 1998).

In contrast, the ‘hot’ system becomes more active as stress levels increase. The reason for this increasing responsiveness is that as stress levels increase, the release of norepinephrine and cortisol facilitate the functioning of the amygdala, or more specifically the BLA (Roosendaal et al., 2009). Thus, at low to moderate levels of stress both the ‘cool’ contextual and narrative features and the ‘hot’ fear-provoking features of the situation show enhanced encoding. At unusually high or traumatic levels of stress, however, the ‘hot’ system becomes hyper-responsive, where, in contrast, the ‘cool’ system breaks down and becomes dysfunctional. Thus, hot-cool systems theory predicts that at unusually high levels of stress, memory should be fragmentary rather than spatio-temporally bound, replete and coherent (Jacobs & Metcalfe, 1998; Kim, Lee, Han, & Packard, 2001; Schwabe, Bohbot, & Wolf, 2012; Schwabe et al., 2007).

Hot-cool theory incorporates the inverted-U relationship discussed above in its “cool” system, but expands the relationship with the introduction of the additional elements of emotional arousal and activation of the BLA in the “hot” system. Hot-cool theory therefore endeavors to incorporate the workings of both the fast and slow stress systems on memory, and to describe the resulting effects on the quality of memory. However, in a similar way to the inverted-U hypothesis, hot-cool theory groups episodic memory as a single entity and does not distinguish between the different phases.<sup>6</sup> In addition, although hot-cool theory may explain the memory enhancements generally seen in consolidation (and sometimes seen in encoding) for emotional material, it cannot account for the impairments seen on retrieval for emotional material. Thus, although hot-cool theory provides a fuller picture of the effects of stress hormones on associated brain regions, it may not be able to explain completely the empirically observed effects of stress on memory.

**The vertical and horizontal perspective theory.** The integrated vertical and horizontal perspective of stress on memory function (Schwabe et al., 2012) is a relatively recent addition to the literature. It incorporates two models of stress on memory functioning. The first, ‘vertical’ model, concentrates mainly on mechanisms that underlie the effects of

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<sup>6</sup>However, as with the inverted-U hypothesis, the theory was formulated before the different effects on memory phases had been established.

stress on memory (Roosendaal, 2002; Roosendaal et al., 2006). The second, ‘horizontal’, model focuses on the dynamics of the effects of stress over time (Joëls et al., 2006). Thus, this integrated perspective aims to explain the underlying mechanisms of stress that result in enhancements and impairments in memory.

The vertical perspective of the integrated model highlights how the main modulators of stress on memory are GCs and adrenergic activation. As introduced above, a large body of research shows that the effects of stress on memory require both GC and adrenergic activation in the BLA (for more-in depth reviews, please see Roosendaal et al., 2006, 2008, 2009). Activation of the BLA is believed to help modulate memory formation in other parts of the brain, such as the hippocampus and prefrontal cortex (Arnsten 2009; Schwabe et al., 2012). As discussed previously, stress effects are reduced or increased in both humans and animals following GC blockade or stimulation, and after a decrease or increase of noradrenergic arousal (de Quervain et al., 2009; Roosendaal et al., 2009; Wolf, 2008, 2009). In addition, BLA lesions or inactivation have also been shown to reduce the effects of stress on memory (La Bar & Cabeza, 2006). Consequently, the vertical perspective of stress on memory focuses on the main stress hormones, and their interactions with the BLA and medial temporal lobes, as the primary mechanisms that shape memories under stress (Schwabe et al., 2012).

In contrast to the vertical perspective’s focus on *the mechanisms* that shape memories under stress, the horizontal perspective focuses on *why* stress sometimes impairs and sometimes enhances memories. According to the horizontal perspective, the direction of the effect depends on the timing of the stressor and the learning episode. If stress is experienced within the context of a learning episode (that is, directly linked with the learning task or immediately before or after a stressor), then stress has an enhancing effect on memory. Alternatively, if stress is experience outside of a learning context (that is, with no direct link to the learning episode or long after or before the stressor), then it has an impairing effect on memory (Joëls et al., 2006).

The horizontal perspective assumes that the direction of the effect is due to the different time course of the fast and slow stress systems. The fast system is comprised mainly of the effects of catecholamines and the non-genomic effects on GCs mediated by membrane-bound receptors. The slow system, on the other hand, focuses on the genomic effects of GCs, which tend to be delayed and long lasting (Groeneweg, Karst, de Kloet & Joëls, 2011; Joëls, Fernandez, & Roosendaal, 2011; Karst et al., 2005, 2010). The effects of the fast stress system are beneficial to memory in the short-term. Both catecholamines and GCs facilitate

learning and memory. Conversely, the slow system affects memory negatively. The genomic actions of GCs suppress the processing of new information and therefore impair the memory process in a way that is unrelated to the GC release (Schwabe et al., 2012).

The horizontal perspective model therefore predicts that if an individual is stressed immediately before, during, or immediately after a learning episode, the beneficial effects of the fast stress system will facilitate attention and encoding processes. In addition, the slow genomic effects of the slow system will suppress competing new information, thereby impairing new learning and enhancing consolidation (Buchanan & Lovallo, 2001; Cahill et al., 2003). However, if an individual is stressed long before or after the learning episode (when the fast stress system has returned to baseline and the genomic effects of the slow stress system are active) then stress can impair memory encoding and consolidation (Joëls et al., 2006).

According to the horizontal model, the disruptive effects on retrieval could occur for two reasons: (i) the stressor is experienced out of context, or (ii) memory retrieval is suppressed in order to facilitate learning (Schwabe et al., 2012). If the stressor is out of context, then the retrieval deficits might be due to there being no direct relationship between the stressor and the memory task. According to this model, studies conducted in laboratory settings are particularly sensitive to 'out of context' stressors (Buchanan et al., 2006; de Quervain et al., 1998; Kuhlmann et al., 2005). Alternatively, stressor-induced retrieval deficits could be due to the facilitation of the new learning process. That is, attention and cognitive memory capacities are directed toward encoding and consolidating the stressful episode at the expense of other cognitive activities, such as retrieval of previously learned information (de Kloet et al., 1999; Diamond et al., 2004; Roozendaal, 2002).

Correspondingly, memory retrieval that follows a stressor can focus cognitive capacities towards storage of the event at the expense of restabilization of reactivated information, thereby resulting in impaired reconsolidation (Schwabe & Wolf, 2010b).

Evidence that supports the horizontal model is found at both a cellular and behavioral level. From a cellular perspective, stress hormones (such as catecholamines and GCs) appear to enhance learning at a synaptic level. Norepinephrine has been shown to (a) strengthen synaptic connections in the hippocampus (Katsuki, Izumi, & Zorumski, 1997), and (b) be involved in facilitating the induction of long-term potentiation (Gelinas & Nguyen, 2005; Hopkins & Johnston, 1984; Huang & Kandel, 1996). Long-term potentiation (LTP) is widely considered to be a fundamental cellular mechanism that is responsible for learning and memory (Diamond et al., 2007). In addition, the rapid non-genomic effects of GCs also

appear to play a role in facilitating glutamatergic transmission in the hippocampus and amygdala (Karst et al., 2005, 2010). In contrast, the slow genomic effects of GCs seem to suppress LTP in the hippocampus and the amygdala (Diamond et al., 2007; Kavushansky & Richter-Levin, 2006; Kim & Diamond, 2002). Evidence supporting the genomic and non-genomic effects of GCs has also been found in functional imagining studies (e.g., see Henckens, Wingen, Joëls, & Fernández, 2010; Lovallo, Robinson, Glahn, & Fox, 2010). Thus, at a cellular level, stress hormones have been shown to enhance memory in the immediate stages surrounding the stressful episode and to suppress memory at later stages following that episode.

Behavioral evidence that supports the horizontal perspective has been alluded to above. The overwhelming trend in the literature suggests that the effects of stress are dependent on timing. As discussed previously, stress and GC treatment are generally reported as having enhancing effects on consolidation and impairing effects on retrieval and reconsolidation. Inconsistent findings with regard to encoding have been theorized to result from differences in the time interval between the stressor and learning task (Diamond et al., 2007; Joëls et al., 2006). Some studies that have reported encoding enhancements have administered the stressor immediately before the learning task (e.g., Domes et al., 2002; Nater et al., 2007; Schwabe et al., 2008a; Smeets et al., 2007), whereas other studies that have reported impairments have used long delays (more than 20 minutes) between the stressor and the learning task (e.g., Elzinga et al., 2005; Kim et al., 2001; Kirschbaum et al., 1996, Taverniers et al., 2011a).<sup>7</sup>

In addition, the context of the stressor and the learning task has also been shown to be a powerful mediator in the direction of the effect on memory. Several studies have reported enhancements in learning when the stressor task and learning task share the same spatial-temporal context (Salehi et al., 2010; Sandi, Loscertales, & Guaza, 1997; Smeets et al., 2007). Smeets et al. (2009) demonstrated that stress administered before learning only enhanced memory when the learning material was related to the stressor and was high in arousal value. However, a more recent study found that the recall of both stress-related and stress-unrelated words were impaired as a result of stress occurring during learning (Schwabe & Wolf, 2010a).

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<sup>7</sup>However, some studies that have administered stress immediately before the learning task have shown impairments (e.g., see Diamond et al., 2006, Schwabe & Wolf, 2010a), whereas some studies that have used long delays between stressors and learning have shown enhancements (e.g., Taverniers et al., 2011b).

In summary, the integrated vertical and horizontal perspective combines two separate models of stress and memory functioning. The first, the vertical model, explains the mechanisms believed to underlie stress effects on memory. Those mechanisms are believed to be concurrent GC and adrenergic activation of the BLA, which in turn interacts with the medial temporal lobe structures (specifically, the hippocampus). The second, the horizontal model, aims to provide an explanation as to why stress can have both a positive and a negative influence on memory. According to the horizontal model, the effects of stress are dependent on the time of the stress exposure. Stress is proposed to exert positive effects on memory if the stressor and memory task occur within a short space of time from each other and/or are in the same spatiotemporal context. These beneficial effects are suggested to be due to the rapid effects of catecholamines and the non-genomic effects of the GCs, described in the vertical hypothesis. Impairing effects are suggested to be due to the genomic effects of the GCs, where the stressor is being experienced out of context, or due to the facilitation of new learning.

Given that it is the most recent theory, the *integrated perspective* seems best poised to describe the general effects of stress on memory. Despite some studies having reported findings that do not confirm predictions derived from this theory, the integrated perspective effectively describes the biological mechanisms and actions that account for: (i) the inconsistent effects of stress that are seen with memory encoding, (ii) the generally positive effects on memory consolidation, and (iii) the generally negative effects found with retrieval and reconsolidation. However, in the present dissertation I will compare the predictions derived from the integrated vertical and horizontal perspective against those derived from the inverted-U hypothesis and hot-cool theory. Given that state-dependent learning has largely been refuted as an explanation for the effects of stress on memory (Coluccia et al., 2008; Wolf et al. 2002), I will not discuss this theory in relation to the findings in later chapters.

An explanation for the effects of stress on memory common to the inverted-U hypothesis, hot-cool theory, and the integrated vertical and horizontal perspective is that GCs have both positive and negative effects on the hippocampus, thereby significantly influencing the functioning of this structure. The hippocampus is a structure that is directly involved in episodic memory, although some amount of controversy surrounds the temporal aspect of hippocampal involvement in episodic memory.

## The Hippocampus and Episodic Memory

The hippocampus is critically involved in certain aspects of memory function. That is, the structure is essential for the acquisition, retention, and retrieval of declarative memories that deal with conscious recollection of facts and episodes. In contrast, the hippocampus is less critically involved in non-declarative memory forms, such as motor and perceptual learning, priming, and the learning of habits, skills and rules (Winocur, Moscovitch & Bontempi, 2010). Again, this review will focus primarily on hippocampal-dependent episodic memory, and spatial memory in particular.

The initial evidence that the hippocampus was involved in memory functioning came from the study of amnesic patients. Scoville and Milner (1958) were the first to describe how bilateral lesions in the medial temporal lobes (including the hippocampus) resulted in profound anterograde amnesia. Patients with these lesions were incapable of learning and recalling new memories. In addition, patients also showed a striking temporal graded retrograde amnesia. That is, they seemed to have no memory for recent events prior to the trauma/operation/disease that resulted in their medial temporal lobe lesions. However, their memories for more remote events (i.e., those encoded prior to the onset of their amnesia) were retained (Penfield & Milner, 1958; Squire & Bayley, 2007). Since this discovery, a large number of human and animal studies have shown recent memory to be impaired and remote memory to be intact (although varying temporally and qualitatively) following hippocampal lesions (e.g., Frankland & Bontempi, 2005; Squire & Bayley, 2007; Sutherland & Lehmann, 2011; Winocur et al., 2010a).

The discrepancy between retrieval of recent and remote memories following hippocampal lesions has led to considerable debate over the role of the hippocampus and the long-term storage and retrieval of memories. The crux of this debate surrounds the topic of the role of the hippocampus in remote memory; consequently, several theories have emerged that attempt to explain this role in recent and remote memory. Two of the more notable theories are *Standard Consolidation Theory* and *Multiple Trace Theory*.

**Standard Consolidation Theory.** The central premise underlying Standard Consolidation Theory (SCT; Burnham, 1904; Muller & Pilzecker, 1900; Ribot, 1882) is that the movement of transient short-term memories to durable long-term memories is a time-dependent process (Hebb, 1949). Although this theory has evolved since its conception, the central idea is the initial retention and retrieval of recently formed memory is reliant on the hippocampus. As the memory becomes consolidated, it is presumed to be stored in neocortical areas. Over time this memory becomes less dependent on the hippocampus until

the durable long-term memory is no longer reliant on the hippocampus for activation (Milner, Squire, & Kandel, 1998; Scoville & Milner, 1957; Squire & Bayley, 2007).

Research has distinguished between two different types of consolidation. The first type is a rapid initial process that follows encoding. This type of consolidation entails cellular and synaptic reorganization and appears to occur over a time range that last seconds to hours, depending on the information. It is this type of consolidation, and the interaction with acute stress, that has been discussed above. The second type of consolidation is a more prolonged process that can extend over a time span ranging from days to years. It is related to changes in the distribution of the memory trace across neural systems (Winocur et al., 2010a). The change in the representation of a long-term episodic memory across brain regions is referred to as ‘systems level consolidation’. It is this second type of consolidation that is the central concern of SCT (Dudai, 2004). Thus, according to SCT, the hippocampus plays a time-limited role in the retrieval of episodic memory and is only involved until the memory trace has consolidated in the neo-cortex.

**Multiple Trace Theory.** According to Multiple Trace Theory (MTT; Nadel & Moscovitch, 1997; Nadel & Moscovitch, 1998), once an event that has been experienced is represented as an episodic memory, a link or trace is formed between the hippocampus and the neocortical neurons. Each time the memory is retrieved, it is automatically re-encoded by the hippocampus along with the context in which the retrieval occurred. The more times a memory is retrieved, the more traces it has and the stronger it is, as there are more trace opportunities for retrieval.

According to MTT, neocortical structures extract the common features of the mature memory across the different spatio-temporal contexts and form the gist of the event, which is independent of context. The memory therefore moves farther away from being an episodic memory, towards being a semantic memory that is not dependent on the hippocampus. Thus, in terms of the MTT, the hippocampus is always necessary for the representation of detailed episodic memories about an event (Winocur et al., 2010a).

Winocur et al. (2010a) recently expanded MTT with *the transformation hypothesis*. This hypothesis has three main elements. First, the memory of a recent event that contains episodic and contextual information remains dependent on the hippocampus for as long as the memory retains episodic features. Second, with experience, and over time, the memory is represented in the neocortex. However, unlike the hippocampal version of the memory, the neocortical version is devoid of spatio-temporal context and is instead a schematic memory that retains only some of the essential features and meanings. The third element of the

transformation hypothesis outlines a dynamic interplay between the hippocampal version and the neocortical version of the memory; that is, either version of the memory can be dominant, depending on the relative strength of the memory trace and the circumstances that elicit the memory at the retrieval phase. The two versions of the memory can therefore interact with and influence each other, given that retention and retrieval are constantly evolving processes (Winocur et al., 2010a). Thus, according to the transformation hypothesis, the hippocampus is engaged even in remote memories, but the extent of engagement depends on which version is dominant at the time of retrieval.

***Standard Consolidation Theory versus Multiple Trace Theory.*** Support for both SCT and MTT have been presented in patient studies, imaging studies, and in animal lesion studies.<sup>8</sup> The crux of the debate between the theories lies in the role of the hippocampus in remote memory. However, in line with consistent research findings, both theories share the common understanding that the hippocampus is fundamental for the encoding and consolidation of new episodic memories, as well as the retrieval of recent memories.

A second minor area of disagreement between SCT and MTT is the topic of spatial memory. Whereas SCT does not distinguish between spatial and non-spatial memories, and predicts hippocampal involvement for recent memory, MTT and the transformation hypothesis view spatial memory as special and *always* reliant on the hippocampus.

### **Hippocampus and Spatial Memory**

O'Keefe and Nadel's (1978) pioneering work distinguished between two forms of spatial memory, namely, allocentric and egocentric spatial memory. *Allocentric spatial memory* refers to the memory for spatial layout of an environment and the configural spatial relationships between locations within that layout. *Egocentric spatial memory*, on the other hand, refers to memory for landmarks and routes in an environment, and to memory from an individual's point of view. Research from animal, lesion, and imaging studies, has implicated the hippocampus in being instrumentally involved in allocentric spatial memory (Squire & Bayley; 2007; Winocur et al., 2010a), whereas the caudate nucleus is implicated in egocentric spatial memory (Bohbot, Gupta, Banner & Dahmani, 2011; Packard & McGaugh, 1996).

Early studies that examined spatial memory in patients with medial temporal lobe lesions showed that despite not being able to learn new or recall recent spatial environments,

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<sup>8</sup>See reviews supporting these theories; for SCT, Squire & Bayley; 2007, for MTT and the transformation hypothesis see Winocur et al., 2010a.

these patients were capable of navigating in environments in which they had considerable amounts of pre-morbid experience (Beatty, Bierley & Boyd, 1985; Milner, Corkin & Teuber, 1968; Zola-Morgan, Squire & Amaral, 1986). More recent studies of patients with well-documented bilateral hippocampal lesions have reported similar findings (Maguire, Nannery & Spiers, 2006; Rosenbaum et al., 2000; 2008; Teng & Squire, 1999). Despite the patients being incapable of learning or recalling new spatial environments, they showed excellent recall of neighborhoods where they had lived for some time prior to their brain injuries. However, the patients showed missing details for the finer points (such as the inability to recognizing familiar landmarks), and for some allocentric spatial information regarding the environments (Winocur et al., 2010a).

Imaging studies have confirmed that the hippocampus is essential for recent, but not for remote, spatial memory in both patients and healthy controls (Maguire, Woollett & Spiers, 2006; Rosenbaum, Winocur, Grady, Ziegler, & Moscovitch, 2007). In a recent fMRI study, Hirshhorn, Grady, Rosenbaum, Winocur, and Moscovitch (2012) examined memory for a large-scale city environment (Toronto, Canada) in healthy participants who had moved to the city within the previous 6 months. This memory was then examined again when these same individuals had been living in the city for a year. Consistent with findings from prior research, when participants had just moved to the city they showed hippocampal activation when performing mental navigation tasks. However, after living in the city for a year, hippocampal activation was not detected. Instead, only neocortical activation in the brain regions associated with remote memory were detected. These same neocortical regions were identified in a prior study using the same tasks (Rosenbaum et al., 2005).

Consistent with patient and imaging studies, rodent studies have reported that hippocampal lesions produce both anterograde and temporally-graded retrograde amnesias. Rats that had been trained in a complex environment (such as the Morris Water Maze [MWM] or cross maze) prior to hippocampal lesions displayed loss of spatial memory for the environment when tested post-surgically. Interestingly, the retrograde amnesia had a temporal quality that encompassed both recent and remote memory (Broadbent, Squire, & Clark, 2006; Clark, Broadbent, & Squire, 2005a, 2005b; Epp et al., 2008; Sutherland et al., 2001; Winocur, Moscovitch, Caruana, & Binns, 2005).<sup>9</sup> However, a few recent studies have shown that if rats are given sufficient time to train in a (non-water) environment, they retain the ability to navigate in the environment following hippocampal lesions. These rats, however,

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<sup>9</sup>Although see Ramos (1998) for an exception to this common finding.

display considerably less flexibility in using spatial cues when navigating (Wang, Teixeira, Wheeler, & Frankland, 2009; Winocur, Moscovitch, Fogel, Rosenbaum, & Sekeres, 2005; Winocur, Moscovitch, Rosenbaum, & Sekeres, 2010).

It is interesting to note that the vast majority of rodent studies that have shown remote memory retrieval impairments following hippocampal lesions have used water mazes such as the MWM (for example, see Clark et al., 2005a, and Martin, de Hoz, & Morris; 2005). A typical MWM paradigm involves a rat being placed into a small pool of water that contains an escape platform hidden a few millimeters below the water's surface. The rat learns the location of the platform by using distal cues located around the pool. Studies using the MWM have shown that even with extensive training (that is, rats trained daily from 21-90 days of age), hippocampal lesions still impair navigational performance in the MWM task (Clark et al., 2005b). Consistent with this finding, Lopez et al. (2012) recently demonstrated using *c-Fos* imaging in rats, that hippocampal activation was present for both recent and remote retrieval in a MWM task. Two possible explanations for the remote memory impairments seen in water maze tasks are: (i) the hippocampal lesion might result in the finer details of spatial memory being lost, which results in the rat being unable to navigate effectively (Squire & Bayley, 2007), or (ii) water maze tasks require that the rat constantly update its position in the water in order to find the hidden platform. The updating of its position requires an element of learning from the rat; such learning is impaired in the case of hippocampal lesions (Knowlton & Fanselow, 1998). Thus, regardless of the explanation for the remote memory impairments seen in water-maze studies, it seems that a functional hippocampus is vital in order for a rodent to successfully retrieve spatial memory in order to navigate in a complex environment, such as the MWM (Lopez et al., 2012).

According to *cognitive map theory*, the hippocampus is essential for learning and retrieving recent and remote spatial memory (O'Keefe & Nadel, 1978). Thus, in a similar vein to the MTT and the transformation hypothesis, cognitive map theory views spatial memory as being always dependent on the hippocampus (to some degree). Standard Consolidation Theory, as mentioned previously, does not differentiate between spatial and non-spatial memories, and only attributes hippocampal involvement to recent memories. Therefore, as with general episodic memory, the debate between the theories is again between whether or not the hippocampus is involved in the retrieval of remote memories.

It is not exactly clear what temporal quality separates recent from remote memories. The time it takes for a memory (spatial or not) to be stored in the neo-cortex, and to become independent of the hippocampus, is believed to depend on several factors. These factors

include the species involved, and complexity of environment (Winocur et al., 2010a). For instance, in humans, it takes from 6 months to 1 year to form a working representation of a complex large-scale environment (Hirshhorn et al., 2012), while in rats, daily exposure over several weeks to months may be sufficient (Winocur et al., 2005b; 2010b).

However, in order to avoid uncertainty over hippocampal involvement in the retrieval of remote memories, this dissertation will only attempt to examine recent memory and the effects of acute stress and GCs on it. As discussed above, there is overwhelming support (from both research and theory) that the hippocampus is vital for the retrieval of recent memory and, most relevantly to this thesis, for the retrieval of recent visual and spatial memory.

## Summary

This chapter provided an introduction to the topic of the acute stress response and its effects on episodic memory. The stress response consists of two separate yet interacting responses: one rapid and one slow. The rapid stress response is coordinated by the autonomic nervous system and is associated with adrenergic activation of the basolateral amygdala, as well as with the non-genomic effects of GCs on the membrane receptors of the hippocampus. In contrast, the slow stress response is orchestrated by the HPA axis, and is associated with the genomic effects of GCs.

The effects of the stress responses on memory depend on when the individual is stressed. The general pattern seen in the literature is that acute stress and GCs have an enhancing effect on memory consolidation, while impairing memory retrieval and reconsolidation. The reported effects on encoding have been inconsistent largely due to the confounding influence of the other phases involved in memory formation. In recent years, several theories have been developed in attempts to explain the workings of stress and GCs on episodic memory; these include *state dependent learning*, the *inverted-U hypothesis*, *hot-cool theory* and the *vertical and horizontal perspective theory*. The latter is the most recently developed and is currently best suited to explain fully the influence of stress on memory functioning. The predictions derived from this recent theory will be compared against those derived from the inverted-U hypothesis and hot-cool theory.

Common to the inverted-U hypothesis, hot-cool theory and, the vertical and horizontal perspective theory is that stress and GCs exert both positive and negative effects on the hippocampus, thereby exerting significant influence over the functioning of this structure. The hippocampus is a brain structure that is crucial for the acquisition, retention

and retrieval of episodic memories (including visual and spatial memories). Despite debate over the role of the hippocampus in remote memory (there are at least two competing theories, *Standard Consolidation Theory* and *Multiple Trace Theory*), it is widely accepted that intact hippocampal functioning is essential for the retrieval of recent memories.

### **Aims and Rationale**

The aim of the current series of studies is to explore the effects of stress on memory retrieval of visual and spatial material. As described above, previously published research suggests that stress and GCs generally have a negative effect on memory retrieval. Although the negative effects, according to the horizontal and vertical perspective, are due either to memory retrieval being suppressed in order to facilitate learning, or due to the stressor being experienced out of context, these findings are surprising, especially when considering visual and spatial memory. As highlighted previously, a threat to the homeostasis of an individual (both human and animal) triggers the release of stress hormones, which act on the body to give rise to the *fight-or-flight* response. From a spatial cognition point of view, it would seem to counter evolutionary adaptation that the triggering of the fight-or-flight response would be coupled with impairment in the retrieval of spatial memory. How would an organism escape a threatening situation if s/he is unable to retrieve the visual and spatial information that allows safe navigation out of the perilous situation? (In Chapter 4, I discuss memory from functional perspective in more detail).

Overall, this set of studies aims to investigate two neglected areas of research on stress and memory. First, the effects of stress on the cognitive domain of visual and spatial memory are relatively unexplored in humans. The vast majority of human studies have looked at the effects of stress or GCs on verbal memory. Those few studies that have looked at visual memory have usually used pictures (e.g., Buchanan & Tranel, 2008), while few have looked at spatial memory using tabletop neuropsychological tests (e.g., Schwabe & Wolf, 2009; Quesada et al., 2012). However, there is a notable absence of studies investigating the effects of stress on memory retrieval for an interactive three-dimensional spatial environment.<sup>10</sup> Examining the effects of stress on this kind of spatial memory in humans will give a better understanding of the effects of stress on cognition and provide clearer comparisons with animal research findings, as this is the principal area of cognition investigated in animal research.

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<sup>10</sup> Guenzel et al. (2013) recently explored the effects of stress on non-hippocampal spatial memory retrieval using an interactive virtual environment. However, no studies (to my knowledge) have examined the effects of stress on hippocampal-dependent spatial memory retrieval using an interactive virtual water maze task.

Second, this set of studies aims to investigate spatial learning and memory using landmarks that are of an arousing nature and that vary in valence. Landmarks help maintain orientation within an environment, and also act as primary organizing features in cognitive maps. They therefore play a pivotal role in spatial navigation through both novel and familiar environments. Although the physical qualities of landmarks are fairly well understood, relatively little is known about the emotional qualities of landmarks. In fact, to my knowledge, no other study has looked at the emotional quality of landmarks. The aim of the current studies is to compare visual and spatial memory retrieval for landmarks of varying arousal (high arousal versus low arousal) and valence (positive, neutral, and negative valence). These emotional landmarks should tap into the most basic of emotional/survival responses and thus should give a better understanding of human spatial behavior under conditions of stress/arousal. (In Chapter 2, I discuss in more detail the relevance for a better understanding of the different qualities of landmarks).

To investigate the effects of stress on visual-spatial cognition, the current series of studies aims to replicate, systematically, the paradigm used by de Quervain et al. (1998). As mentioned briefly above, de Quervain and colleague's pioneering study was the first to report the negative effects of stress on retrieval in rodents in a MWM study.<sup>11</sup> de Quervain et al. demonstrated, importantly, that both stress (in the form of foot-shocks) and GC treatment impaired performance in a MWM that was learned 24 hours before.

To examine visual and spatial memory retrieval in humans, the current set of studies substituted the traditional MWM used by de Quervain and colleagues with a virtual MWM environment. In addition, I also substituted the foot-shock stressor with a more appropriate stressor. Chapters 2 and 3 of this dissertation aim to validate the instruments used to test the research question, while Chapters 4 and 5 test the actual question by either administering stress (Chapter 4) or cortisol (Chapter 5) treatment.

This research is important in obtaining a better understanding of memory under conditions of stress. We are all susceptible to a multitude of stressful episodes through our lives in which we have to remember information successfully. In most of these episodes, the failure to remember relevant information can make the difference between success and failure. If we are able to better understand how memory works under stress, then we may be able to identify what areas of memory are most affected by stress and, in turn, find ways of encoding information that may be more resilient under stressful conditions.

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<sup>11</sup>Rodent studies have also shown that a functional hippocampus is needed in order to successfully complete the MWM, irrespective of when the maze was learned (that is, whether memory for its layout is recent or remote).

## CHAPTER TWO:

### STUDY A – VALIDATION OF THE SPATIAL ENVIRONMENTS

As stated in Chapter 1, the present dissertation aims to explore the effects of stress on memory retrieval of visual and spatial material. To do so, I aim to systematically replicate the pioneering paradigm used by de Quervain et al. (1998). Those researchers were the first to report the negative effects of stress on memory retrieval in rodents and, importantly, demonstrated that both stress (in the form of foot-shocks) and glucocorticoid (GC) treatment impaired performance in a Morris Water Maze (MWM; Morris, 1984) environment that had been learnt 24 hours prior. Because it is not feasible to use the MWM, constituted in the conventional way, in human research, the aim of the present chapter is to describe the manner in which I developed a spatial navigation task formally similar to that used by de Quervain et al., but more appropriate for use with human participants. I will first introduce the topic of spatial navigation and then describe the process of validation of the spatial tasks that will be used in the subsequent studies.

Being able to successfully navigate an environment is crucial to ensuring the survival of any mobile animal. Humans and animals must learn something about the layout of their environment so that they can locate nutritional sites and other important resources; remember and avoid dangerous locations; return home; or migrate between known places (Foo, Warren, Duchon, & Tarr, 2005). To accomplish these tasks, a reliable cognitive system is needed to represent the elements of the external world. This system should represent these elements in relation to the organism itself, as well as in relation to other elements of the environment (Roche, Mangaoang, Commins, & O'Mara, 2005). This internal representation of the external environment can be compared to a cartographic map. Indeed, this metaphor was originally used by Tolman (1948), who coined the term “cognitive map.”

#### **Cognitive Maps**

Downs and Stea (1973, p. 9) define cognitive mapping as “a process composed of a series of psychological transformations by which an individual acquires, stores, recalls, and decodes information about the relative locations and attributes of phenomena in his/her everyday spatial environment”. Golledge and Stimson (1997) elaborated on that idea, stating that the process of cognitive mapping is a way to structure, interpret, and cope with a vast and complex set of information that exists in different environments. This process exists partly in

service of wayfinding, which may be defined as the manner in which organisms orient and navigate in order to accurately relocate between places in the environment and to recognize when a destination has been reached (Gluck, 1990; Peponis, Zimring, & Choi, 1990).

From a neurophysiological viewpoint, the development of a cognitive map begins with sensory inputs from the environment. These inputs include visual input from the occipital cortex, balance and topographical information from the vestibular system, auditory information from the temporal association areas, proprioceptive feedback from the somatosensory areas concerning muscles and joints, and (to a lesser degree in humans) olfactory information from the olfactory bulb. All these inputs allow an animal to create an accurate cognitive representation of the environment. The process whereby these stimuli are converted into a stored representation, model, or map of the environment has been referred to as a *spatial strategy* (Roche et al., 2005).

**Route-, survey-, and landmark-based information.** Two possible navigational learning strategies when exploring the layout of new, novel or altered environments include a physical search and exploration of the environment (route or egocentric knowledge) or a priori familiarization through secondary information (survey or allocentric knowledge; Levelt, 1982; Linde & Labov, 1975; O'Keefe & Nadel, 1978). This secondary information may include maps, books, photographs, videos, or any other source that may describe the appearance of the environment (Golledge & Stimson, 1997). Roche et al. (2005) describe route-based knowledge as knowledge of the spatial layout from an individual's perspective (egocentric or ground-level view); it is acquired as a result of physical navigation through the environment. Route knowledge thus involves information about the order and sequence of locations or landmarks, and the actions taken at each landmark. This form of knowledge, which can be thought of in terms of a quick trip to the local supermarket, is acquired and used almost unconsciously (McNamara & Shelton, 2003). Subsequent trips along the route will increase the individual's knowledge of the slopes, distances, and vectors associated with the environment surrounding those landmarks (Brunyé, Gardony, Mahoney, & Taylor, 2012; Foo et al., 2005; Roche et al., 2005).

Survey knowledge, on the other hand, is allocentric knowledge of the spatial layout of the landmarks, gathered via an external perspective of the environment, creating something closer to a map like-view. Thus, the contents of the environment are incorporated and related to each other, irrespective of the position of the individual. So, finding a new supermarket in a familiar city would entail developing a geographic representation of landmarks and the

directions in relation to these landmarks. Survey knowledge underlies what we know as a cognitive map (Brunyé et al., 2012; McNamara & Shelton, 2003; Roche et al., 2005).

An increase in survey knowledge enables an individual to create an increasingly accurate cognitive representation of any given environment (Golledge & Stimson, 1997). However, the formation of a cognitive map (through the use of the constituent landmark, route, and survey knowledge) is more abstract than the sum of the component parts, as cognitive maps have “image-like” properties. They allow individuals to estimate distances, plan short cuts or detours, and obtain bearings from any location within the map (Peruch, Gaunet, Thinus-Blanc, & Loomis, 2000).

An important common feature of using either route or survey knowledge is the utilization of landmarks. Specifically, as an individual travels along a route, s/he will become familiar with the landmarks along that route. Subsequent trips along that route could possibly lead to an increase in survey knowledge, which will relate those landmarks to each other irrespective of the individual’s position.

**Landmarks in cognitive maps.** Landmarks are essential components of cognitive maps. Previous empirical and theoretical work has established that the acquisition and development of both route and survey knowledge invariably involves some landmark recognition, as well as recognition that paths or routes develop between these landmarks. Furthermore, knowledge of landmarks plays an important role in maintaining orientation during navigation (Chan, Baumann, Bellgrove, & Mattingley, 2012; Jansen-Osmann & Wiedenbauer, 2004; Siegel & White, 1975). From this point of view, physical landmarks are one of the most important features of wayfinding.

Before proceeding further, it is useful to define exactly what is meant by “landmark” in this context. One early, basic definition is that a landmark is any element of an environment that acts as a reference point; it can be drawn from the natural, built, or cultural environment (Lynch, 1960). Golledge (1999) added to this definition by saying that landmarks might be the strategic focus points towards or away from which an individual may travel; intermediate focus points on routes that may assist in spatial decision making; or significant physical structures, buildings, or culturally defined objects that stand out in the environment. Roche et al. (2005) pointed out that landmarks have two distinct components when being used: (a) they are capable of drawing attention and being recognized by many people on the basis of visibility, pertinence, distinctiveness and permanence, and (b) they accrue significance in an idiosyncratic way.

In summary, landmarks not only help maintain orientation but also act as a primary organizing feature in cognitive maps. That is, they usually act as anchor points for organizing other spatial information into a cognitive layout of the environment (Couclelis, Golledge, Gale, & Tobler, 1987). Landmarks are often noticed or remembered because they are visibly dominant and easily identifiable in terms of shape, structure, or social significance. Coincidentally, factors like size, visual form, clarity, dominance, color, architectural design, location, proximity to other cues, functional class, and shape are all points advertisers stress in creating an advert that will draw the public's attention (Chan et al., 2012; Golledge & Stimson, 1997; Rossiter & Percy, 1997).

The above factors are useful in determining why people choose between different visually distinctive landmarks (e.g., selecting a petrol station rather than an office block). Under conditions of navigating with visually similar landmarks, however, the idiosyncratic meaning of a landmark may be the most important factor influencing an individual's memory and use of the landmark (Roche et al., 2005). This idiosyncratic meaning might derive, for instance, from prior history (e.g., either direct or indirect contact that will give an individual a narrative by which a landmark comes to have particular meaning).

A closely related concept that also influences the memory and use of landmarks is the individual's schemas. Neisser (1976) proposed the concept of the schema as a cognitive construct that mediates perception. That is to say, a schema is a mental framework for organizing knowledge (Sternberg, 2006). Schemas accept some pieces of perceptual information as a given concept, and focus an individual's attention on other aspects. Schemas underlie, for instance, stereotypes that individuals hold about particular places or situations. Schemas influence memory in that, when a person with an activated schema enters a new environment, s/he will look for schema-expected elements (Zimring & Gross, 1991). In the context of spatial navigation, these processes might lead an individual to focus on certain landmarks that are consistent with his/her schema.

One can safely conclude, therefore, that landmarks are chosen for use in cognitive mapping and consequent spatial navigation either because they are visually distinctive or because they hold some sort of idiosyncratic significance. This study seeks to delve even further into the nature of landmarks by examining their emotional qualities and the impact of those qualities on navigation. Although some studies (McGregor, Hayward, Pearce, & Good, 2004; Paz-Villagran, Save, & Poucet, 2004; Wiener, Berthoz, & Zugaro, 2002) have found that different environmental features and shapes can influence firing rates of hippocampal

neurons in rats, relatively little is known about human spatial cognition using landmarks that contain emotional or arousing qualities.

As mentioned in Chapter 1, a reasonably large body of literature has shown that memory is usually stronger for emotionally arousing material than for neutral material (La Bar & Cabeza, 2006; Packard & Goodman, 2012; Payne et al., 2006; Reisberg & Heuer, 2004; Wolf, 2008). In addition, the effects of stress are often more pronounced for emotional material (de Quervain et al., 2009; La Bar & Cabeza, 2006; Roozendaal et al., 2004, 2009; Schwabe et al., 2012; Wolf, 2008, 2009).

Given the empirical results comparing neutral to emotionally significant material, the question arises for those interested in spatial navigation: If people remember arousing material better than neutral material, then would this beneficial effect be transferred to spatial learning or memory when using landmarks that contain emotional content?

Before attempting to answer that question, one must look, first, at some factors that influence spatial cognition, and, second, at the apparatus that can be used to investigate the question.

### **Sex Differences in Spatial Memory**

Sex differences in spatial memory are among the most robustly demonstrated effects in the psychological literature (for meta-analyses, see Linn & Petersen, 1985; Voyer, Voyer, & Bryden, 1995). Although there is some debate concerning the actual magnitude of the differences, in general, men perform better than women on tests of spatial rotation and navigation (Andreano & Cahill, 2009; Johnson & Bouchard, 2005, 2007). However, women generally perform better than men on tests of object location (Andreano & Cahill, 2009). Because spatial navigation is the primary focus of the present dissertation, this area of spatial cognition is discussed below.

Consistent male advantages in both accuracy and completion time have been reported for tasks of navigation that entail reconstruction of a path on a two-dimensional map (Choi & Silverman, 1996; Dabbs, Chang, Strong, & Milun, 1998; Galea & Kimura, 1993; Postma, Jager, Kessels, Koppeschaar, & van Honk, 2004; Rahman, Andersson, & Govier, 2005), tasks involving experimentally manipulated virtual environments (Astur, Ortiz, & Sutherland, 1998; Chai & Jacobs, 2009; Iaria, Petrides, Dagher, Pike, & Bohbot, 2003; Moffat, Hampson, & Hatzipantelis, 1998; Mueller, Jackson, & Skelton, 2008; Ross, Skelton, & Mueller, 2006; Sandstrom, Kaufman, & Huettel, 1998), and tasks involving real-world space (Malinowski & Gillespie, 2001; Saucier, Green, Leason, MacFadden, & Elias, 2002; Silverman et al., 2000).

However, it must be noted that some studies have not found sex differences in navigation (Andersen, Dahmani, Konishi, & Bohbot, 2012; Astur, Tropp, Sava, Constable, & Markus, 2004).

In addition to notable sex differences in navigational performance, men and women appear to use different cognitive navigational strategies (Andreano & Cahill, 2009). Several studies have indicated that men prefer to use allocentric or Euclidian strategies, whereas women prefer egocentric or topographic strategies (Barkley & Gabriel, 2007; Chai & Jacobs, 2009; Choi & Silverman, 1996; Dabbs et al., 1998; Lawton, 1994; Lawton, Charleston, & Zieles, 1996; Rahman et al., 2005). Topographic strategies engage the use of landmarks, whereas Euclidian strategies involve the use of distances and directions.

The explanations for these differences in spatial cognition and spatial strategies have been attributed to both developmental reasons, such as age (Dabbs et al., 1998; Joshi, Mac Lean, & Carter, 1999), and biological reasons, such as variations in testosterone levels (Clint, Sober, Garland, & Rhodes, 2012; Hampson, Finestone & Levy, 2005; Kimura, 2004; Kimura & Hampson, 1994; Leplow et al., 2003). However, the correlation of circulating testosterone with navigation performance is disputed by some researchers (Driscoll, Hamilton, Yeo, Brooks, & Sutherland, 2005; Burkitt, Widman, & Saucier, 2007).

Although a full review of these differences are outside the scope of this dissertation (for a detailed review, see Andreano & Cahill, 2009), the important note here is that sex differences in spatial cognition and spatial navigation strategies do exist and have been well documented.

### **The Use of Virtual Environments in Cognitive Neuroscience Research**

Spatial cognition can be researched in at least two ways: in a naturalistic setting or in laboratory experiments (Jansen-Osmann & Wiedenbauer, 2004). With advances in technology, computer-based virtual environments provide a means of combining these two ways (i.e., by simulating naturalistic settings for use in laboratory experiments). Virtual environments (VEs), therefore, provide a convenient means of investigating human spatial behavior (Thomas, Hsu, Laurance, Nadel, & Jacobs, 2001). The use of VEs not only allows for reproduction of both novel and realistic naturalistic settings in experimental research, but also allows for control of extraneous variables and of financial costs (Frey, Hartig, Ketzler, Zinkernagel, & Moosbrugger, 2007; Sandstrom et al., 1998).

VEs have been shown to simulate naturalistic real-world environments accurately. Péruch, Vercher, and Gauthier (1995) reported that learning in VEs predicted accurate

judgments about metrics in real space. People also acquire knowledge about distances and directions in VEs, and develop route and survey knowledge in these environments (Jansen-Osmann & Wiedenbauer, 2004). In addition, the advantages of using VEs in spatial cognitive research are: (1) they provide a good transfer of spatial information (Wilson, Foreman, & Tlauka, 1997), (2) VE and virtual reality technology have been shown to help in neurological and neuropsychological rehabilitation (Brooks et al., 1999), (3) they allow for spatial relations and environmental features to be varied in a quick and economic way, (4) they allow participants to operate within the environment in a self-determined way, (5) they allow for all kinds of real-world environments to be simulated, and (6) navigation may be measured on-line (Peruch et al., 2000).

Although it can be deduced from the above that VEs are a convenient and efficient way to study human behavior, they are not without their disadvantages. For instance, VEs typically fail to provide proprioceptive feedback information that is associated with spatial learning (Witmer, Bailey, Knerr, & Parsons, 1996).

**The Computer-Generated Arena.** One non-immersive VE desktop simulation that has been used to measure human spatial navigation is called the Computer-Generated (CG) Arena (Jacobs, Laurance, & Thomas, 1997; Jacobs, Thomas, Laurance, & Nadel, 1998; Kallai, Makany, Karadi, & Jacobs, 2005; Skelton, Bukach, Laurance, Thomas, & Jacobs, 2000; Thomas et al., 2001). The CG Arena is a human analog of the MWM, and was developed in order to satisfy the need for a measure of hippocampal functioning and spatial cognition in humans. The CG Arena has been shown to have solid reliability and good construct and external validity, as data obtained from the CG Arena closely resemble those found in the MWM and in dry-land mazes (Thomas, 2003).

The CG Arena requires subjects to view a conventional computer monitor that displays a circular arena within a square room. On each wall of the room is a set of distal cues (landmarks) that may be varied by the researcher. The subject navigates through the room from a first-person perspective by manipulating the display so as to search for a square target located on the arena floor. In some conditions, the target is visible and the subjects have to locate it by visually scanning the Arena and finding it on the floor (proximal cue). In other conditions, the target is invisible and subjects have to locate it by using the distal cues on the wall.

Studies conducted by Jacobs et al. (1997, 1998) helped elucidate the differences between proximal and distal spatial orientation in the CG Arena. Proximal orientation requires cues from the actual object one is navigating towards. Distal orientation requires

gaining cues from fixed places that may be some distance from the object toward which one is navigating. Distal cues can therefore be thought of in terms of orientating landmarks.

*Place learning* in the CG arena typically entails participants using distal cues to find an invisible target. Consequently, individuals should display accurate navigation from distal cues if they take a direct path to locate an invisible target. Jacobs et al. (1997) found that (a) place learning in the CG Arena can occur on the basis of distal cues alone, and (b) place learning based on distal cues does not disengage when proximal cues are present. Jacobs et al. (1998) established that (c) place learning does not rely on any single set of distal cues, but that (d) navigation may be disrupted when changes in topographical relations among distal cues are introduced.

In summary, the research reviewed above highlights the importance of distal cues in cognitive maps and human navigation, strongly suggests that landmarks form an integral part of cognitive maps (and so play an important role in human spatial navigation), and shows that there are methods and apparatus available by which further research into the nature of landmarks may be investigated. That is to say, use of the CG Arena may allow for further investigation into what sorts of distal cues are remembered and used in navigation. As mentioned earlier, successful navigation of our environment is crucial for our survival; therefore, a thorough understanding of the qualities of landmarks with which we use to navigate is needed.

### **Aims, Rationale, and Hypotheses**

The rationale for the following comparative study was to determine whether and how effectively people can successfully navigate, learn, and remember environments containing emotionally arousing landmarks. As mentioned above, landmarks serve as markers to help maintain orientation within an environment and also act as primary organizing features in cognitive maps. They therefore play a pivotal role in spatial navigation and wayfinding. The emotional landmarks that were used in this study were chosen to tap into the most basic of emotional/survival responses.<sup>12</sup> From an evolutionary perspective, survival of both humans and animals depends on avoiding threatening stimuli and being able to locate stimuli that promote survival. Thus, the location of both defensive and appetitive stimuli should be

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<sup>12</sup>Lang, Bradley, and Cuthbert (1997) view emotion arousal as comprising two fundamental systems, one appetitive and one defensive. These systems have evolved through situational interactions with the environment that either threaten or promote survival. A review of the literature surrounding the appetitive and defensive motivational systems is provided in Appendix A.

successfully learned and remembered to ensure survival. Using landmarks that heavily draw upon the basic survival systems should, thus, give a better understanding of human spatial behavior under these conditions.

I created three separate CG Arena environments. The first, *the Cool room*, featured landmarks that were neutral pictures. The second, *the Hot Appetitive room*, featured landmarks that were selected as a means to activate the appetitive emotional system. The appetitive system is primarily activated in contexts that promote survival, such as procreation, sustenance, and nurturance. These contexts promote a basic survival behavior repertoire based on copulation, ingestion, care giving, and exploration (Bradley, Codispoti, Cuthbert, & Lang, 2001). The third, *the Hot Defensive room*, featured landmarks that were selected as a means to activate the defensive emotional system. The defensive system is activated in situations of threat that trigger such basic behaviors as escape, avoidance, attack, or defence (Bradley et al., 2001). The pictures used in this study were rated in terms of their arousal and valence qualities in a separate study, presented in Appendix A.

The aim of the present study was to compare, in human subjects, spatial navigational behavior using landmarks that are neutral versus landmarks that are emotionally arousing. The study tested these hypotheses:

- (1) Navigation in the three rooms will be equally effective. This is because there will be no acute or chronic disruption of hippocampal activity (e.g., due to increased cortisol levels, or due to organic damage) in the current study.
- (2) Memory for the different rooms, however, will be influenced by the differing arousal content of the pictures across rooms. As reviewed in Chapter 1, humans process and remember emotional information more robustly than neutral material (Dolan, 2002; La Bar & Cabeza, 2006; Phelps, 2004; Reisberg & Heuer, 2004, Wolf, 2008, 2009). People should, therefore, have stronger memory for the picture stimuli that contain the arousing content versus the neutral content.
- (3) Women's navigation performance and memory will be worse than that of men, across all of the CG Arena rooms. The rationale behind this hypothesis is that previous literature (e.g., Andreano & Cahill, 2009) suggests that men perform better at tests of spatial navigation than women.

## Methods

## Participants

Twenty-four participants (12 male; mean age = 19.42 years;  $SD = 1.10$ ) were recruited from the University of Cape Town undergraduate population through the Department of Psychology's Student Research Participation Program (SRPP). All received course credit in exchange for participation. Individuals with a history of neurological illness, substance abuse or psychiatric disorders, were excluded from the study. Individuals with a prior history of visiting [www.rotten.com](http://www.rotten.com) or [www.charonboat.com](http://www.charonboat.com), or who were familiar with the images displayed on these websites, were also excluded from the study. These participants were excluded because of the chance that people with prior exposure to the 'hot' images would be desensitized to the graphic nature of their content.

## Stimulus Selection

The stimulus selection for this study was based on the results of the picture validation study presented in Appendix A. In that study, 58 participants rated 50 pictures on measures of *pleasure*, *arousal* and *dominance* using the Self-Assessment Manikin (SAM), a rating scale employed in the International Affective Picture System (IAPS; Lang et al., 1999, 2005, 2008) and in other emotional motivation studies. Each picture was classified as either:

(1) *Hot appetitive*, a category consisting of pictures that were pleasant to view (to arouse appetitive motivation). These pictures featured content showing solo and couple erotica and nudity. Previous research has shown that these kind of pictures lead to the greatest subjective ratings of pleasure and arousal (Bradley et al., 2001a, 2001b; Lang et al., 1999, 2005, 2008).

2) *Hot defensive*, a category consisting of pictures that were unpleasant to view (to arouse defensive motivation). These pictures featured content showing human attack, death, mutilation, and disease. Pictures containing these contents have previously been shown to have the lowest subjective rating of valence and the highest arousal ratings (Bradley et al., 2001a, 2001b; Lang et al., 1999, 2005, 2008).

3) *Cool*, a category consisting of pictures that were neither unpleasant nor pleasant to view, and that did not contain an active motivational content (i.e., were neutral). These pictures were selected to contain unfamiliar views of common objects (such as fruit and household appliances). Pictures of this nature were rated in the stimulus selection study as being neither high nor low in valence. Unfamiliar views of these objects were chosen so that they would also not be rated as too low in arousal (i.e., considered so familiar or mundane that participants would pay no attention to their content).

Findings from the picture validation study showed that the three groups of pictures were rated as significantly different in term of valence and arousal. Importantly, the study also validated that the sample viewed the pictures in the intended emotion and valence direction. That is, the participants judged the hot appetitive pictures as being pleasurable and arousing, and found the hot defensive pictures to be unpleasant and slightly more arousing than the appetitive pictures. The cool pictures were rated as almost neutral in pleasure, but slightly non-arousing.

In addition, four findings from the SAM data indicated that the affective ratings of the pictures in that sample are comparable with the IAPS. First, the reliability coefficients show these ratings to be internally consistent, and in line with Lang and colleagues' (2005) samples. Second, the ratings of pleasure and arousal plotted in two-dimensional affective space support the biphasic organization of emotion along the hypothetical core appetitive (upper half of the plot) and defensive (lower half of the plot) motivational systems (Lang et al., 1997). Third, the association between pleasure and arousal was found to be stronger for negative stimuli than for positive stimuli. Finally, the predictions of a negativity bias and a positivity offset were confirmed within the sample.<sup>13</sup>

The pictures chosen for use in the present study were therefore selected from the set of pictures rated in the study presented in Appendix A. More specifically, the 8 pictures used in the Cool room were selected from the 16 cool pictures rated in that study. Those 8 pictures were those judged as being the most 'neutral' (mean nearest to 5) in terms of pleasure and arousal. The mean (and standard deviation) ratings for these cool pictures were 4.94 (1.58) for valence and 3.85 (1.94) for arousal. The Hot Defensive room, in turn, contained the 8 pictures rated as being the most unpleasant and the most arousing. These pictures were selected from the group of 17 hot defensive pictures, and had mean ratings of 2.01 (1.25) for valence and 7.20 (1.73) for arousal. Finally, the Hot Appetitive room contained the 8 most pleasurable and arousing pictures from the group of 17 hot appetitive pictures. Those 8 pictures had a mean valence of 6.10 (1.93) and a mean arousal of 6.20 (1.92). The Cool, Hot Defensive and Hot Appetitive room pictures are presented in Appendix B.

### **Apparatus: The CG Arena**

This research was conducted using the CG Arena software (Jacobs et al., 1997, 1998; Thomas, 2003; Thomas et al., 2001). Participants sat in front of a computer containing the

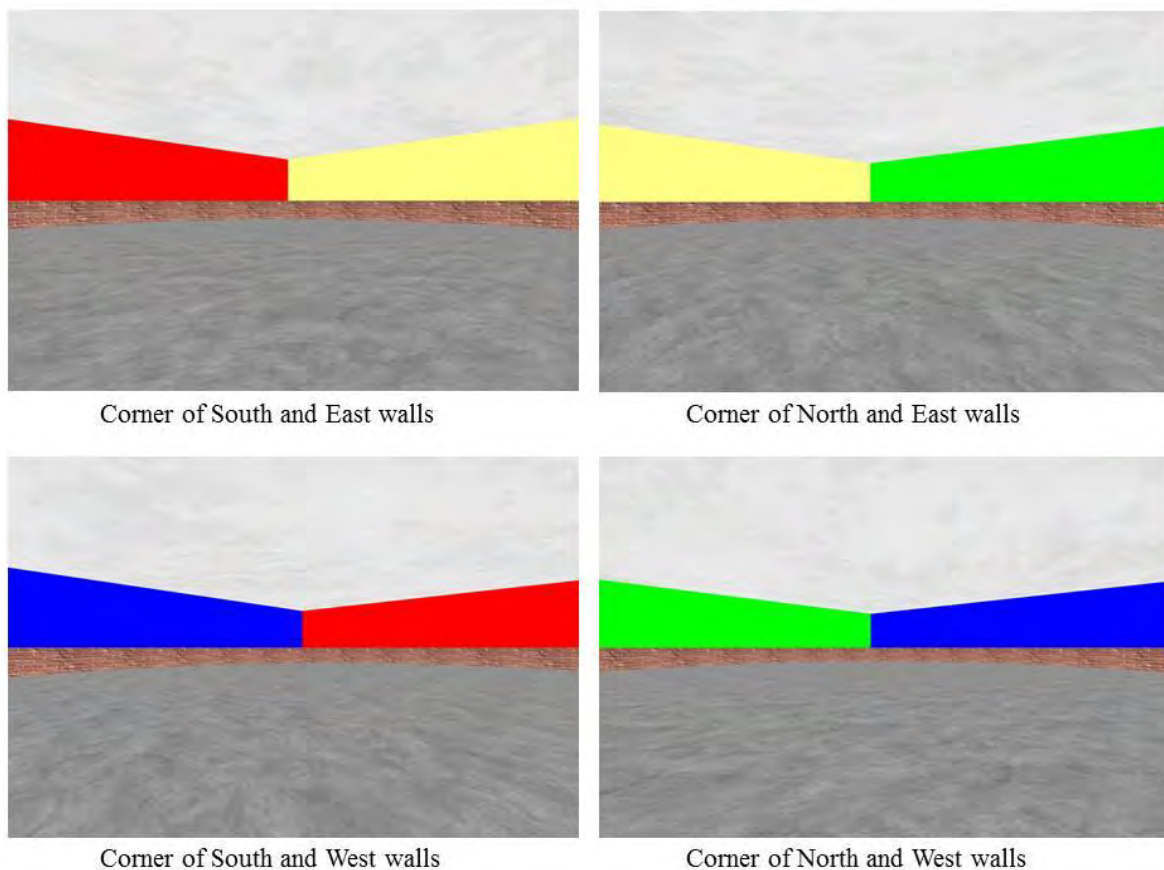
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<sup>13</sup>These results are presented in full in Appendix A.

custom-designed software. A conventional computer monitor displayed a view of a circular arena contained within one of five square rooms: a waiting room and four experimental rooms (a training room, a Cool experimental room, a Hot Defensive experimental room, and a Hot Appetitive experimental room).

**Movement in the CG Arena.** Participants were able to move within the CG Arena by manipulating a joystick manually. Moving the joystick forward or backward moved the participant's view of the Arena forward or backward. The movement in the Arena was at a constant rate until a new movement was initiated, or until the participant returned the joystick to its rest position. Moving the joystick left or right rotated the participant's view of the display left or right, respectively. This movement continued at a constant rate until the participant returned the joystick to its rest position or initiated a new movement.

**The waiting room.** Figure 1 shows the layout of the waiting room. This room was a computer-generated display of a large square room containing an arena. A circular arena wall, featuring a face brick texture, enclosed the central section of the waiting room. No distal cues were displayed on the walls of this room. The waiting room signified the start of each trial in the training, Cool, Hot Defensive and Hot Appetitive rooms.



*Figure 1.* The layout the waiting room.

**The CG Arena experimental rooms.** Each experimental room was similar to the waiting room in that it consisted of a computer-generated display of a large square room containing a face brick circular arena wall. Each wall of each experimental room was black in color, and was labeled arbitrarily either North, East, South, or West. In the Cool, Hot Defensive, and Hot Appetitive rooms, each wall offered either one or three distal cues, so that a total of eight such cues were displayed in each of those rooms. In training room, each wall featured only one distal cue.

***Quadrants of the CG Arena Experimental Rooms.*** For the purpose of data analysis, each CG Arena experimental room was divided into four quadrants: the north-west quadrant (located in the corner which is formed by the intersection of the north and west walls), the north-east quadrant, the south-east quadrant, and the south-west quadrant. Divisions between the quadrants were not apparent to the participants.

***Trials in the CG Arena experimental rooms.*** Twenty-eight trials were conducted in the CG Arena experimental rooms. Table 1 shows the parameters for those trials. The dimensions for the Cool, Hot Defensive, and Hot Appetitive rooms are presented in Appendix C. On each trial, participants had to search for a target that was either visible or invisible. If the participant moved onto the target within the allotted time, the target would become visible (if the participant was searching for an invisible target), and s/he would be locked on the target. The participant would only be able to move within the boundaries of the target until s/he pressed the spacebar or until the display changed to the waiting room of the next trial. If, however, the participant was unable to locate the target within the allocated time, s/he was transported to the waiting room of the next trial. In the waiting room, the participant would then start the next trial in the experimental room by pressing the spacebar, or wait 20 seconds before being transported to the next trial.

***The training room.*** Figure 2 shows the layout of the training room. Trials 1-4 were conducted in this room. In this room, a visible target was situated on the floor in one of the quadrants of the room. The purpose of the training room was to familiarize participants with the joystick movements within the CG Arena and with the tasks required of them. The training room also allowed the researcher to gauge if the participant was capable of performing the tasks in the CG Arena. If the participant was unable to successfully navigate to the target in the allotted time, s/he was not permitted to continue onto the remaining trials.

Table 1  
*CG Arena Trial Parameters for the Acquisition Phase*

Parameter	Type of Room/Trial						
	Training	Cool	Probe	Hot Defensive	Probe	Hot Appetitive	Probe
Number of trials	4	7	1	7	1	7	1
Sequence of start locations <sup>a</sup>	N, E, W, S	W, S, E, N	Random	W, S, E, N	Random	W, S, E, N	Random
Target condition	Visible	Invisible	Absent	Invisible	Absent	Invisible	Absent
Time limit (sec)	120	120	45	120	45	120	45

*Note.* <sup>a</sup>The N (North) starting location was near the middle of the North wall of the arena, the S (South) starting location was near the middle of the South wall, and so on. The full sequence of start locations is presented in Appendix D.

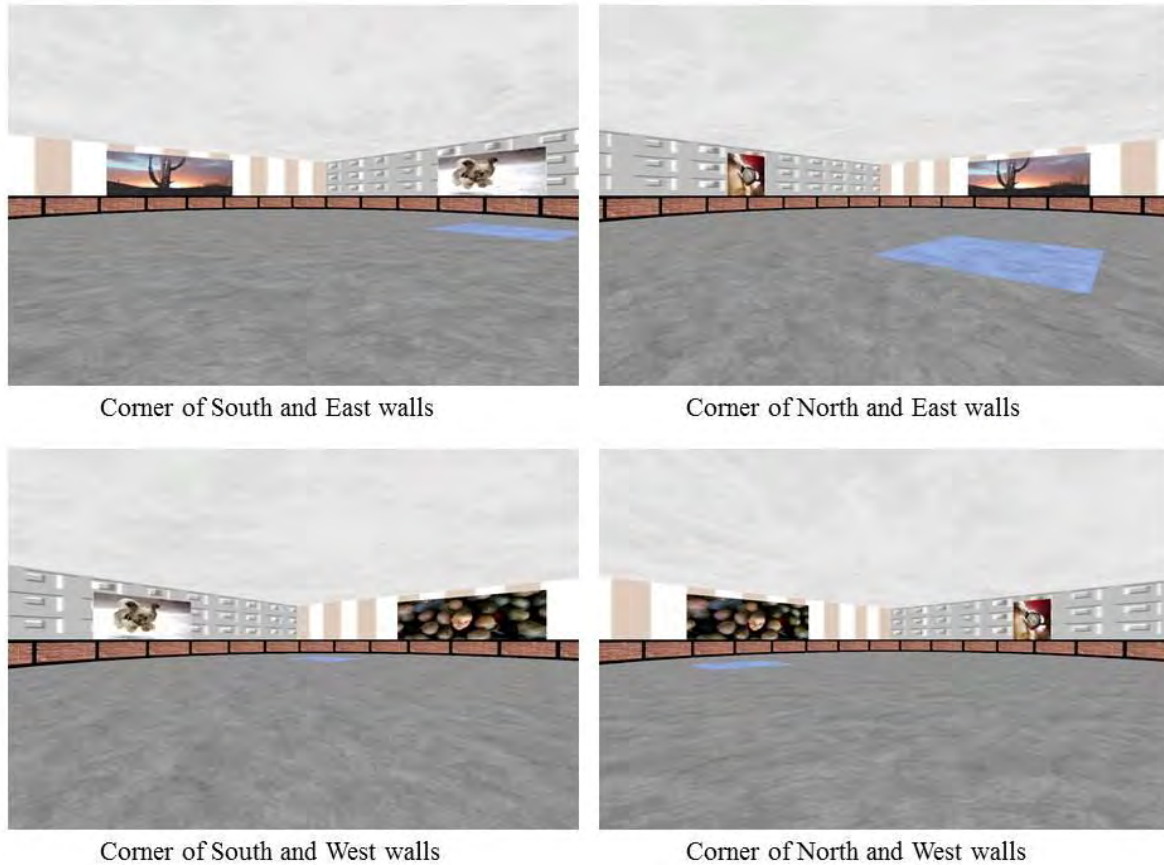


Figure 2. The layout the training room.

***The Cool experimental room.*** Figure 3 shows the layout of the Cool experimental CG Arena room. Eight trials were conducted in this room. The walls of this room displayed the eight Cool images (i.e., unfamiliar views of common objects). The first seven trials required participants to find an invisible target that was situated in a fixed location on the CG Arena floor. The eighth trial, however, was a ‘probe’ trial in which the target was absent. The purpose of the probe trial was to determine if the participants were, in fact, using distal cues to locate the target and not simply locating the target by moving about the room randomly. In other words, the purpose of the probe trial was to determine the degree of participants’ reliance on spatial versus non-spatial navigation strategies (Vorhees & Williams, 2006)

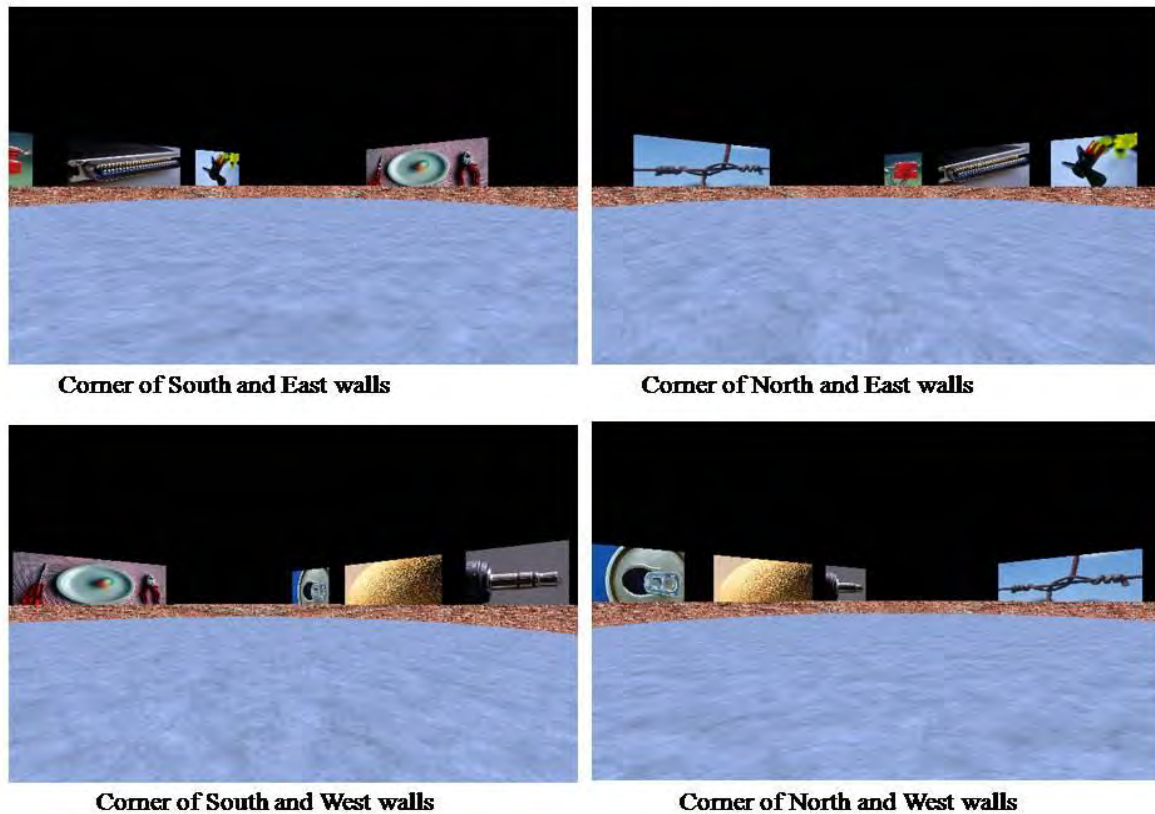
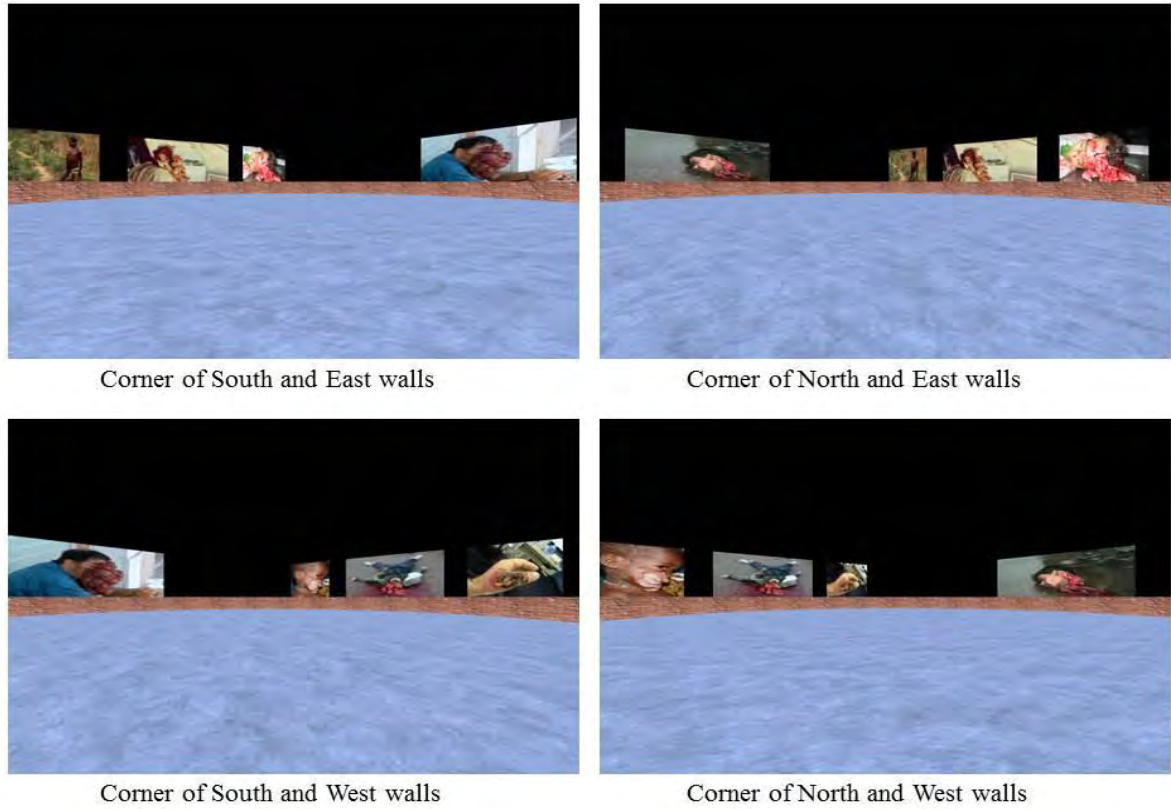


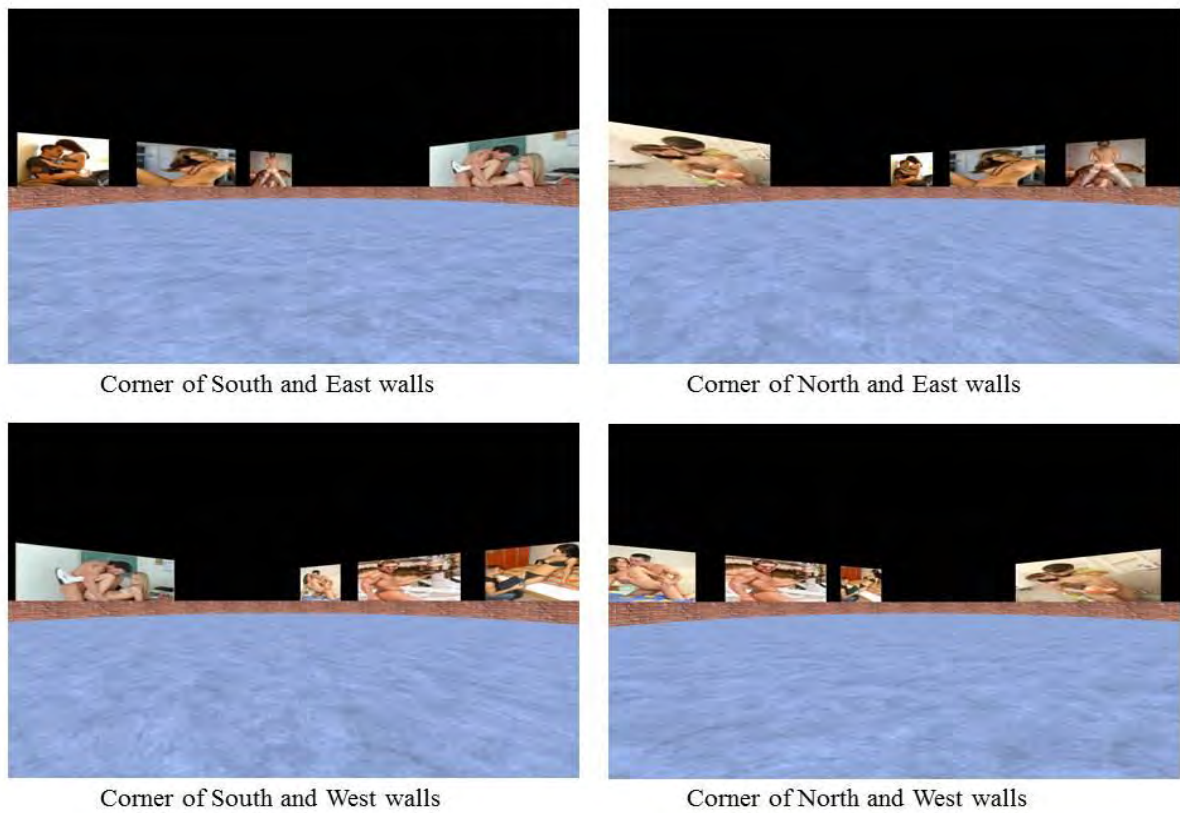
Figure 3. The layout the Cool CG Arena experimental room.

***The Hot Defensive experimental room.*** Figure 4 shows the layout of the Hot Defensive experimental CG Arena room. Eight trials were conducted in this room. The walls of this room displayed eight unpleasant arousing images (i.e., depictions of scenes of human death, attack, mutilation, and disease). These stimuli acted as fearful arousing distal cues. As in the Cool experimental room, the first seven trials featured an invisible target that was always located in the same place, and the eighth trial was a probe trial.

***The Hot Appetitive experimental room.*** Figure 5 shows the layout of the Hot Appetitive experimental CG Arena room. Eight trials were conducted in this room. The walls of this room displayed eight images that contained erotic pictures of couples or individuals. Because solo erotic pictures are often rated as slightly unpleasant and unarousing by individuals of the same sex (as the pictured individuals; see Appendix A), only two solo pictures were included (one attractive male and one attractive female erotic picture). As in the Cool and Hot Defensive experimental rooms, the first seven trials featured an invisible target that was always located in the same place, and the eighth trial was a probe trial.



*Figure 4.* The layout the Hot Defensive CG Arena experimental room.



*Figure 5.* The layout the Hot Appetitive CG Arena experimental room.

## **Other Apparatus**

Two tasks developed in conjunction with the CG Arena were administered to participants. Previous studies have shown that these tasks are good visual memory supplements to CG Arena testing (Skelton et al., 2000; Thomas, 2003; Thomas et al., 2001).

**Object Recognition Task (ORT).** The ORT is a forced-choice picture recognition test that assesses memory for the distal cues on the walls of the CG Arena experimental rooms. In the version used in this study, the participant was seated in front of a computer containing E-prime software (Psychological Software Tools, 2002). The researcher explained to the participants that a slide with two pictures was to be displayed on the screen in front of them. Each picture was labeled as either 1 or 2. One of the pictures was in the CG Arena experimental room they had just encountered and the other was not. Participants were asked to select the picture that had been in the room by pressing '1' or '2' on the computer keyboard, for 16 forced-choice slides. Eight of those images shown were those on the walls of an experimental room and the other eight were distracter objects similar to those in the experimental rooms. The cool, hot appetitive and hot defensive distracter pictures can be seen in Appendix E. Participants were thus shown each Arena picture twice, but paired with a different distracter object. A separate ORT was administered for the Cool, Hot Defensive, and Hot Appetitive experimental rooms.

**Arena Reconstitution Task (ART).** The ART is a visuospatial task that aims to assess memory for the layout of the distal cues in a CG experimental room. Its purpose is to measure the quality of the participant's cognitive map for that room. The researcher showed the participant a 3-dimensional cardboard model of the CG Arena. On each wall of the model were three strips of Velcro, indicating possible places where a distal cue could have been. In addition, on the floor of the model were four strips of Velcro (one in each quadrant of the model), which indicated possible places where the target could have been. The participant was then provided with laminated cutouts of the distal clues in the experimental room, as well as a laminated grey square representing the target. Both the pictures and the target had Velcro on their reverse side. The participant was then asked to reconstruct the room as best as s/he could by sticking the pictures on the walls of the model and placing the target on the floor. The researcher then recorded the participant's reconstruction on a sheet of paper that depicted a top down view of the layout of the model (see Appendix F). A separate ART was administered for each of the three experimental rooms.

## Procedure

The study procedures were conducted in the ACSENT Laboratory in the Department of Psychology at the University of Cape Town (UCT). The research described here followed the ethical guidelines for research subjects outlined by the Health Professions Council of South Africa and the UCT Codes for Research. The Research Ethics Committee of the UCT Department of Psychology approved all study procedures.

All testing sessions were run between 14h00 and 18h00. Once the participant and I had met, the participant was asked to read a consent form and was given a chance to ask questions concerning it. The participant was then asked to sign the form. After the participant had read and signed the consent form (see Appendix G), I administered a basic socio-demographic questionnaire (see Appendix H).

Immediately after completing the questionnaire, the participant was seated in front of a computer. I then read a set of standardized instructions, which were designed to prepare the participant for the tasks required of him/her in the CG Arena. These instructions also explained the relationship between movements of the joystick and changes in the display on the screen. After being given a chance to ask any questions concerning the instructions or the experimental procedure, the participant was then asked to complete the CG Arena tasks. As noted above, the appropriate ORT and ART was administered after each of the Cool, Hot Defensive, and Hot Appetitive rooms.

Table 2  
*Possible Sequence of Training and Experimental CG Arena Rooms*

Group	Sequence of Testing Phase			
	Trials 1-4	Trials 5-12	Trials 13-20	Trials 21-28
1	Training Room	Hot+ Room	Cool Room	Hot- Room
2	Training Room	Hot+ Room	Hot- Room	Cool Room
3	Training Room	Cool Room	Hot+ Room	Hot- Room
4	Training Room	Cool Room	Hot- Room	Hot+ Room
5	Training Room	Hot- Room	Cool Room	Hot+ Room
6	Training Room	Hot- Room	Hot+ Room	Cool Room

*Note.* H+ = Hot Appetitive; H- = Hot Defensive.

The order of presentation of the rooms was counterbalanced across participants. Table 2 shows six different sequences in which the three rooms were administered. Participants were pseudo-randomly assigned to one of the sequences on the basis of their participant numbers (i.e., participant number 1 completed sequence 1, participant number 2 completed

sequence 2, participant number 7 completed sequence 1, and so on). This counterbalancing sought to alleviate any confounding influence of the sequence of experimental room tasks.

At the completion of testing, I debriefed the participant and the study was concluded. The length of time for testing each participant was no more than 90 minutes.

### **Data Analysis**

**The CG Arena.** The CG Arena software produces a data file for each participant. This file collects data concerning different aspects of the participant's performance on each of the trials. This file therefore includes, for each CG Arena trial, information about (1) path length (i.e., the distance of the route the participant took from starting point to the target), (2) latency (i.e., the time the participant required to find the target), and (3) dwell time (i.e., the amount of time the participant spent in each quadrant of the Arena).

For each trial, the major outcome variable I used to estimate spatial navigation performance was deviation from the optimal path length. Optimal path length on any trial was calculated by modifying the CG Arena program file to make the target position visible. The trial was then completed three times by moving as directly as possible to the target each time. An average path length for each of those three trials was calculated and deemed the optimal path length for that trial. The optimal path length was then subtracted from the actual path length on each trial to obtain the variable *deviation from the optimal path length*.

**ORT score.** An accuracy score for the ORT responses was created by giving correct choices 1 point and incorrect choices 0 points. The points were added up and divided by the total number of choices participants had to make (16). The resulting score would then range between 0 (all incorrect choices) and 1 (all correct choices).

**ART score.** The ART was scored using a displacement score, similar to that used by Skelton et al. (2000) and Thomas et al. (2003). In this case, the ART score sheet was a model depicting a top-down view of a CG Arena experimental room (see Appendix F). Each wall of this model had three Velcro strips where pictures could be placed; hence, there were 12 possible locations for pictures.

Scoring of the model entailed counting the distance (i.e., number of locations on the wall) the participant placed a particular picture from the actual location of that picture in the CG Arena room. In this way, each picture in the reconstruction of the room was scored separately. The total ART score was therefore the sum of the displacement scores for each of the pictures in the reconstruction of the room. Higher scores therefore indicated poorer performance, and a score of zero indicated perfect reconstruction of the spatial layout of the

experimental room. Appendix F provides a worked-through example for calculating a displacement score in the Cool CG Arena room.

All statistical analyses were conducted using Statistica 8 (StatSoft Inc., 2007). Details of each analysis are given at the appropriate point in the Results section. All decisions about statistical significance were made at the conventional alpha level of  $p < .05$ .

## Results

### Sample Characteristics

Table 3  
*Demographic frequencies for the entire participant sample (N = 24)*

		Count	Cumulative Count	Percentage
Sex	Male	12	12	50.00
	Female	12	24	50.00
Handedness	Right handed	21	21	87.50
	Left handed	3	24	12.50
	Ambidextrous	0	24	0.00
Computer Usage	Every day	24	24	100.00
	Once a week	0	24	0.00
Amount of Computer Experience	50-100 Hours	1	1	4.17
	>100 Hours	23	24	95.83
Shock Web-site Experience	Yes	0	0	0.00
	None	24	24	100.00

### Training Trials

The a priori prediction here (based on previous work in the CG Arena; see, e.g., Jacobs et al., 1997; Thomas et al., 2003) was that there would be no statistically significant performance differences across the four trials in the training room. Figure 6 shows the average deviation from the optimal path length across each training room trial. As can be seen, there was consistently good performance from the first to the fourth trial in this room.

A repeated-measures ANOVA confirmed there were no statistically significant differences in path length (deviation from the optimal) across the four trials,  $F(3, 69) = 2.25$ ,  $p = .09$ ,  $\eta_p^2 = .09$ . This set of data illustrates that prior experience with computers did not give some participants an advantage over others in the CG Arena.

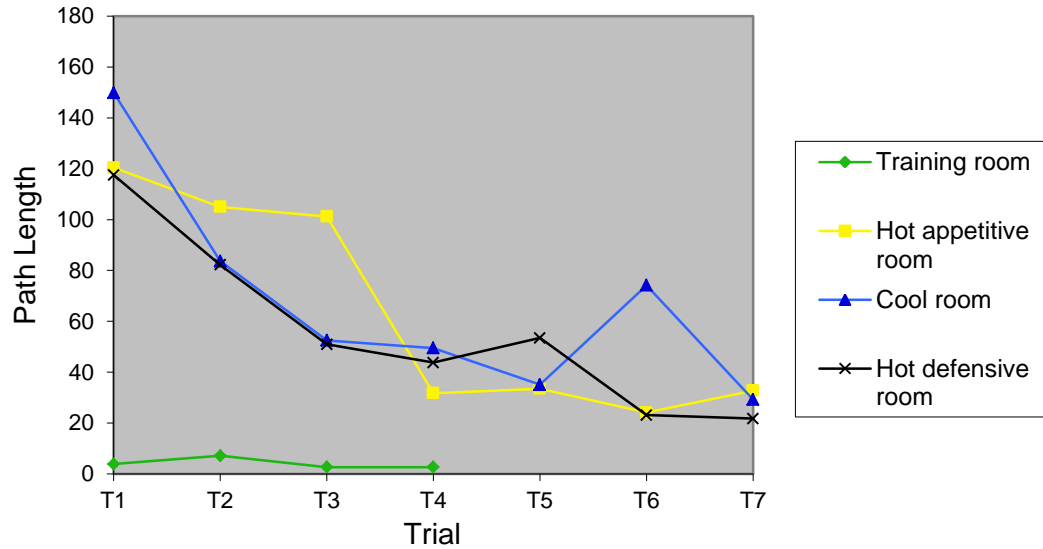


Figure 6. Average path lengths to find the target in four CG Arena rooms.

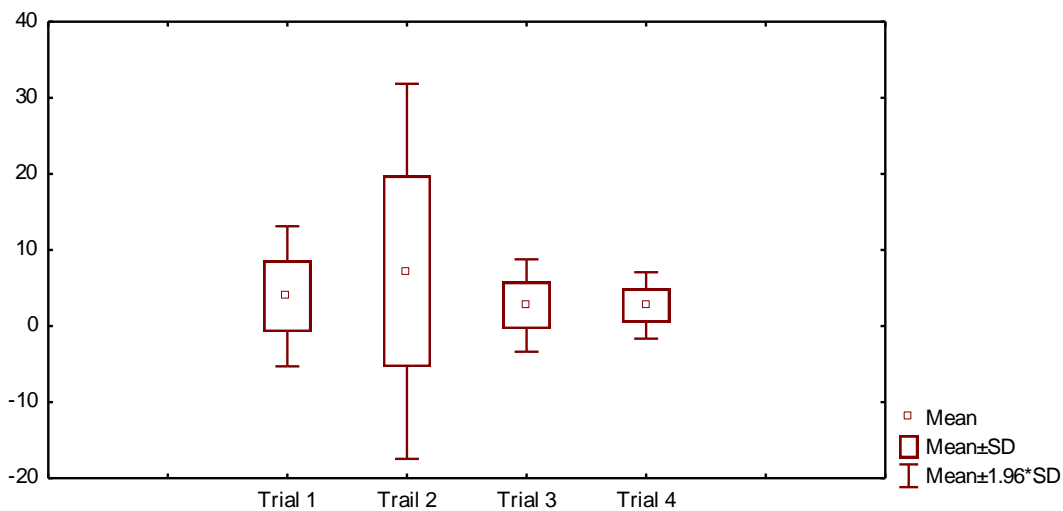


Figure 7. Box and whisker plot showing the deviations from optimal path length across the four trials in the CG Arena training room.

Figure 7, however, illustrates that the variance in deviations from the optimal path length in the four trials of the training room decreased across the trials. The relatively low amount of variance on the last trial in this room indicates that all participants went into the CG experimental rooms with approximately the same level of CG Arena expertise (i.e., the level of expertise was at least sufficient to ensure that they could manipulate the joystick to take the most efficient route to a visible target).

### Hot and Cool rooms: Effects of counterbalancing

I conducted statistical analyses to investigate whether there were any differences in spatial navigational performance due to the order in which the participants experienced the Cool, Hot Defensive, and Hot Appetitive rooms. If the order of the rooms did influence performance in some way, one would expect to see a difference in overall path length deviations between the six counterbalanced sequences in the Cool, Hot Appetitive, and Hot Defensive rooms. To test this prediction, I conducted one-way ANOVAs (independent variable: the six different room presentation sequences) on the average path length (deviation from optimal) data in the Cool, Hot Appetitive, and Hot Defensive rooms. The analysis did not detect any significant between-sequence differences in the Cool room,  $F(5, 18) = 1.69$ ,  $p = .187$ ,  $\eta_p^2 = .13$ , the Hot Defensive room,  $F(5, 18) = 0.81$ ,  $p = .557$ ,  $\eta_p^2 = .04$ , or in the Hot Appetitive room,  $F(5, 18) = 2.22$ ,  $p = .097$ ,  $\eta_p^2 = .18$ .

A second set of analyses sought to determine if there was any effect on ORT scores due to the order of presentation of rooms. Again, a one-way ANOVA detected no statistically significant between-sequence difference in the Cool ORT,  $F(5, 18) = 1.49$ ,  $p = .243$ ,  $\eta_p^2 = .09$ , the Hot Defensive ORT,  $F(5, 18) = 0.64$ ,  $p = .676$ ,  $\eta_p^2 = .08$ , and the Hot Appetitive ORT,  $F(5, 18) = 1.49$ ,  $p = .234$ ,  $\eta_p^2 = .09$ .

A third set of analyses sought to determine if there was any effect on ART scores due to the order of presentation of rooms. Once again, a one-way ANOVA detected no statistically significant between-sequence difference in the Cool ART,  $F(5, 18) = 0.56$ ,  $p = .732$ ,  $\eta_p^2 = .06$ , the Hot Defensive ART,  $F(5, 18) = 0.68$ ,  $p = .643$ ,  $\eta_p^2 = .07$ , and the Hot Appetitive ART,  $F(5, 18) = 1.71$ ,  $p = .183$ ,  $\eta_p^2 = .13$ .

In summary, these analyses suggest that the order in which the participants experienced the Cool, Hot Defensive, and Hot Appetitive rooms had no effect on their spatial navigational performance, their recognition for the distal cues, or their reconstruction of the rooms.

### Invisible Target Trials

To confirm that learning occurred in the Cool, Hot Appetitive, and Hot Defensive CG Arena rooms (i.e., the rooms that featured an invisible target), the data were analysed to see if participants found the target using progressively shorter path length (deviation from optimal) across trials. Table 3 presents average deviation from the optimal path length on the seven acquisition trials in the Cool, Hot Appetitive, and Hot Defensive rooms. Figure 8 shows these data graphically. Repeated-measures ANOVAs confirmed that learning, in the form of

shorter path lengths, occurred in all three rooms: in the Cool room,  $F(6, 138) = 3.32$ ,  $p = .004$ ,  $\eta_p^2 = .13$ , in the Hot Appetitive room,  $F(6, 138) = 4.18$ ,  $p < .001$ ,  $\eta_p^2 = .15$ , and in the Hot Defensive room,  $F(6, 138) = 3.59$ ,  $p = .002$ ,  $\eta_p^2 = .14$ .

Table 4  
*Performance in the Three CG Arena experimental rooms (N = 24)*

Variable	Room			F	p	$\eta_p^2$
	Cool	Hot Appetitive	Hot Defensive			
Path Length						
Trial 1	149.88 (186.36)	120.40 (111.99)	117.49 (111.44)	0.38	.680	.01
Trial 2	83.65 (126.36)	105.00 (158.62)	82.22 (206.16)	0.14	.869	<.01
Trial 3	52.56 (87.40)	101.24 (162.70)	50.97 (98.65)	1.34	.268	.04
Trial 4	49.55 (128.14)	31.79 (38.14)	43.77 (71.56)	0.26	.774	<.01
Trial 5	35.12 (62.62)	33.51 (50.98)	53.49 (83.89)	0.65	.523	.02
Trial 6	74.17 (136.88)	24.14 (35.06)	23.18 (33.10)	2.91	.061	.08
Trial 7	29.23 (51.54)	32.82 (58.58)	21.77 (36.54)	0.31	.736	<.01
Dwell Time	30.47 (10.86)	28.05 (9.63)	30.09 (9.35)	0.41	.666	.01
ORT Scores	0.84 (0.127)	0.92 (0.11)	0.91 (0.16)	2.45	.094	.07
ART Scores	15.46 (7.86)	16.75 (7.84)	17.13 (7.34)	0.32	.731	<.01

*Note.* For the *Path Length* variable, the data are deviation from the optimal path length. For the *Dwell Time* variable, the data are seconds. For the *ORT Scores* variable, data are accuracy scores. For the *ART score* variable, data are displacement scores. Means are presented with standard deviations in parentheses. For each between-trial comparison,  $df = (2, 69)$ .

Table 4 also shows that there were no significant differences in deviation from optimal path length when comparing, using one-way ANOVA, the analogous trials across room (i.e., Trial 1 in each of the Cool, Hot Appetitive, and Hot Defensive rooms compared against one another).

In summary, the emotional qualities of the distal cues did not affect participants' finding, learning, and remembering a hidden location in a VE.

One trial does, however, stand out from the rest. On trial 6, participants seemed to take a longer path length to find the target in the Cool room than in the other two rooms (see Table 4 and Figure 8). A planned contrast analysis sought to determine whether participants took significantly longer to find the target in the Cool room than they did in the other two rooms. The contrast analysis was done on the basis that it is not necessary to have a significant omnibus  $F$  in order to find differences between means, as contrast analysis gives greater substantive interpretation of results and greater power for tests of significance (Rosenthal, Rosnow, & Rubin, 2000). The planned contrast weighted path length in the Cool, Hot Appetitive, and Hot Defensive rooms as 2, -1, and -1, respectively. The result of this

planned comparison showed that participants did in fact take a statistically significantly longer route to find the target in the Cool room than they did, on average, in the other two rooms,  $F_{\text{contrast}}(1, 69) = 5.81, p = .019, d = 0.60$ .

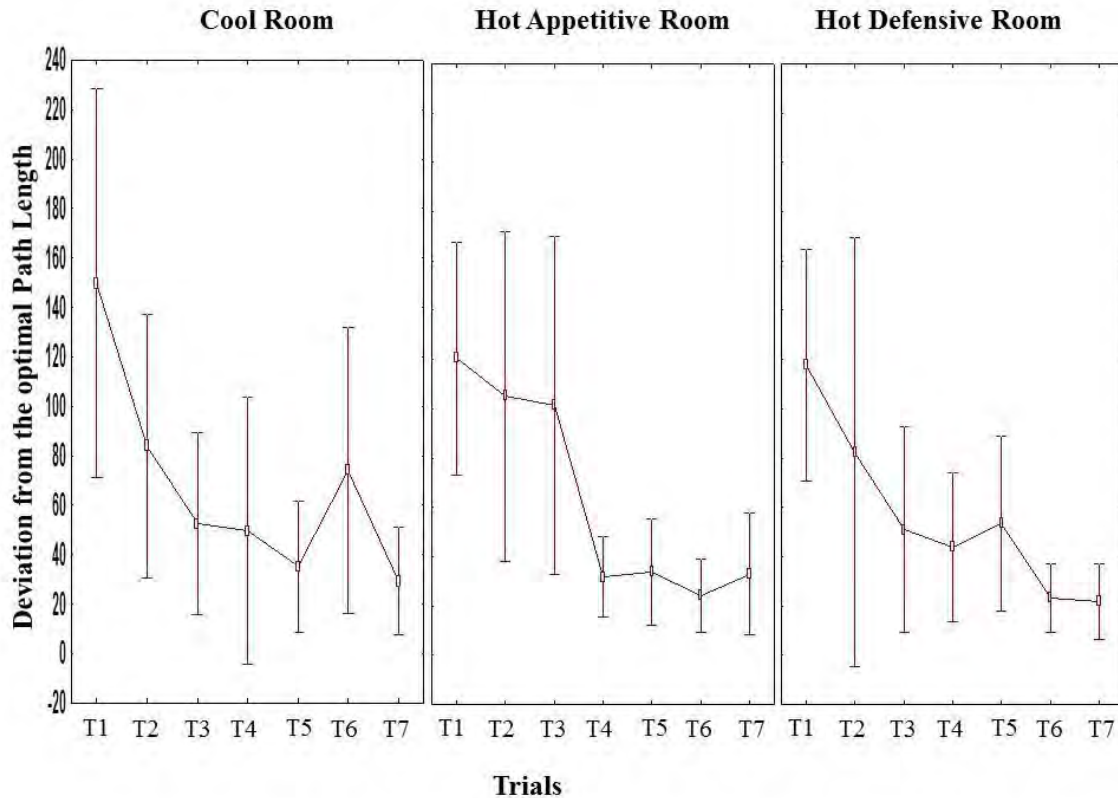


Figure 8. Deviations from the optimal path length across the 7 trials in the Cool, Hot Appetitive and Hot Defensive rooms. Error bars indicate standard deviation of the mean.

Table 4 also displays dwell time data for the probe trial. ‘Dwell time’ refers to the amount of time the participant spent in the target quadrant of the Arena (i.e., searching for the target in the place where it had previously been located). During the 45-s probe trials, participants spent, on average, roughly two-thirds searching the target quadrant. As the Table shows, dwell time was not statistically significantly different across rooms.

### Object Recognition Task

Accuracy score data for the ORT are presented in Table 4 and in Figure 9. As Table 4 shows, a one-way ANOVA detected no statistically significant across-room differences. A planned contrast analysis, weighting the Cool, Hot Appetitive, and Hot Defensive ORT scores as  $-2, 1, \text{ and } 1$ , further tested the hypothesis that memory will be better for emotionally arousing stimuli than neutral stimuli. As predicted, participants’ recognition

memory was stronger for the emotionally arousing material than the neutral material,  $F_{\text{contrast}}(1, 69) = 4.78, p = .032, d = 0.57$ .

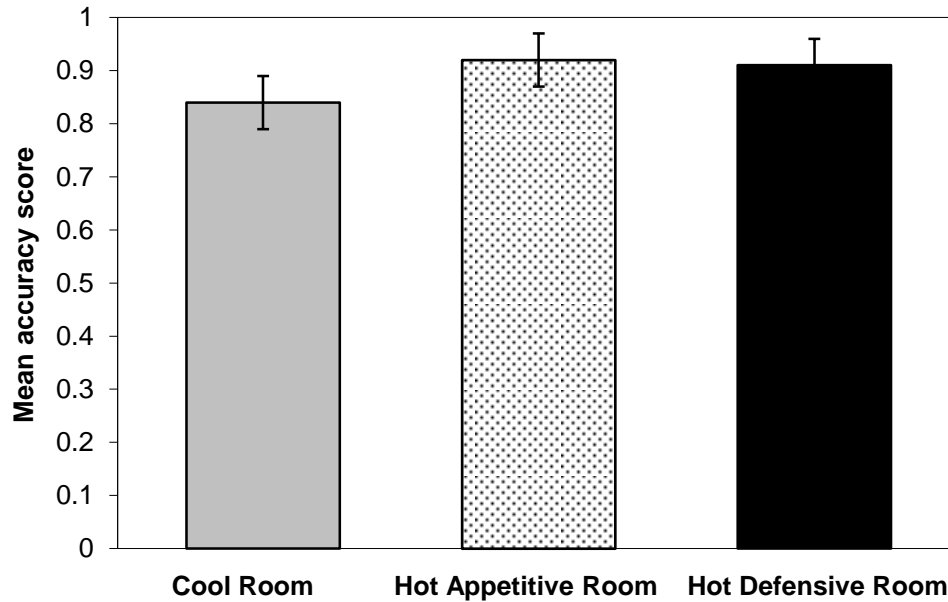
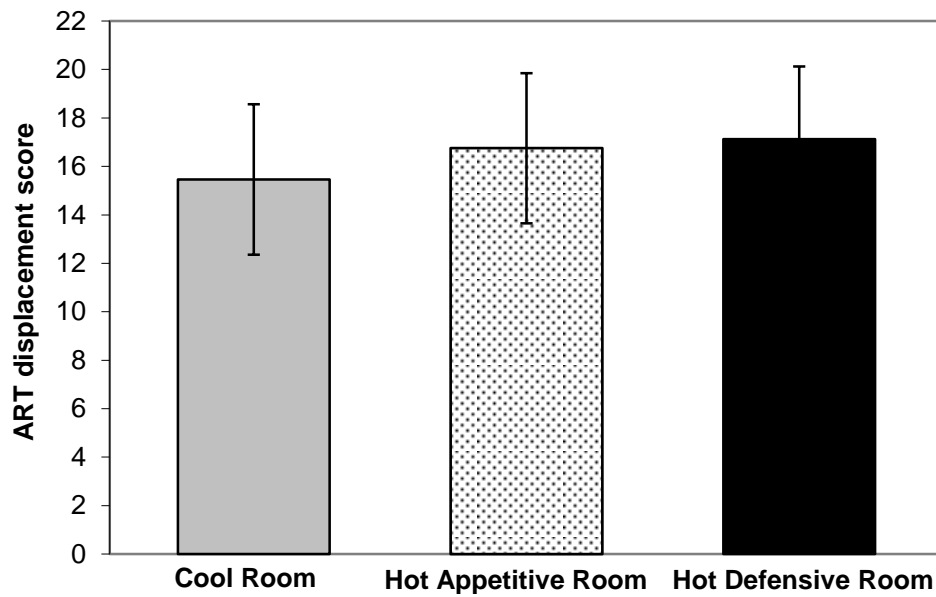


Figure 9. Object Recognition Task (ORT) accuracy scores for the three CG Arena experimental rooms. Error bars indicate standard error of means.

### Arena Reconstitution Task

The ART displacement score data are shown in Table 4 and in Figure 10. As Table 4 shows, a one-way ANOVA detected no statistically significant cross-room differences. A planned contrast analysis, weighting the Cool, Hot Appetitive, and Hot Defensive ORT scores as  $-2, 1,$  and  $1,$  further tested the hypothesis that memory will be better for emotionally arousing stimuli than neutral stimuli. Here, the hypothesis was not confirmed: There was no significant performance difference between the rooms that contained arousing content compared with the one that contained neutral content,  $p = .441$ .



*Figure 10.* Arena Reconstitution Task (ART) scores for the three CG Arena experimental rooms. Error bars indicate standard error of means.

### Sex Differences

**Between-sex comparisons.** Table 5 presents means and standard deviations for CG Arena performance (the average deviation from path length on the acquisition trials), ORT score, and ART score broken down by sex. The Table also presents results of independent samples t-tests conducted to determine whether there were sex differences on any of the outcome variables. Figure 11 presents graphic comparison of male and female performance with regard to deviations from the optimal path length on each invisible-target.

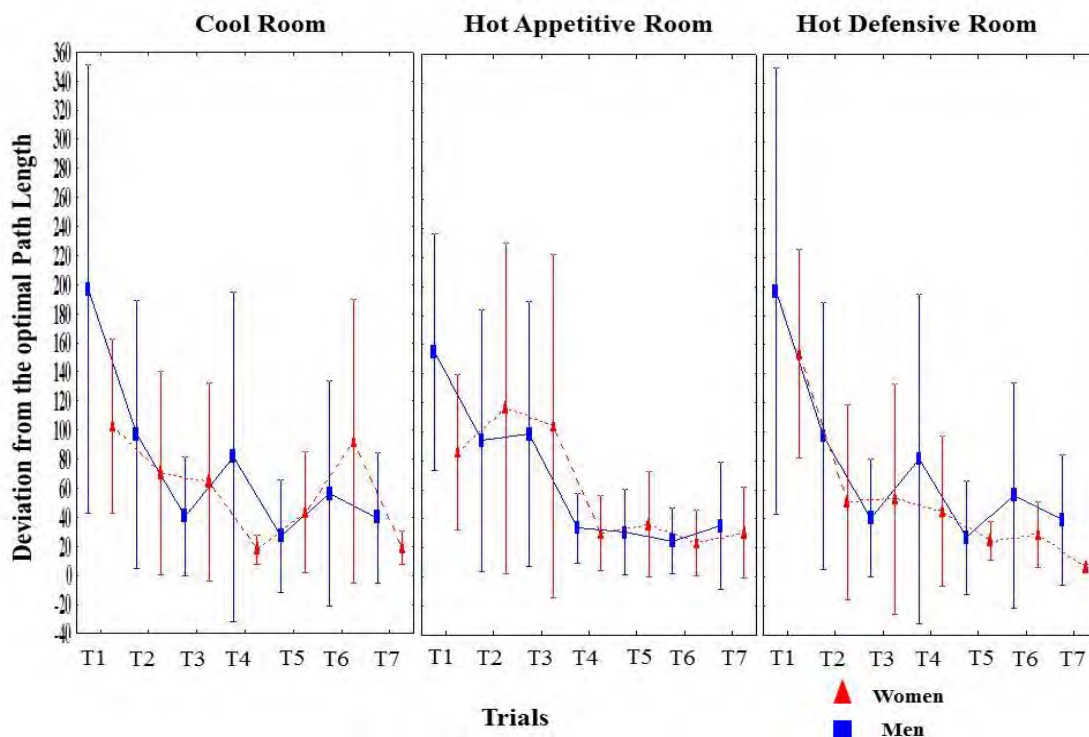
As Table 5 shows, there were no sex differences with regard to performance on either the visible- or invisible-target trials, regardless of room. These results disconfirm the a priori hypothesis, based on data from previous studies (see, Andreano & Cahill, 2009) that men would display superior spatial navigation performance, particularly in the invisible-target rooms.

Table 5

*Between-sex Comparisons: CG Arena performance, ORT score, and ART score (N = 24)*

Variable	Sex		<i>t</i>	<i>p</i>	<i>d</i>
	Male ( <i>n</i> = 12)	Female ( <i>n</i> = 12)			
<b>Path length<sup>a</sup></b>					
Training trials	4.66 (4.70)	3.61 (1.99)	0.71	.484	0.29
Cool room	76.99 (64.71)	58.49 (59.85)	0.73	.475	0.30
Hot Appetitive room	67.39 (30.14)	60.87 (48.55)	0.39	.697	0.16
Hot Defensive room	60.06 (79.28)	52.19 (59.85)	0.27	.787	0.11
<b>Dwell time</b>					
Cool room	31.50 (9.23)	29.44 (11.22)	0.49	.628	0.20
Hot Appetitive room	30.51 (6.51)	28.58 (9.27)	0.59	.561	0.24
Hot Defensive room	31.79 (5.81)	29.38 (10.91)	0.68	.507	0.28
<b>Object Recognition Task</b>					
Cool room	0.83 (0.15)	0.85 (0.10)	-0.38	.707	0.16
Hot Appetitive room	0.92 (0.15)	0.92 (0.06)	0.13	.900	0.00
Hot Defensive room	0.88 (0.22)	0.94 (0.08)	-0.93	.363	0.36
<b>Arena Reconstitution Task</b>					
Cool room	17.42 (9.12)	13.50 (5.65)	1.26	.219	0.52
Hot Appetitive room	17.25 (8.80)	16.25 (7.12)	0.31	.762	0.12
Hot Defensive room	17.92 (8.13)	16.33 (6.76)	0.52	.609	0.21

*Note.* Means are presented with standard deviations in parentheses. <sup>a</sup>Deviation from optimal path length. For each comparison, *df* = 22.



*Figure 11.* Deviations from the optimal path length across the 7 acquisition trials in the Cool, Hot Appetitive, and Hot Defensive rooms for men and women. Error bars indicate standard deviation of the mean.

**Within-sex comparisons.** Tables 6 and 7 present data regarding deviation from the optimal path length for male and female participants, respectively, on each of the seven acquisition trials in the Cool, Hot Appetitive and Hot Defensive rooms. Tables 6 and 7 also present results of one-way ANOVAs comparing performance, across rooms, on each acquisition trial. As the Tables show, there were no within-sex differences in terms of path length (deviation from the optimal) for each trial in all rooms. These results suggest that, overall, the spatial navigational performance of both men and women was not influenced by the content of the landmarks used to find the invisible target.

Table 6

*Male Participants: Performance on outcome variables (n = 12)*

Variable	Room			<i>F</i>	<i>p</i>	$\eta_p^2$
	Cool	Hot Appetitive	Hot Defensive			
Path length <sup>a</sup>						
Trial 1	197.09 (242.56)	155.05 (128.46)	81.27 (101.65)	1.44	.250	.08
Trial 2	96.96 (144.84)	93.86 (141.82)	112.90 (274.83)	0.03	.968	<.01
Trial 3	40.65 (64.09)	98.61 (144.04)	48.09 (68.44)	1.21	.310	.07
Trial 4	81.40 (178.52)	33.47 (37.46)	42.29 (63.36)	0.63	.540	.04
Trial 5	27.02 (61.49)	30.63 (46.48)	81.98 (111.89)	1.84	.174	.10
Trial 6	56.30 (122.24)	24.80 (35.64)	17.22 (30.53)	0.90	.415	.05
Trial 7	39.49 (70.67)	35.29 (68.94)	36.66 (47.94)	0.01	.986	<.01
Dwell time						
Probe trial	31.50 (9.23)	30.51 (6.51)	31.79 (5.81)	0.53	.592	.03
ORT score	0.83 (0.15)	0.92 (0.15)	0.88 (0.22)	0.77	.473	.04
ART score	17.42 (9.12)	17.25 (8.79)	17.92 (8.13)	0.02	.981	<.01

*Note.* Means are presented with standard deviations in parentheses. <sup>a</sup>Deviation from optimal path length. ORT = Object Recognition Test. ART = Arena Reconstitution Test. For each comparison, *df* = (2, 33).

Tables 6 and 7 also present, for men and women respectively, descriptive statistics and results of one-way ANOVAs for dwell time, ORT accuracy score, and ART displacement score. Regarding dwell time and ART displacement score, there were no significant across-room differences for either men or women.

Regarding ORT accuracy scores, however, there was a significant across-room difference for women but not for men (see Figure 12). A set of post hoc comparisons revealed that women recognized significantly more of the hot defensive pictures than the cool pictures,  $p = .016$ , and significantly more of the hot appetitive pictures than the cool pictures,  $p = .040$ . This pattern of data was not replicated in the male sample: Men recognized a similar number of hot defensive and cool pictures,  $p = .521$ , and a similar number of hot appetitive and cool pictures,  $p = .225$ .

Table 7  
 Female Participants: Performance on outcome variables ( $n = 12$ )

Variable	Room			$F$	$p$	$\eta_p^2$
	Cool	Hot Appetitive	Hot Defensive			
Path length <sup>a</sup>						
Trial 1	102.67 (94.46)	85.75 (84.28)	153.72 (113.02)	1.57	.224	.08
Trial 2	70.34 (109.63)	116.15 (179.52)	51.54 (106.21)	0.72	.496	.04
Trial 3	64.46 (107.50)	103.87 (185.96)	53.85 (125.08)	0.40	.670	.02
Trial 4	17.69 (15.75)	30.11 (40.40)	45.24 (81.78)	0.80	.458	.04
Trial 5	43.22 (65.38)	36.39 (57.05)	25.00 (20.67)	0.38	.685	.02
Trial 6	92.03 (153.41)	23.49 (36.04)	29.14 (35.79)	2.00	.152	.11
Trial 7	18.98 (18.20)	30.35 (49.07)	6.88 (3.10)	1.80	.180	.10
Dwell time						
Probe trial	29.44 (11.22)	28.58 (9.27)	29.38 (10.91)	0.06	.944	<.01
ORT score	0.85 (0.1)	0.92 (0.06)	0.94 (0.08)	3.73	.035	.18
ART score	13.50 (5.65)	16.25 (7.12)	16.33 (6.76)	0.73	.490	.04

Note. Means are presented with standard deviations in parentheses. <sup>a</sup>Deviation from optimal path length. ORT = Object Recognition Test. ART = Arena Reconstitution Test. For each comparison,  $df = (2, 33)$ .

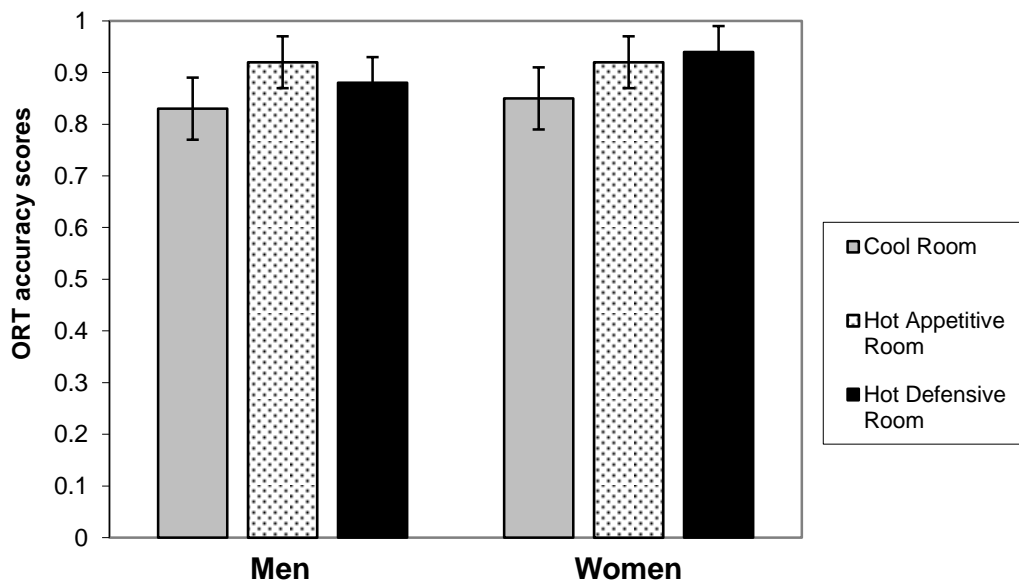


Figure 12. Object Recognition Test (ORT) accuracy scores for men and women in the three CG Arena experimental rooms. Error bars indicate standard error of means.

## Discussion

The purpose of the present study was to determine whether people could successfully navigate, learn, and remember locations within virtual environments using landmarks that varied, across environments, in valence and arousal intensity. These landmarks had been rated by a separate sample in a previous study (see Appendix A) as being significantly different in terms of valence and arousal qualities.

I created three different virtual environment (VE) rooms within the CG Arena (Jacobs et al., 1997, 1998; Skelton et al., 2000; Thomas et al., 2001). The first room contained pictures that were rated in the previous study as being almost neutral in pleasure and arousal. The second room contained pictures that had been rated as being both highly pleasurable and highly arousing; these were chosen as landmarks that might activate the appetitive motivation system. The third room contained pictures that had been rated as being both highly unpleasant and highly arousing; these were chosen as landmarks that might activate the defensive motivational system. The current results with regard to general CG Arena performance are consistent with results obtained in previous CG Arena studies. That is, the current data show that people are capable of forming a cognitive map of the VE, that they can learn and remember the location of a particular place (the target) in that map, and that they use the relations among the distal cues in the CG Arena to recall and locate the target (Jacobs et al., 1997; 1998; Thomas et al., 2001; Thomas, 2003).

The first prediction tested in this study was that people would display equally effective navigation in the three rooms. This prediction was made on the basis that the emotional stimuli used as distal cues would not be considered a proximal threat, and thus would not stress the participant enough to cause memory problems. Lang et al. (1997) suggest that a participant reacting to highly arousing pictures in a laboratory setting is in an attentional freezing state; that is, the participant is oriented to the stimulus, will process the contextual details, and will retrieve any relevant information from memory. This attentional state would not, however, be enough of a stressor to activate the hypothalamic-pituitary-adrenal axis, and thus result in the release of cortisol (Lovallo & Thomas, 2000). As discussed in Chapter 1, stress-induced effects on spatial/episodic memory occur when there is a sufficient release of stress hormones (i.e., cortisol) to disrupt the functioning of brain structures such as the hippocampus (de Kloet et al., 1999; de Quervain et al., 2009; Jacobs & Metcalfe, 1998; Roozendaal et al., 2009; Schwabe et al., 2012; Wolf, 2009). Thus, the present study did not attempt to explore the effects of stress, but rather attempted to explore the effects of the content of the landmarks on place learning and memory.

As predicted, there were no between-room differences in navigational performance. The data analyses detected no significant between-room differences in path length on each of the seven acquisition trials. Furthermore, on the probe trial, there were no between-room differences in dwell time (i.e., the amount of time participants searching for the target where it had been located previously). These results suggest that, in a VE, people are just as capable of finding, learning, and remembering the location of a target in a room featuring ‘cool’ (neutral) landmarks as in a room featuring ‘hot’ (emotionally arousing) landmarks. In addition, participants’ navigation performance was not affected by the use of Hot Appetitive versus Hot Defensive pictures as landmarks.

The second hypothesis tested here was that the content of the stimuli would influence participants’ recognition memory for the landmarks in the room. Specifically, the prediction was that participants would have stronger recognition memory for the pictures featuring arousing content than those featuring neutral content. Consistent with this prediction, participants’ ORT recognition scores were higher for the (arousing) pictures in the Hot Defensive and the Hot Appetitive rooms than for the (neutral) pictures in the Cool room. This finding is consistent with a large body of previous research showing that memory for emotionally arousing material is stronger than memory for neutral material (e.g., Heuer & Reisberg, 1990; La Bar & Cabeza, 2006; Packard & Goodman, 2012; Payne et al., 2006; Reisberg & Heuer, 2004; Wolf, 2009). However, further analyses revealed that this effect was seen only in the women and not the men.

The third hypothesis tested here was derived from previous literature showing that there are robust sex differences in spatial cognition (e.g., Andreano & Cahill, 2009; Clint et al., 2012; Johnson & Bouchard, 2005, 2007). Specifically, the prediction was that men’s navigational and memory performance would be superior to that of women in all rooms of the CG Arena. This hypothesis was not confirmed; there were no sex differences on any of the outcome measures.

It would be premature to draw definite conclusions concerning sex differences owing to the small sample size used in this study. There were only 12 men and 12 women in the sample, and hence there may not have been enough statistical power to detect sex differences. Chapter 6 gives further elaboration and discussion of sex differences in relation to the findings presented in this dissertation.

**Conclusion**

The present study attempted to examine navigation, learning and memory in three virtual environment rooms that contained distinctly different landmarks. Although the stimuli employed as landmarks had been judged in a previous study (presented in Appendix A) as being significantly different in pleasure (being either highly unpleasant, neutral, or pleasant) and arousal (being either highly arousing or neutral), the current study showed that these emotionally-charged landmarks did not influence spatial navigation performance. This lack of influence existed despite the fact that participants had better recognition memory for the arousing stimuli than the neutral stimuli. In conclusion, the results obtained from this study verify that the Hot Defensive, Hot Appetitive, and Cool rooms created in the CG Arena are appropriate tools to use in subsequent studies investigating the effects of stress on visual and spatial memory retrieval.

### **CHAPTER THREE: STUDY B – VALIDATION OF THE STRESSOR**

As introduced in previous chapters, the current dissertation aims to explore the effects of stress on visual and spatial memory retrieval in humans by systematically replicating de Quervain et al.'s (1998) pioneering (rodent) study. The previous chapter in this dissertation endeavored to create and verify the visual and spatial tasks to be used in Chapters 4 and 5. The present chapter aims to formulate and validate a suitable substitute stressor for the foot-shocks administered to rodents in de Quervain et al.'s study. As foot-shocks are absolute stressors (i.e., physiological stressors), the aim of this study is formulate a stressor that contains a physical stressor component *and* induces a moderate to large cortisol response.

As discussed in Chapter 1, exposure to both absolute and relative stressors activates two primary stress response systems in the body. Both these systems are characterized by the release of stress hormones that facilitate adaptation to the threatening situation (de Kloet et al. 2005; Herbert et al., 2006; McEwen, 1998). The first system is orchestrated primarily by the sympathetic nervous system and sees the rapid release of catecholamines (e.g., epinephrine and norepinephrine) that produce increases in heart rate, respiration, and blood pressure. The second system is activated more slowly, and is initiated solely by the hypothalamic-pituitary-adrenal (HPA) axis (Roozendaal et al., 2006, 2009). This activation results in the release of glucocorticoids (corticosterone in non-human animals; cortisol in humans) from the adrenal cortex.

#### **Laboratory Stressors**

Empirical study of the ways in which stress affects human psychobiological, cognitive, and affective processes (and, therefore, the ways in which stress affects human health) demands that researchers have reliable methods of experimentally stimulating the HPA axis. The Trier Social Stress Test (TSST; Kirschbaum, Pirke, & Hellhammer, 1993) and the Cold Pressor Test (CPT; Hines & Brown, 1932) are two methods that neuroscientists use frequently to induce stress in the laboratory. The TSST involves participants undergoing a mock job interview; it consists of a short preparation period, a 5-minute speech and a 5-minute verbal arithmetic task. The CPT, in contrast, requires participants to hold their hands and forearms in ice water for up to 3 minutes. These two methods, therefore, induce stress responses differently: Whereas the TSST manipulates psychological and social-evaluative elements, the CPT manipulates physiological elements.

Neither method, however, consistently activates the HPA axis in all participants. Typically, the CPT elicits strong SNS activation but only moderate HPA-axis responses (Duncko, Cornwell, Cui, Merikangas, & Grillon, 2007; Schwabe, Haddad, & Schachinger, 2008). Typically, the TSST elicits a stronger HPA-axis response than the CPT (McRae et al., 2006), but it does not elicit consistent HPA-axis responses across participants. For example, some researchers (e.g., Buchanan & Tranel, 2008; Schoofs & Wolf, 2009) have reported low numbers of cortisol responders to the TSST, while others (e.g., Kuhlmann et al., 2005; Luethi et al., 2009; Nater, 2007; Schoofs et al., 2008) have chosen to use male-only samples because the TSST typically elicits a larger stress response in men than in women. These sex differences in TSST response appear related to HPA-axis (re)activity (Kudielka et al., 2009). Furthermore, potential explanations for the TSST's ability to induce a greater HPA-axis response than the CPT include the nature (psychosocial versus physiological), duration (20 min versus 3 min), and uncontrollability/unpredictability of the procedures (Dickerson & Kemeny 2004; Smeets et al., 2012).

Recently, at least two different studies have investigated the question of whether combining elements of the TSST and CPT might lead to stronger, and more consistent, HPA-axis responses. The rationale for combining elements of the two stress-induction procedures is this: The CPT induces, because of the experience of physical pain, a rapid stress response via activation of the autonomic nervous system and HPA axis. Neural correlates believed to underlie this reflexive physical response are the brainstem and hypothalamus (Ulrich-Lai & Herman, 2009). In contrast, the TSST utilises psychosocial stress elements that require cognitive appraisal. This cognitive evaluation of the stressor is associated with activity in the frontal lobes and thalamus, which sees resulting connections from prefrontal and limbic regions to the hypothalamus activating the HPA axis (Dickerson & Kemeny, 2004; Ulrich-Lai & Herman, 2009). Combining psychosocial and physical stressors can, therefore, be expected to strongly activate both autonomic and HPA-axis responses.

Consistent with this expectation, several new stress induction methods that combine psychological and physiological elements of the TSST and CPT have reported encouraging results. For example, Schwabe et al. (2008c) demonstrated that adding a socio-evaluative component to the CPT (i.e., being watched by a confederate and being videotaped while dipping a hand into ice water) increased HPA-axis response over the standard CPT. Similarly, Smeets et al. (2012) demonstrated that the Maastricht Acute Stress Test (MAST), which features the addition of another component of the TSST (a socially evaluated mental arithmetic task) to Schwabe et al.'s Socially Evaluated CPT (SECPT), elicited even greater

HPA-axis activation than the standard CPT and than the SECPT. However, cortisol elevations in response to the MAST were similar to those elicited by the TSST.

### **Aims and Hypotheses**

In the current study, I ask if combining *all* the components of the TSST with those of the CPT will elicit a greater cortisol response than the standard TSST. Hence, I describe an ecologically valid procedure that contains the *entirety* of both the CPT and the TSST, and that maintains, to a large degree, the fiction set forth in the latter. The method, which involves participants undergoing a mock audition for the reality television show *Fear Factor*, combines the psychological aspects of the TSST and the physiological aspects of the CPT into a single, believable, and ethical procedure. I compared changes in subjective anxiety, heart rate, and cortisol levels produced by the *Fear-Factor Stress Test* (FFST), the TSST, and a control procedure with similar mental and physical demands to the FFST but devoid of its stress-inducing features.

I tested the prediction that the Fear-Factor Stress Test produces greater increases in subjective anxiety, heart rate, and cortisol than the Trier Social Stress Test or a no-stress Control condition. Hence, I expected this pattern of data for all outcome variables: FFST > TSST > Control.

## **Methods**

### **Participants**

Ninety healthy university students (45 men, 45 women) between the ages of 18 and 27 years ( $M = 19.76$ ;  $SD = 1.82$ ) met the eligibility criteria for participation. Exclusion criteria included smoking tobacco, using any prescription medication (including oral contraceptives), and scoring  $\geq 29$  on the Beck Depression Inventory - Second Edition (BDI-II; Beck et al., 1996). Participants were asked to refrain from eating, drinking, or doing physical exercise for at least 2 hours before testing.

### **Experimental Manipulations**

Participants were pseudo-randomly assigned to one of three experimental groups: Fear-Factor Stress Test (FFST;  $n = 30$ ); Trier Social Stress Test (TSST;  $n = 30$ ); and Control ( $n = 30$ ). Each group contained equal numbers of men and women because previous studies in this field have reported sex differences in the magnitude of HPA-axis activation following stress induction in the laboratory (e.g., Kirschbaum et al., 1992; Kudielka & Kirschbaum,

2005). I did not include a CPT group because previous studies demonstrate that stress-induction methods that include social evaluative components (e.g., TSST, SECPT) elicit greater HPA-axis responses than the standard CPT (McRae et al., 2006; Schwabe et al., 2008c; Smeets et al., 2012). Figure 13 depicts the sequence of experimental procedures for the FFST, TSST and Control procedures.

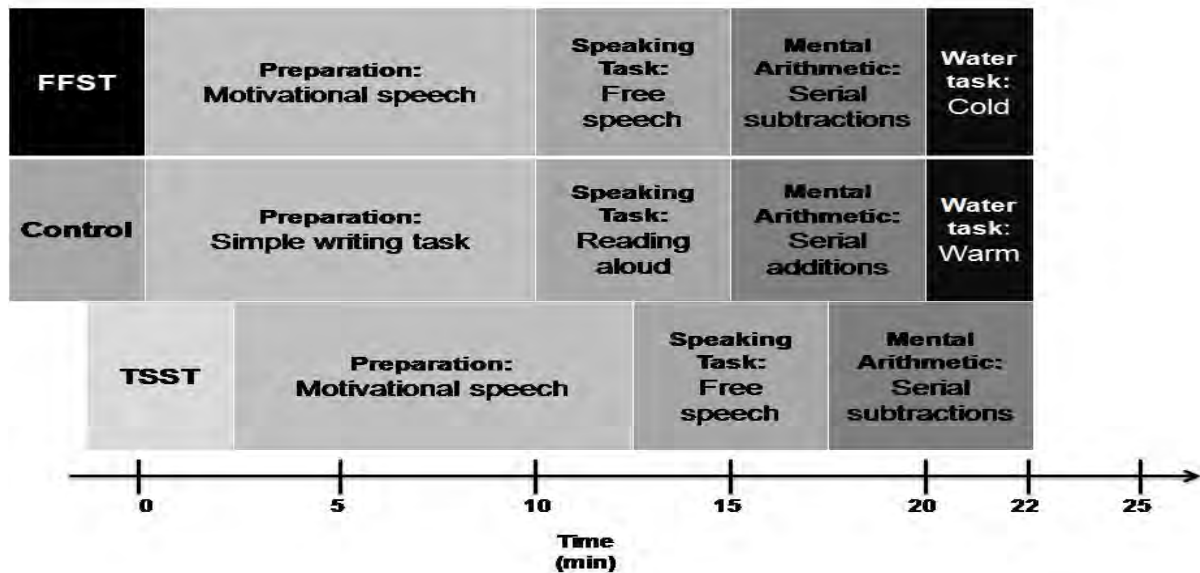


Figure 13. Sequence of tasks for the Fear-Factor Stress Test (FFST), Trier Social Stress Test (TSST) and Control experimental procedure.

In the FFST group, I instructed participants to imagine auditioning for the reality television show *Fear Factor*, and then read a set of standardized instructions detailing the process of the audition. Participants were informed that they would complete three tasks: (1) a 5-min free motivational speech as to why they should appear on *Fear Factor*; (2) a 5-min mental arithmetic task to test thinking under pressure; and (3) a test of pain resilience that measured their ability to withstand the physical demands of the show. I told participants they would complete the three tasks in front of a panel of two judges, who would decide on their suitability for the show.

Participants received a blank sheet of paper and were given 10 minutes to prepare the speech. After preparation, I took them to a room illuminated by a halogen lamp; this room contained a video camera and a panel of judges. Two undergraduates (one man, one woman) served as judges. They were smartly dressed and seated behind a desk. The participants were given 5 minutes to present their speech extemporaneously; if they stopped speaking before 5 minutes elapsed, the judge of the opposite sex to the participant asked a set of standard

prompting questions (e.g., “You still have time left, please continue” or “What is your ultimate fear and how do you think you will be able to overcome it in front of the camera?”). Following the speech, participants performed the mental arithmetic task (subtractions of 17 starting from 2043). If the participant answered incorrectly, the same judge asked him/her to restart at 2043. Finally, the judge of the same sex as the participant asked him/her to submerge their dominant arm, up to the elbow, in cold water (between 0° and 4°C) for as long as possible, up to a maximum of 2 minutes. Participants remained standing for all three tasks, with the judges watching throughout.

In the TSST group, participants underwent a standard TSST that differed only slightly from the original (Kirschbaum et al., 1993). First, I instructed participants to write and present a speech detailing their suitability for a job of their choice. The participants prepared the speech for 10 minutes and were then taken to an interview room where the two judges were seated behind a desk. The interview room was identical to that described for the FFST group. The remaining protocol, including the extemporaneous speech and the arithmetic task, proceeded precisely as Kirschbaum et al. (1993) described. Participants remained standing for both tasks.

In the Control group, I provided participants a blank sheet of paper and instructed them to write a summary of everything they had done on that day. The participants wrote for 10 minutes and were then taken to a well-lit room, where they were told to stand and read aloud from a general-interest magazine. I left the room and permitted the participants to read aloud and alone for 5 minutes. I then re-entered the room and instructed the participant to count upwards in multiples of five, starting from zero. I then left the room and permitted the participants to perform this task aloud and alone for 5 minutes. I then re-entered and instructed the participant to submerge his/her dominant arm into warm water (34-38 °C) for as long as possible, up to a maximum of 2 minutes. I remained in the room but did not directly watch the participant, who remained standing.

## **Materials**

Both physiological and self-report measures were collected from the participants across the testing session. These measures are described below.

**Physiological measures.** A measure of heart rate (HR) was collected using the Vrije Universiteit Ambulatory Monitoring System (VU-AMS, Version 5fs; de Geus and van Doornen 1996). In addition, saliva samples were collected using *Salivettes*.

**VU-AMS.** Heart rate/ electrocardiography (ECG) data was collected using the VU-AMS via three electrodes that were attached to the upper torso of each participant. The VU-AMS is a portable device that allows recording of the electrocardiogram (ECG) and impedance cardiogram (ICG). Heart rate decreases in response to parasympathetic nervous system activation, and increases in response to sympathetic nervous system activation. Time markers were inserted during the measurement process to indicate points of interest in order to assist with data analysis. VU-DAMS software suite was used to extract indicators of HR (i.e., number of heartbeats per unit of time) from the VU-AMS ECG and ICG signal recordings. Heart rate was compared at three points of interest:

- 1)  $HR_B$ . The average HR recorded over 2 minutes at the start of the session represented a baseline HR measure for each participant.
- 2)  $HR_1$ . The average HR sampled throughout the final 12 minutes (10 minutes for the TSST group) of the FFST stress or Control manipulations. The average during this period, which encompassed the speaking and mental arithmetic tasks, as well as the water immersion task for the FFST and Control groups, represented HR during the manipulation.
- 3)  $HR_2$ . The average HR sampled for 2 minutes starting at 35 minutes after the manipulation ended, taking the average of those 2 minutes as the final representation of HR.

**Salivette.** Saliva samples were collected using Sarstedt Salivette® Cortisol swabs (Sarstedt, Nümbrecht, Germany) in order to measure cortisol concentrations. At each collection, I instructed participants to chew gently on the cotton swab for a full minute. Thereafter, I immediately placed the swab into a storage tube and placed the tube in a freezer where it remained until transported to a laboratory for salivary cortisol analyses. The assay used the Roche E170 platform; further details are provided by Pillay, Haumann, Bonito Attwood, Omar, and Thomas, (2008). Saliva samples were taken at three points of interest from each participant.

- 1)  $CORT_B$ . At the start of the session represented a baseline cortisol measure for each participant.
- 2)  $CORT_1$ . Five minutes after the FFST, TSST or Control manipulation ended.
- 3)  $CORT_2$ . Thirty-five minutes after the end of the FFST, TSST or Control manipulation.

**Self-report measures.** Two self-report measures were collected, a depression screening measure and a measure of self-reported anxiety. These measures are described below.

***The Beck Depression Inventory-II.*** The Beck Depression Inventory-II (*BDI-II*; Beck, Steer, & Brown, 1996) is a self-rated multiple-choice questionnaire that was developed to measure the intensity, severity and depth of depression in both patients and the general population. Higher reported scores on the BDI-II indicate greater severity of depressive symptomatology and therefore a more intense depression. Each item on the questionnaire consists of four statements that correspond to ratings from 0 to 3, with higher ratings indicating characteristics of more severe depression.

The BDI-II has been shown to have good psychometric properties; it has a high internal consistency ( $\alpha = .91$ ; Dozois, Dobson, & Ahnberg, 1998) and good test-retest reliability (Pearson  $r = .93$ ; Beck et al., 1996). In addition, it also shows a strong positive correlation with other depression measures, such as the Hamilton Depression Rating Scale (Pearson  $r = .71$ ; Weeks & Heimberg, 2005).

In the present study, the BDI-II was used as a screening measure. Any participant that scored above 28 was excluded from the study. Screening of depression was included due to the link between depression and cognitive deficits (Austin, Mitchell, & Goodwin, 2001).

***The Spielberger State Anxiety Inventory.*** The Spielberger State Anxiety Inventory (*STAI-State*; Spielberger, Gorsuch, Lushene, Vagg, & Jacobs, 1983) consists of a 20-item self-report scale that measure in-the-moment state anxiety. The 20-item State scale requires the participant to indicate the intensity of his/her feelings of anxiety at the current time.

The STAI-State shows a high degree of internal consistency ( $\alpha = .92$ ), as well as high test-retest reliability (Spielberger & Vagg, 1984). In addition, the scale shows strong positive correlations with the Taylor Manifest Anxiety Scale and the IPAT Anxiety Scale, both of which are reliable measures of anxiety levels (Spielberger & Vagg, 1984).

For the purposes of the present study, the STAI-State scale was used to assess participants' subjective experiences of anxiety throughout the experimental session. As with HR and saliva samples, three STAI-State measures were collected at three points of interest from each participant:

- 1) *STAI<sub>B</sub>*. At the start of the session represented a baseline self-report anxiety measure for each participant.
- 2) *STAI<sub>I</sub>*. Five minutes after the FFST, TSST or Control manipulation ended.

3) *STAI*<sub>2</sub>. Thirty-five minutes after the end of the FFST, TSST or Control manipulation.

### **Procedure**

The study procedures were conducted in the ACSSENT Laboratory in the Department of Psychology at the University of Cape Town (UCT). Figure 14 illustrates the timeline of events during the experimental procedure. All test sessions started at either 14h00, 16h00, or 18h00. The last session each day ended at 19h30. At the start of the session the participant was asked to read and sign an informed consent form (Appendix I). The consent form described the study procedures clearly, assured the confidentiality of participation, outlined what would be expected of participants, stated they could end their participation at any time without penalty or prejudice, and confirmed they would receive course credit as compensation. No participant took the option to withdraw, and none reported remaining in a subjectively distressed state at the end of the study. Had any been in such a state, a clinical psychologist was on stand-by, and contact details of other counselling services would have been provided. The research described here followed the ethical guidelines for research subjects outlined by the Health Professions Council of South Africa and the UCT Codes for Research. The Research Ethics Committee of the UCT Department of Psychology approved all study procedures.

Following the consent form, the participant rated his/her current level of anxiety (*STAI*<sub>B</sub>) and was then fitted to the VU-AMS. The participant then sat quietly for 5 minutes, in order to acclimatise to the device, before *HR*<sub>B</sub> was obtained. Following the baseline measure of HR, I collected a first saliva sample (*CORT*<sub>B</sub>). I then read a set of instructions to the participant detailing either the FFST, TSST or Control conditions. The participant then performed the assigned condition and HR was measured during the performance segment of the condition (*HR*<sub>1</sub>). Five minutes after the FFST, TSST or Control conditions, the participant provided measure of self-reported anxiety (*STAI*<sub>1</sub>) and a second cortisol sample (*CORT*<sub>1</sub>). The participant then completed cognitive memory tasks for 30 minutes. The participant then provided a final saliva sample (*CORT*<sub>2</sub>), as well as measures of HR (*HR*<sub>2</sub>) and self-report anxiety (*STAI*<sub>2</sub>). Immediately following data collection, I debriefed the participant completely, and the study concluded.

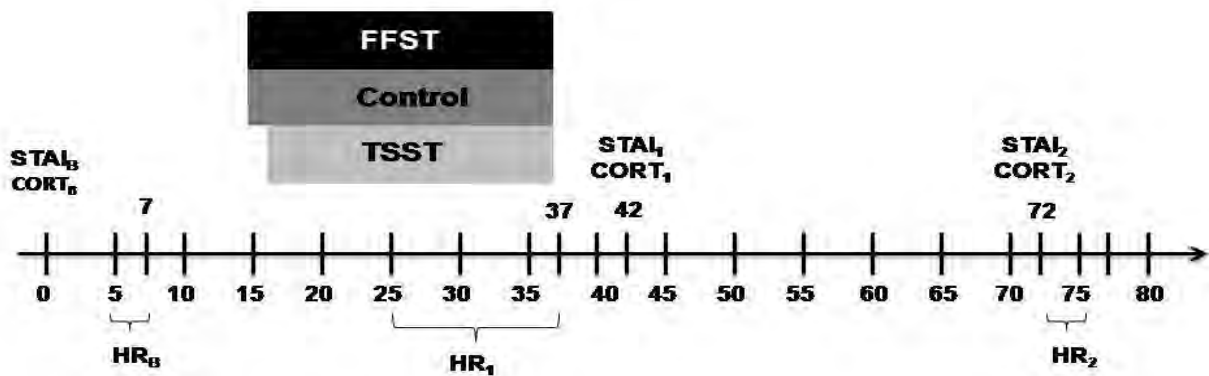


Figure 14. Timeline of events, from 0 minutes to 80 minutes, during the experimental procedures. FFST = Fear-Factor Stress Test group; TSST = Trier Social Stress Test group; STAI = Spielberger State Anxiety Inventory; HR = heart rate (measured in beats per minute); CORT = salivary cortisol (measured in nmol/l). Subscripts represent measurement point (e.g., STAI<sub>B</sub> is the first STAI measurement point, or baseline).

### Data Analysis

Statistical analysis followed two broad analytic strategies. First, I used three separate repeated-measures ANOVAs (one for each class of outcome variable). Between-subject variables were Group (FFST versus TSST versus Control) and Sex (male versus female). The within-subject variable was Time; measurement points for this variable were once before the manipulation (baseline) and twice post-manipulation (5 and 35 minutes after the end of the manipulation). Second, due to significant between-group differences in baseline levels of cortisol, I used six separate 3 (Group: FFST versus TSST versus Control) x 2 (Sex: male versus female) factorial ANOVAs to examine between-group differences on the outcome variables of interest. For the latter analyses, I derived outcome variables by subtracting the baseline measure from those at the second and third measurement points, as follows:

$$\begin{aligned}
 \text{STAI}_{\Delta 1} &= \text{STAI}_1 - \text{STAI}_B \\
 \text{STAI}_{\Delta 2} &= \text{STAI}_2 - \text{STAI}_B \\
 \text{HR}_{\Delta 1} &= \text{HR}_1 - \text{HR}_B \\
 \text{HR}_{\Delta 2} &= \text{HR}_2 - \text{HR}_B \\
 \text{CORT}_{\Delta 1} &= \text{CORT}_1 - \text{CORT}_B \\
 \text{CORT}_{\Delta 2} &= \text{CORT}_2 - \text{CORT}_B
 \end{aligned}$$

To analyze the CORT data further, I split the groups, on a post-hoc basis, into cortisol responders and cortisol non-responders. Following Fehm-Wolfsdorf et al. (1993), I classified participants as *cortisol responders* if their CORT<sub>1</sub> or CORT<sub>2</sub> values represented a 2 nmol/l or more increase over baseline (CORT<sub>B</sub>). In the current sample, an increase of 2 nmol/l relative

to baseline was equivalent to a 49% cortisol increase. I analyzed between-group differences in number of cortisol responders using Pearson's  $\chi^2$  tests of independence.

I conducted all statistical analyses using SPSS21. I set the threshold level of statistical significance ( $\alpha$ ) at .05. In most cases, data distributions met the required assumptions for the relevant inferential statistical analyses; I made necessary adjustments where assumptions were violated (e.g., the use of Greenhouse-Geisser degrees of freedom corrections).

## Results

### Subjective Anxiety

Table 8 provides descriptive statistics for the STAI-State scores. Repeated-measures ANOVA detected significant main effects of Time,  $F(1.58, 132.42) = 75.83, p < .001, \eta_p^2 = .47$ , and Group,  $F(2, 84) = 7.40, p = .001, \eta_p^2 = .15$ , in the absence of significant main effect of Sex,  $p = .431$ . Additionally, the analysis detected a significant Group x Time interaction,  $F(3.15, 132.42) = 23.80, p < .001, \eta_p^2 = .36$ , in the absence of a significant Time x Sex interaction,  $p = .896$ , Group x Sex interaction,  $p = 1.00$ , or Time x Group x Sex interaction,  $p = .114$ .

Table 8  
*Subjective anxiety, heart rate, and cortisol descriptive data (N = 90)*

Variable	Group		
	FFST (n = 30)	TSST (n = 30)	Control (n = 30)
Subjective Anxiety			
STAI <sub>B</sub>	29.13 (7.42)	34.07 (6.81)	31.70 (6.50)
STAI <sub>1</sub>	45.30 (12.89)	44.10 (11.78)	29.33 (6.41)
STAI <sub>2</sub>	28.53 (6.31)	31.57 (6.92)	28.57 (6.35)
Heart rate			
HR <sub>B</sub>	74.78 (11.72)	74.76 (12.82) <sup>b</sup>	73.27 (18.22) <sup>a</sup>
HR <sub>1</sub>	94.13 (15.06)	103.93 (19.61) <sup>b</sup>	85.48 (21.69) <sup>a</sup>
HR <sub>2</sub>	71.78 (11.54)	71.74 (9.92) <sup>b</sup>	70.03 (17.33) <sup>a</sup>
Salivary cortisol			
CORT <sub>B</sub>	3.71 (1.43) <sup>a</sup>	1.96 (1.94)	4.55 (5.42)
CORT <sub>1</sub>	6.01 (2.83) <sup>a</sup>	5.61 (4.18)	3.41 (2.87)
CORT <sub>2</sub>	7.90 (7.20) <sup>a</sup>	2.23 (2.19)	2.46 (2.00)

*Note.* Means are presented, with standard deviations in parentheses. FFST = Fear-Factor Stress Test group; TSST = Trier Social Stress Test group; STAI = Spielberger State Anxiety Inventory; HR = heart rate (measured in beats per minute); CORT = salivary cortisol (measured in nmol/l). Subscripts represent measurement point (e.g., STAI<sub>B</sub> is the first STAI measurement point, or baseline). <sup>a</sup>n = 29, <sup>b</sup>n = 21.

Bonferroni post-hoc within-group analyses across Time showed that the FFST group displayed a significant increase in self-reported anxiety from STAI<sub>B</sub> to STAI<sub>1</sub>,  $p < .001$ , but returned to near baseline levels by STAI<sub>2</sub>,  $p = 1.00$  (see Table 8). The TSST group showed a similar significant increase from STAI<sub>B</sub> to STAI<sub>1</sub>,  $p < .001$ , and also returned to near baseline levels by STAI<sub>2</sub>,  $p = 1.00$ . The Control group, in contrast, displayed a non-significant decrease in self-reported anxiety from STAI<sub>B</sub> to STAI<sub>1</sub>,  $p = .251$ , and reported significantly decreased anxiety levels by from STAI<sub>B</sub> to STAI<sub>2</sub>,  $p = .022$ .

Factorial ANOVA of mean STAI<sub>Δ1</sub> scores detected a significant main effect of Group,  $F(2, 83) = 26.03, p < .001, \eta_p^2 = .39$ . That analysis detected no main effect of Sex,  $p = .837$ , and no significant Group x Sex interaction,  $p = .193$ . Post-hoc pairwise comparisons detected a significant difference for the mean of the FFST group versus that of Control group,  $p < .001$ , but not for the mean of the FFST and Control groups taken together versus that of the TSST group,  $p = .10$ . This set of decisions implies the following order of true means:  $FFST > TSST > Control$ , a pattern that matches the sample data displayed in Table 8.

Factorial ANOVA of mean STAI<sub>Δ2</sub> scores detected no significant main effects of Group,  $p = .292$  or of Sex,  $p = .759$ , and no significant Group x Sex interaction effect,  $p = .784$ . These analyses confirm the pattern of data shown in Table 8, where it appears that, at STAI<sub>2</sub>, self-reported anxiety levels returned to, and dipped below, baseline in all groups.

### Heart Rate

I visually inspected the recorded interbeat interval time series for implausible ( $> 3 SD$  from the mean) readings. These implausible readings can result from hardware failures, or from electrodes not making full contact with a participant's skin. If more than 10% of the data over a critical period consisted of artefacts, I excluded the variable for that participant. I excluded 10 participants (9 in the TSST group and 1 in the Control group) following this reasoning.

Table 8 provides descriptive statistics for the measure of HR. Repeated-measures ANOVA detected significant main effects of Time,  $F(1.57, 115.85) = 351.11, p < .001, \eta_p^2 = .83$ , and Sex,  $F(1, 74) = 16.08, p < .001, \eta_p^2 = .18$  (Men:  $M = 75.75, SD = 12.48$ ; Women:  $M = 85.44, SD = 12.52$ ), in the absence of a significant main effect of Group,  $p = .276$ . Additionally, the analysis detected significant interactions between Group and Time,  $F(3.13, 115.85) = 15.56, p < .001, \eta_p^2 = .30$ , and between Time and Sex,  $F(1.57, 115.85) = 8.23, p < .001, \eta_p^2 = .10$ , in the absence of a significant Time x Group x Sex interaction,  $p = .084$ .

Bonferroni post-hoc within-group analyses across Time showed that, on average, participants in all three groups showed a significant increase in heart rate levels from  $HR_B$  to  $HR_1$ , all  $p$ 's  $< .001$ , and returned to below baseline levels by  $HR_2$ , all  $p$ 's  $\leq .001$  (see Table 8).

Factorial ANOVA of mean  $HR_{\Delta 1}$  values detected a significant main effect of Group,  $F(2, 74) = 17.41, p < .001, \eta_p^2 = .32$ . That analysis detected no significant main effect of Sex,  $p = .144$ , and no significant Group x Sex interaction,  $p = .849$ . Post-hoc pairwise comparisons detected a significant difference for the mean of the FFST group versus that of the Control group,  $p = .022$ , but not for the mean of the FFST and Control groups taken together versus that of the TSST group,  $p = .234$ . This set of decisions implies the following order of true  $HR_{\Delta 1}$  means:  $FFST > TSST > Control$ , a pattern that matches the sample data displayed in Table 8.

Factorial ANOVA of mean  $HR_{\Delta 2}$  values detected no significant main effects of Group,  $p = .731$ , or of Sex,  $p = .535$ , and no significant Group x Sex interaction effect,  $p = .110$ . These analyses confirm the pattern of data shown in Table 8, where it appears that, at  $HR_2$ , heart rate returned to, and dipped below, baseline in all groups.

### Cortisol Responses

Due to experimenter error, cortisol data for one man in the FFST group were lost. Table 8 provides descriptive statistics for the measure of cortisol. Repeated-measures ANOVA detected significant main effects of Time,  $F(1.75, 145.34) = 6.39, p = .003, \eta_p^2 = .07$ , and of Group,  $F(2, 83) = 7.35, p = .001, \eta_p^2 = .15$ , in the absence of a significant main effect of Sex,  $p = .362$ . Additionally, the analysis detected a significant Group x Time interaction,  $F(3.50, 145.34) = 12.66, p < .001, \eta_p^2 = .23$ , in the absence of a significant Time x Sex interaction,  $p = .184$ , Group x Sex interaction,  $p = .631$ , or Time x Group x Sex interaction,  $p = .888$ .

Bonferroni post-hoc within-group analyses across Time showed that the FFST group displayed a significant increase in cortisol levels from  $CORT_B$  to  $CORT_1, p < .001$  (see Table 8). FFST participants' cortisol levels continued to show a sustained increase at  $CORT_2$ , when they were significantly higher than at baseline,  $p = .010$ . The TSST group also showed a significant increase in cortisol levels from  $CORT_B$  to  $CORT_1, p < .001$ . By  $CORT_2$ , however, average levels in the TSST group had returned to near baseline levels, and were not significantly different from  $CORT_B, p = 1.00$ . The Control group, in contrast, displayed a

non-significant decrease from  $CORT_B$  to  $CORT_1$ ,  $p = .262$ . By  $CORT_2$ , average levels in the Control group were significantly lower than at  $CORT_B$ ,  $p = .011$ .

Between-group analysis at  $CORT_B$  showed a significant main effect of Group,  $F(2, 86) = 4.42$ ,  $p = .019$ ,  $\eta_p^2 = .09$ . Bonferroni post-hoc comparisons confirmed a significant difference between cortisol levels for the TSST and Control groups,  $p = .010$ , but not between the FFST and TSST groups,  $p = .157$ . It is largely due to these pre-existing between-group differences at  $CORT_B$  that further between-group comparisons at  $CORT_1$  and  $CORT_2$  were performed using change scores.

Figure 15 illustrates these change scores, and shows there were noteworthy differences in cortisol responding among the groups across time. A visual impression of the figure suggests that 5 minutes after the end of the manipulation (i.e., at  $CORT_1$ ), both stress manipulations resulted in cortisol levels greater than those in the Control group. Thirty minutes later, however, cortisol *declined* in the TSST group but *continued to increase* in the FFST group.

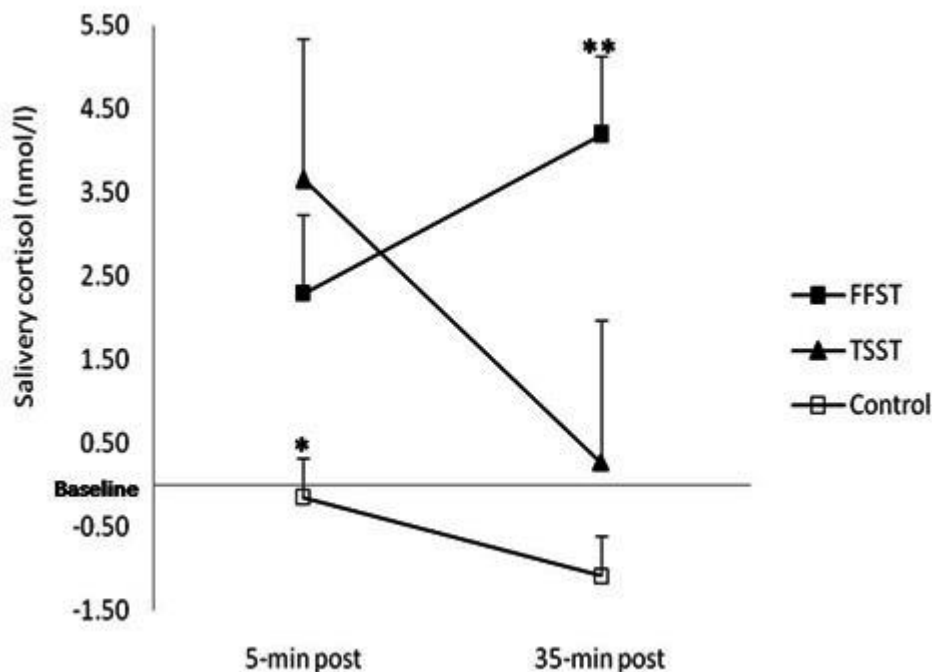


Figure 15. Salivary cortisol in nanomoles per liter (nmol/l; mean + standard error) at two measurement points in the study. \*Significant difference between the Control group and the other two groups,  $p = .004$ . \*\*Significant difference between FFST group and other two groups,  $p < .001$

Statistical analyses confirmed this impression. Factorial ANOVA of mean  $CORT_{\Delta 1}$  values detected a significant main effect of Group,  $F(2, 83) = 9.80$ ,  $p < .001$ ,  $\eta_p^2 = .19$ . That

analysis detected no significant main effect of Sex,  $p = .166$ , and no significant Group x Sex interaction,  $p = .079$ . Post-hoc pairwise comparisons detected no significant difference for the mean  $CORT_{\Delta 1}$  value obtained from the FFST group versus that obtained from the TSST group,  $p = .130$ , but a significant difference for the mean of the  $CORT_{\Delta 1}$  values obtained from the FFST and TSST groups taken together versus that of the Control group,  $p < .001$ . This set of decisions implies the following order of true  $CORT_{\Delta 1}$  means:  $FFST = TSST > Control$ , a pattern that matches the sample data displayed in Table 8.

Factorial ANOVA of mean  $CORT_{\Delta 2}$  values also detected a significant main effect of Group,  $F(2, 83) = 11.30$ ,  $p < .001$ ,  $\eta_p^2 = .21$ . That analysis detected no significant main effect of Sex,  $p = .582$ , and no significant Group x Sex interaction,  $p = .368$ . Post-hoc pairwise comparisons detected a significant difference for the mean  $CORT_{\Delta 2}$  value obtained from the FFST versus that obtained from the TSST group,  $p < .001$ , and a significant difference for the mean of the  $CORT_{\Delta 2}$  values obtained from the FFST and TSST groups taken together versus that of the Control group,  $p < .001$ . This set of decisions implies the following order of true means:  $FFST > TSST > Control$ , a pattern that matches the sample data displayed in Table 8.

### **Cortisol Responders**

At  $CORT_1$ , 14 of the 29 (48%) participants in the FFST group (8 men, 6 women) were cortisol responders. Similarly, 17 of the 30 (57%) participants in the TSST group (11 men and 6 women) were responders. Only 1 of the 30 (3%) participants in the Control group (1 man) was a responder. A chi-squared test of independence confirmed that the overall proportion of responders between groups differed significantly,  $\chi^2(2) = 18.38$ ,  $p < .001$ , Cramer's  $V = .45$ . The proportion of responders in the FFST and TSST groups did not differ significantly,  $\chi^2(1) = 0.42$ ,  $p = .519$ , Cramer's  $V = .08$ .

In contrast, at  $CORT_2$ , 15 of the 29 (52%) participants in the FFST group (9 men, 6 women) were cortisol responders. Only 4 of the 30 (13%) participants in the TSST group (4 men) were responders. A chi-squared test of independence confirmed that the overall proportion of responders between groups differed significantly,  $\chi^2(2) = 21.99$ ,  $p < .001$ , Cramer's  $V = .50$ . The proportion of responders in the FFST group differed significantly from that in TSST group,  $\chi^2(1) = 9.95$ ,  $p = .002$ , Cramer's  $V = .41$ . Importantly, there was no significant difference between the proportion of men and women responders within the FFST group,  $\chi^2(1) = 1.71$ ,  $p = .192$ , Cramer's  $V = .24$ .

I observed individual differences in maintenance of cortisol response over time. In the FFST group, 10 of the 14 participants who responded initially maintained or increased that

response from  $CORT_1$  to  $CORT_2$ , whereas 4 returned to baseline. In contrast, 4 of the 17 participants in the TSST group sustained responding from  $CORT_1$  to  $CORT_2$ , whereas the remaining 13 returned to baseline. The solitary cortisol responder in the Control group also did not sustain responding from  $CORT_1$  to  $CORT_2$ ; he returned to baseline. Naturally, this indicates that 6 participants in the FFST group were new responders at  $CORT_2$  (i.e., they had been classed as non-responders at  $CORT_1$ ), whereas there were no new responders in the TSST or Control groups. A chi-squared test of independence detected a significant between-group difference in terms of sustained responders,  $\chi^2(2) = 10.61, p = .005$ , Cramer's  $V = .24$ .

### Discussion

In the present study I have described the Fear-Factor Stress Test (FFST), a method of stress induction that combines a commonly used physiological stressor (the Cold Pressor Test) and a commonly used psychosocial stressor (the Trier Social Stress Test). The FFST draws on both the uncontrollable and social evaluative elements present in the TSST and features tasks (public speaking and mental arithmetic) known to increase cortisol levels reliably (Biondi & Picardi, 1999; Dickerson & Kemeny, 2004). I sought to determine if the FFST produces a more robust stress response than the TSST. I also compared the FFST and the TSST to a control version of the FFST procedure, similar in physical and mental demands but without negative stress-inducing components.

Participants in the FFST group did not show increased sympathetic activation (as measured by heart rate) relative to those in the TSST group, and did not rate the combined stressor experience as more anxiety-inducing than did those in the TSST group. In contrast, participants in the FFST group showed increased cortisol responding, which I assume is a marker of increased HPA-axis activity, relative to those in the TSST group. Specifically, although the FFST and TSST groups were not distinguishable in terms of magnitude of cortisol response from baseline to 5 minutes post-manipulation, they were statistically distinct in terms of change from baseline to 35 minutes post-manipulation. On average, participants in the FFST group sustained a relatively high level of cortisol responding, whereas those in the TSST group returned to baseline. Similarly, the proportion of cortisol responders (defined as those with 2 nmol/l increase over baseline) in the TSST and FFST groups did not differ significantly at the 5-min measure, but did differ significantly at the 35-min measure. Taken together, the absence of a sustained heart rate response, the decline of subjective anxiety, and the sustained cortisol response, permits the inference that the FFST increases HPA-axis activation without additional psychological discomfort.

The present data indicate that psychosocial stressors and physiological stressors are distinct, and not merely alternative, methods of activating the HPA axis, and that there is increased HPA-axis response when activated in conjunction. This conclusion is consistent with those reached by Schwabe et al. (2008c) and Smeets et al. (2012). The FFST, however, appears to deliver a more sustained cortisol response than that achieved by the Maastricht Acute Stress Test or the TSST (Smeets et al., 2012, Study 2). Direct comparisons of the three procedures remain to be described, however.

Consistent with the finding of the present study and with those of Schwabe et al. (2008c) and Smeets et al. (2012), cognitive appraisal of a stressful event appears to have a large effect on the physiological response of an individual to that event (Dickerson et al., 2008). The current data indicate that the inclusion of psychosocial component to a physiological stressor results in a more robust stressor. Thus, it appears that if an individual perceives a stressor as a physical, intellectual, and social threat, then the physiological response to that stressor is greater than when the stressor incorporates merely a physical component.

Typically, research in this area reports means, or describes patterns of mean group differences, treating individual differences in cortisol response as unsystematic variance or error. However, it is possible that these reported means hide important individual differences in cortisol responding. I found that most individuals in the FFST group who were responders at the 5-min measure continued to respond at the 35-min measure. In contrast, most of those in the TSST group who responded at the 5-min measure returned to baseline at the 35-min measure. In light of the statistical results for those in the FFST group, I consider it unlikely these individual differences represent unsystematic variance. Possible sources of systematic variance include traits (temperament, personality), recent or remote life experiences, phase of the menstrual cycle, or other pre-existing differences distributed unevenly across groups (Kudielka et al., 2009). Programmatic investigation of these possibilities may be a rewarding area of inquiry, as might be studies that determine why about 50% of individuals exposed to laboratory-based stress tests do not show a significant cortisol response (Kudielka & Kirschbaum, 2005; Kudielka & Wüst 2010).

Studies using the TSST frequently report sex differences in cortisol responses. Moreover, women are less likely than men to show an HPA-axis response to the TSST (Kirschbaum et al., 1992; Kirschbaum et al., 1999), leading many investigators to include only men in their studies (e.g., Kuhlmann et al., 2005; Schoofs et al., 2008; Smeets et al., 2012). However, analyses in the present study detected no significant sex differences in

response to either the FFST or the TSST. Of note, though, is that I observed a statistically significant increase in the number of female sustained responders in the FFST group over the TSST group, despite the fact that I did not control for phase of the menstrual cycle (Kirschbaum et al., 1999). These data suggest that, by including a combination of stressors, the FFST holds promise as a stress-induction method that might attenuate the sex differences often seen in the TSST.

Interestingly, the women in the current study, irrespective of the experimental group, showed higher heart rate levels than the men. This finding is consistent with previous reports that women have higher resting heart rates than men (Pham, 2003). The higher resting rates in women did not, however, seem to influence autonomic activation in response to the experimental manipulation.

A secondary aim of this study was to create and describe an effective control (placebo) version of the FFST. Any adequate control is identical to the intended treatment and differs only in psychological and/or physical effective characteristics (Mill, 1843; Shapiro & Morris, 1978). In the present case, the uncontrollable, social evaluative, and pain-inducing components were effective characteristics of the FFST. Participants in the Control group did not, on the average, show an increase in cortisol levels, and they reported significantly lower state anxiety levels than those in the FFST and TSST groups after the manipulation. Those in the Control group did, however, show an increase in heart rate during the manipulation, although the increase was significantly less than that observed in the FFST group. The cardiovascular nature of the control task may produce this increase, and the observed increase is consistent with results from the control version of the TSST (Het et al., 2009). Hence, the absence of uncontrollability, social evaluative components, and pain stimuli in the control task produced moderate sympathetic activation without concomitant HPA-axis activation.

### **Limitations**

I acknowledge six factors that may limit the generalizability of the present findings. First, I did not control for participants' body mass index (BMI). Although it appears traditional to control for BMI in this literature (e.g., Schwabe et al., 2008c; Smeets et al., 2012), Wirtz and colleagues (2008) established that BMI and salivary cortisol (either in reaction to stress or in circadian cortisol secretion) are not related. Hence, it is not completely clear that such a control is necessary.

Second, I did not control for phase of the menstrual cycle in the women who participated in this study. Previous studies show that responses to a stressor change as a function of phase of the menstrual cycle (Kirschbaum et al., 1999). Hence, some of the variability I describe in these data may be due to this factor, which is, obviously, interesting in its own right.

Third, I collected a subjective measure of stress at the end of the stress manipulation. Subjective measures of stress are greater when measured *during* the manipulation than when measured *following* it (Hellhammer & Schubert, 2012). Hence, I may have missed differences in participant levels of stress *during* stress-induction.

Fourth, the FFST manipulation tested in the current study was slightly longer (by about 2 minutes) than the TSST. Although there is no suggestion in the literature of an optimal length for a stress-induction procedure, there is a possibility that the length of the manipulation is positively correlated with HPA-axis response. Future studies might serve to tease apart the effects of length of the stressor exposure versus characteristics of the stressor.

Fifth, there were large differences in baseline cortisol levels between the three groups in the current study. Although I am unable to account precisely for the source of these differences, I suggest that they might be associated with (a) variations in phase of menstrual cycle amongst female participants, and (b) variations in time of day at which participants were exposed to the experimental manipulations. Although I am unaware of literature suggesting that such differences at baseline are associated with the magnitude of cortisol response, there nevertheless exists a possibility of such an association. However, given that *magnitude* of response was the critical outcome variable, I am confident that the reported results are sound and valuable. Furthermore, if one argues that higher baseline cortisol values leave less room for a large cortisol response to the stressor (i.e., that individuals with lower baseline cortisol values are farther away from the physiological limits of circulating cortisol, and so can show larger magnitude of cortisol responses relative to individuals with lower baseline values), then my argument for the value of the FFST over the TSST is even stronger: In this study, the TSST group's baseline cortisol values were significantly lower than those of the FFST group.

Finally, cortisol levels of FFST participants did not return to baseline by the end of the study. Hence, the duration of this response remains to be determined.

**Conclusion**

The present study attempted to formulate and validate a suitable replacement stressor for the foot-shock used by de Quervain et al. (1998). The findings from this study demonstrate that the FFST, in tandem with its control comparison, is a promising research tool. Similar cognitive and physical demands characterize the experimental and control conditions; in so doing, they increase internal validity by eliminating confounding variables (Krauth 2000). Differences between the procedural demands and response burden of the FFST and the TSST are trivial (e.g., it takes about 2 minutes longer to administer than the TSST). Importantly, the FFST elicits a more robust and sustained HPA-axis response than the TSST without (a) increasing participant discomfort or (b) requiring increased resources and costs. Such a research tool could prove valuable in helping disentangle the actions of stress and HPA axis-related hormones on human cognitive, affective, and behavioral functioning. The FFST will therefore be utilized as a substitute for the foot-shock stressor (used by de Quervain et al., 1998) in the next study presented in Chapter 4.

## **CHAPTER FOUR:**

### **STUDY 1 - THE EFFECTS OF ACUTE STRESS ON RETRIEVAL OF VISUAL AND SPATIAL MATERIAL**

Chapter 1 provided a broad review of the effects of stress and glucocorticoids (GCs) on memory. As discussed in that chapter, the direction (to enhance or impair) of the effects depends on *when* the individual is stressed. The general pattern seen in the literature is that acute stress or GCs have an enhancing effect on memory consolidation, while impairing memory retrieval and reconsolidation. The reported effects on memory encoding have been inconsistent due, in part, to difficulty in isolating the encoding phase from the other memory phases (de Quervain et al., 2009; Roozendaal et al., 2009; Schwabe et al., 2012, Wolf 2008, 2009).

Chapter 1 also outlined theoretical explanations for the influence of stress and GCs on episodic memory performance. These theories include the *inverted-U hypothesis*, *hot-cool theory*, and the *integrated vertical and horizontal perspective theory*. The following brief review aims to focus specifically on the literature surrounding the effects of stress on visual and spatial memory retrieval in humans. In addition, this review aims to introduce an alternative perspective on memory, one that views memory as having functions shaped by our evolutionary past.

#### **The Effects of Stress on Visual and Spatial Memory**

In a recent review paper outlining 12 years of stress and memory research, Wolf (2009) characterized the workings of stress on memory retrieval in the following way: “In sum, stress as well as cortisol treatment impaired memory retrieval and this effect was especially pronounced for emotional arousing material independent of its valence” (p. 147). This summation of the effects of stress on memory retrieval has also been echoed by other researchers in the field (de Quervain et al., 2009; Roozendaal et al., 2009; Schwabe et al., 2012).

The findings regarding the direction of the effect of stress on memory retrieval are derived from both human and animal studies. However, these human and animal studies have usually employed quite different methodologies, and have examined different domains of memory. Animal studies are typically constrained to the realm of visual and spatial memory, whereas human studies can examine those domains as well as verbal memory. For various reasons (e.g., the ease of testing, and the importance of verbal memory for humans), verbal

memory has received the majority of attention by researchers in this field (Allen, 2003). Unfortunately, the focus on verbal memory has resulted in very few human studies exploring the effects of stress on visual and spatial memory. In addition, the focus on verbal memory has resulted in a substantial gap between findings from human versus animal studies, which in turn makes comparisons between human and animal studies difficult.

Although only a handful of human studies have explored the effects of stress on visual and spatial memory, the findings from these studies seem to be consistent with the generalized effects seen on verbal memory. Consistent with the general (and apparently incoherent) effects of stress observed on the encoding phase of verbal memory, stress has been shown to enhance memory for pictures (Payne et al., 2007, Weymar et al., 2012) and for spatial layouts (Luethi et al., 2009), but has also been shown to impair spatial memory (Elizinga et al., 2005<sup>14</sup>; Taverniers et al, 2011b; Thomas et al., 2010). Consistent with the general enhancing effects of stress on the consolidation phase of verbal memory, similar beneficial effects have been seen for consolidation of spatial memory (Abercrombie et al., 2006; Cahill et al., 2003; Human et al., 2013<sup>15</sup>). Similarly, the impairing effects of stress on the retrieval phase of verbal memory are also prominent when testing visual (Buchanan & Tranel, 2008) and spatial memory retrieval (Quesada et al., 2012; Schwabe & Wolf; 2009). Given that there are only three studies (to my knowledge) that examine the effects of stress on visual and spatial memory retrieval, these studies will be reviewed in greater detail below.

**The effects of stress on visual and spatial memory retrieval in humans.** Buchanan and Tranel (2008) examined the effects of stress on visual memory retrieval for 10 emotional (negative valence) and 10 neutral pictures. Forty participants (20 male) viewed these pictures and recognition memory for the pictures was tested 24 hours later, following the completion of either the Trier Social Stress Test (TSST) or a control task. The authors reported that only those participants that were cortisol responders (5 male and 1 female) showed impaired memory retrieval for both neutral and emotional pictures. Those participants in the TSST condition who did not show a cortisol response showed enhanced memory retrieval for only the emotional pictures. The authors concluded that cortisol was the primary modulator in the

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<sup>14</sup>Elizinga et al.'s (2005) study was in fact a verbal memory test that tested memory for a paragraph description of a short walk along a path with several 'attractions'.

<sup>15</sup>It is possible that the effects of stress in Human et al.'s (2013) study could have influenced both the consolidation and retrieval phases. The authors administered an acute stressor roughly 5 minutes after participants encoded a complex figure. They tested recall of the figure 35 minutes after the end of the stress manipulation. Thus, stress is likely to have had a large influence on both the consolidation and retrieval phases due to the close temporal proximity between encoding, the stress manipulation and retrieval.

stress-induced retrieval impairment. Stress in the absence of the cortisol response (i.e., emotional arousal) was, in turn, associated with a retrieval enhancement.

Buchanan and Tranel's (2008) study demonstrated, importantly, that similar to the widely reported impairing effects of stress on verbal memory retrieval, stress also impaired visual memory retrieval in humans. This effect was, however, only seen in the small group of individuals who showed a substantial increase in cortisol following exposure to the TSST. Those individuals who did not show an increase in cortisol following the stress manipulation displayed no impairment, but rather showed enhanced recall for the emotional pictures. Thus, emotional arousal and consequential adrenergic activation of the BLA was associated with increased memory retrieval for emotional stimuli, while the substantial release of cortisol (and its genomic negative effect on the hippocampus) was associated with an overall impaired memory performance. From a visual memory perspective, Buchanan and Tranel's (2008) finding offers some degree of support for this inverse relationship, often reported in verbal memory retrieval studies (Buchanan et al., 2006; de Quervain et al., 2007; Kuhlmann et al., 2005a; Kuhlmann et al., 2005b; Smeets et al., 2008; Tollenaar et al., 2008).

Unfortunately, the conclusions one can draw from Buchanan and Tranel's (2008) study must be tempered by the low number of cortisol responders. Less than one-third of their participants (6 out of 20) in the TSST condition were classed as responders, and only one of those responders was female. This small sample size compromises the overall generalizability of the results, and does not allow for sex difference comparisons. However, the study nevertheless suggested that stress (and the subsequent release of cortisol) might have an impairing effect on visual memory retrieval, similar to effects reported in the verbal memory domain.

Recently, Schönfeld et al. (2014) also examined the effects of stress on memory retrieval of pictures (and words) learned 24 hours prior. The authors tested memory retrieval both during, and 25 minutes after, a public speaking stress manipulation. When memory was tested 25 minutes after the stressor, the authors reported a similar impairing effect to that found by Buchanan and Tranel (2008). Conversely, when memory was tested during the stressor, it was positively correlated with autonomic activation but not with cortisol response. The authors attribute the findings to the workings of the fast and slow stress response systems on memory (introduced in Chapter 1). However, Schönfeld et al. did not strictly examine spatial memory retrieval as their recall test entailed participants giving a verbal description of the pictures. In addition, the authors only report a combined memory recall performance for

the pictures and words. Thus, one cannot isolate or distinguish the effects of stress on visual memory from Schönfeld et al.'s (2014) study.

In terms of spatial memory, both Schwabe and Wolf (2009) and Quesada et al. (2012) examined spatial memory using a two-dimensional object location task. The task, which was a computerized version of the popular game "Memory", involved the participants learning the position of 15 card pairs over two trials and then being asked to recall the position of the card pairs in a delayed recall trial. In both studies, the card pairs varied in valence and arousal; 5 pairs were positively arousing, 5 were neutral and 5 were negatively arousing.

The primary objective of Schwabe and Wolf's (2009) study was to test the effects of stress on retrieval in congruent and incongruent learning and testing environments. Male and female participants learned the position of the card pairs in a room scented with vanilla. Twenty-four hours later, participants were exposed to either a stress manipulation (Socially Evaluated Cold Pressor Test; SECPT) or a control condition before a recall trial of the object location task. The recall trial was administered either in a room scented with vanilla (familiar, or congruent, context), or in a room without the vanilla scent (unfamiliar, or incongruent, context). The authors reported that stress only impaired retrieval when tested in an unfamiliar context. When stressed participants were tested in a familiar context, no impairments in retrieval were observed. Furthermore, the authors reported no valence, arousal, or sex differences.

Quesada et al. (2012), on the other hand, examined memory retrieval in male and female children aged 8-10 years. Here, the participants learned the position of the card pairs, with retrieval then tested roughly 1.5 hours later. Before retrieval testing, the participants underwent either a children's version of the TSST or a control condition. The authors reported that participants in the TSST condition showed an overall impaired performance on retrieval of card pairs, irrespective of valence and arousal. They reported no sex differences, and no valence or arousal differences.

An obvious methodological problem with Quesada et al.'s (2012) study is that learning and retrieval took place within 1.5 hours of each other. This short time interval between learning and retrieval introduces the confounding effects of stress on the memory consolidation phase, in addition to effects on retrieval. Thus, a short delay between learning and retrieval is not ideal when attempting to isolate the effects of stress on the retrieval phase of memory.

Nevertheless, the studies of both Schwabe and Wolf (2009) and Quesada et al. (2012) suggest that stress can have an impairing effect on spatial memory. In conjunction with

Buchanan and Tranel's (2008) study, these findings regarding the effects of stress on visual and spatial memory seem to be consistent with those reported on verbal memory.

The hypothesis that stress would impair all memory retrieval, however, seems counter-intuitive when thinking in terms of the survival of both humans and animals. As discussed in Chapter 1, a threat to the homeostasis of an individual triggers the release of stress hormones, which act on the body to give rise to the fight-or-flight response. This stress response system is the product of evolutionary adaptation that seeks to ensure the survival of the organism when presented with a threatening situation. It would seem contrary to this adaptation that the triggering of the stress response system would be coupled with an impairment in the retrieval of spatial memory. The individual would not be able to escape the threatening situation if s/he was not capable of retrieving the necessary visual and spatial information that would allow him/her to navigate out of the perilous situation.

From an evolutionary perspective, it makes sense that memory systems have evolved to solve problems that occurred in our ancestral past. The adaptive process of memory would evolve to enable us to remember information that increases our chances of survival and successful reproduction (Nairne, 2005). This view of memory is termed the *functional perspective of memory*.

### **The Functional Perspective of Memory**

To this point, I have not addressed the origins and functions of memory. Rather, the focus of this dissertation has been on the brain structures responsible for episodic memory, along with the (approximate) mechanisms of action and resulting effects of stress on memory. However, one cannot focus exclusively on the structures of memory without considering the function of memory. If memory has evolved through the process of natural selection, then the structural properties of memory should reflect its function (Tooby & Cosmides, 1992). Nairne and Pandeirada (2008b) offer three probable hypotheses regarding the characteristics of an evolved memory system:

- 1) ...it is unlikely that memory and its associated mechanisms evolved simply to remember the past. There is little adaptive value in designing a system to recover the veridical past, given that the past can never occur again (at least in exactly the same form). Instead, our memory systems must be engineered to use the past in the service of the present, or perhaps to predict the likelihood of events occurring in the future...
- 2) ...evolved memory mechanisms are likely to be domain specific, or sensitive to content; they should be tuned to remember certain kinds of information. A memory

system that treats all environmental events the same would be maladaptive because not all events are equally important from a fitness perspective—for example, it is particularly important to remember the food source, the predator, or the appearance of a potential mate...

3) ...memory mechanisms should be geared especially to helping us perform actions that enhance our reproductive fitness. Again, memory did not develop in a vacuum; memory mechanisms evolved as design “solutions” to problems associated with fitness. Remembering the location of food, an activity preferred by a mate, or perhaps individuals who violate social contracts are likely to improve the chances of successful reproduction, which, in turn, sets the stage for structural modification via descent... (p. 240)

Thus, from an adaptive perspective, it seems logical that both humans and animals remember information that is vital for survival and, consequentially, reproductive fitness. Consistent with this perspective, New, Krasnow, Truxaw, and Gaulin (2007) reported that memory for the spatial locations of food items was better for items that had a higher nutritional value. Wilson, Darling, and Sykes (2011) reported that the locations of evolutionarily relevant stimuli (such as images of predators and dangerous animals) were learned more quickly than the locations of evolutionarily irrelevant stimuli that were matched in terms of arousal (such as the image of a gun aimed directly toward the observer, or a knife being held in a ‘stabbing’ position). In addition, processing information from a survival point of view produces superior retention for related and unrelated words (Burns, Burns, & Hwang, 2011; Howe & Derbish, 2010; Kang, McDermott, & Cohen, 2008; Nairne & Pandeirada, 2008a; Otgaar & Smeets, 2010; Weinstein, Bugg, & Roediger, 2008), for pictures (Otgaar, Smeets, & van Bergen, 2010), and for the 2-dimensional spatial locations of food and animal pictures (Nairne, van Arsdall, Pandeirada, & Blunt, 2012).

Thus, the assumption behind the functionalist approach is that memory systems have a purpose. It is probable that we have developed the capacity to remember in order to solve crucial adaptive problems. Problems such as remembering the locations of food sources, or that potential predators or reproductive partners are likely to be found in a certain territory, should increase the chances of survival and, consequently, reproductive fitness (Nairne et al., 2012). It is also probable that survival would depend, to a great degree, on successful recall of relevant visual and spatial information (e.g., the locations of potential predators) under stressful conditions.

However, regardless of these assumptions behind the functioning of memory, most studies have shown that under conditions of stress (associated with an increased cortisol response), memory retrieval is impaired. These findings have been consistently demonstrated in both human (for verbal, visual and spatial memory) and animal studies, and are therefore not disputed in this dissertation. However, a possible reason for the current direction in the effects of stress seen on retrieval could be due to the nature of the memory tasks that are used. As discussed previously, most human studies have tested memory using tasks such as wordlists, pictures, and 2-dimensional object location tasks. These tasks have no evolutionary relevance (that is, they do not resemble critical adaptive problems that could have shaped our evolutionary past) and thus it would be unlikely that memory systems have adapted to solve these kinds of tasks under stress.

In contrast, tasks that are used in animal studies, such as the Morris Water Maze (MWM), have greater evolutionary relevance. Rodents are forced to remember the location of the hidden platform in order to escape a perilous environment. Failure to escape the environment would compromise the survival of the rodent, and so, accordingly, one can assume that remembering the location of the escape route would be an adaptive problem that would set the stage for structural modification. The task is, therefore, more likely to resemble an adaptive problem from the rat's evolutionary past. However, as discussed in Chapter 1, rodent studies have also shown, robustly, that stress impairs retrieval of a previously learned target in the MWM (de Quervain et al., 1998; Diamond et al., 2006).

A possible explanation for this consistent retrieval deficit might be due to the measure of the rodent's memory performance in the MWM. That is, the measure of spatial memory in the MWM is the rodent's wayfinding performance (i.e., its efficiency in locating the hidden platform in the maze). As noted in Chapter 2, wayfinding is the process of orientation and navigation in order to accurately relocate between places in the environment and to recognize when a destination has been reached (Gluck, 1990; Peponis et al., 1990). Therefore, wayfinding cannot be considered a 'pure' measure of spatial memory, as it involves the interpretation of spatial memory through other cognitive processes (such as orientation and navigation) in order to find the platform in the MWM. Thus, heightened attention could be directed to these other cognitive activities at the expense of the spatial memory (de Kloet et al., 1999; Diamond et al., 2004; Roozendaal, 2002).

Similarly, rodent studies have demonstrated that a functioning hippocampus is essential in order for the rat to navigate successfully to the platform, irrespective of the amount of training in the MWM (i.e., whether memory for the environment is recent or

remote). As discussed in Chapter 1, a possible explanation for the remote memory impairments seen in MWM studies is that water-maze tasks require the rodent to constantly update its position in the water in order to find the hidden platform. This updating of position requires an element of learning from the rodent, which is impaired in the case of hippocampal lesions (Knowlton & Fanselow, 1998). Thus, attention and cognitive memory capacities could be directed towards encoding and consolidating the MWM at the expense of wayfinding performance (Joels et al., 2006; Schwabe et al., 2012). However, one cannot be certain that spatial memory is impaired, as memory for the environment cannot be tested outside of the environment; not in animal studies at least. Using a human version of the MWM (such as the CG Arena) might enable different aspects of spatial memory to be tested outside of the environment, in addition to wayfinding performance in the environment.

### **Summary**

Despite being a relatively understudied area, the literature surrounding the effects of stress on visual and spatial memory retrieval appear consistent with the findings on verbal memory. That is, stress is generally reported to have an overall impairing effect on memory retrieval.

From an adaptive perspective, however, the hypothesis that stress causes a global memory retrieval impairment across all domains seems counter intuitive. The functional approach to memory sees memory systems as having a purpose. In other words, memory systems have developed in order to solve critical adaptive problems from our ancestral past. Amongst other factors, successfully remembering the locations of potential predators, or reproductive partners, are likely to increase the chances of survival and reproductive fitness. Under stressful conditions, remembering these locations would, in all likelihood, increase the odds of survival.

Consequently, the overall stress-induced retrieval impairment seen in the literature might possibly be due to the nature of the memory tests that are used or, in the case of animal studies, the measure of spatial memory that is used. The current study aims to explore the effects of stress on visual and spatial memory retrieval by using a 3-dimensional task that contains landmarks drawing on the most basic of emotional/survival responses. In doing so, the aim is that this research might help to better explain the effects of stress on visual and spatial memory retrieval.

### **Aims, Rationale, and Hypotheses**

The aim of the following comparative study was, first, to test the fundamental question asked in this dissertation: What are the effects of acute stress on retrieval of visual and spatial material? Second, the study aimed to determine what additional effects, if any, emotional arousal might have on the quality of visual-spatial memory retrieval under stress. The current study builds on the findings of the first two studies in this dissertation (documented in Chapters 2 and 3). The purpose of those studies was: (a) to identify the stimuli to be used in the current series of studies; (b) to verify that the spatial tasks to be used in these studies would not bias spatial learning and memory; and (c) to employ a stress manipulation that would robustly increase stress (and, importantly, cortisol) levels in the participants.

To investigate the effects of stress on visual and spatial cognition, the present study aimed to systematically replicate the paradigm used by de Quervain et al. (1998). As discussed in Chapter 1, that pioneering study was the first to report the negative effects on retrieval in rodents in a MWM study. These authors demonstrated, importantly, that both stress (in the form of foot shocks) and GC treatment impaired performance in a MWM that had been learned 24 hours previously.

The current study also aimed to bridge the divide between animal and human methodologies used to explore the effects of stress on memory. It does so for two main reasons: First, such bridging will allow for better comparisons between findings from human and animal studies. Second, as mentioned previously, measurement in animal studies is usually confined to examining spatial wayfinding performance. Employing a similar design in human studies will allow for memory for the other aspects of the spatial environment to be examined (e.g., the spatial layout of the environment and recognition of the landmarks in the environment). These other memory details provide a more detailed picture of the quality of visual and spatial memory than if one only examines the spatial wayfinding performance in the environment.

The current study expands on the experimental paradigm used in Study A. However, several adaptations were made to the experimental design so as to focus on the memory retrieval phase. In order to separate memory retrieval from consolidation, the study was conducted over two sessions, with a 24-hour period separating the learning of a spatial environment from retrieval of that environment. In the first session, participants learned the target locations in the three CG Arena rooms described in Study A. In the second session,

participants were assigned to either a *Stress* or *Control* group. Participants in the Stress group were exposed to the Fear-Factor Stress Test (FFST) stress paradigm discussed in Chapter 3; Control participants were exposed to the FFST control paradigm. Following the manipulation, participants were required to undergo tests of memory retrieval (i.e., recall [Arena Reconstitution Task; ART] and recognition [Object Recognition Task; ORT] of the layout of the environment). Wayfinding and dwell time in the CG Arena were also key outcome measures.

Based on the general findings in the literature surrounding stress and memory retrieval (and consistent with the predictions of the integrated vertical and horizontal perspective theory), the study tested these main hypotheses:

1) Stress will have an overall impairing effect on memory retrieval. Specifically, participants in the Stress group will perform more poorly than those in the Control groups on all tests of memory retrieval.

2) Memory for the different rooms will be influenced by the arousal content of the different pictures used as landmarks in the CG Arena. The Stress and Control groups will show a contrasting pattern of retrieval for the arousing versus neutral stimuli. That is, although the Stress groups will show an overall retrieval impairment, a greater retrieval impairment will be present for the arousing pictures than for the neutral pictures.<sup>16</sup> The Control groups, in contrast, were predicted to show enhanced retrieval for the picture stimuli that contained the arousing content versus those with the neutral content.

Despite the primary focus of this dissertation being on broad effects of stress on memory retrieval, differences between men and women have been widely reported in the domains of both emotional arousal and spatial memory.<sup>17</sup> Unfortunately, these differences cannot be ignored, as they may well influence the results of the present studies. Thus, in line with the hypotheses discussed in Chapter 2 (although not confirmed in the chapter), I continued with the hypothesis regarding sex differences. The prediction was that:

3) Women will display inferior spatial memory compared to men.

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<sup>16</sup>As discussed above, the literature and theory both support a disruptive or impairing effect of stress on memory. This impairing effect, according to some authors (i.e., de Quervain et al, 2009; Wolf, 2008, 2009), is directly proportional to the level of emotional arousal. That is, under stressful conditions, there is greater retrieval impairment associated with higher levels of emotional arousal.

<sup>17</sup>Although sex differences are also reported in stress response to psychosocial stressors (Kudielka et al., 2009), Study B showed that the FFST induced a similar autonomic and HPA-axis response in both men and women. Thus, I refrain from formulating hypotheses regarding specific sex differences in stress responding in the present study.

## Methods

### Participants

Seventy participants (32 men) were recruited through the UCT Department of Psychology's Student Research Participation Program (SRPP). Ten participants (2 men) were excluded from the study, either because they met the exclusion criteria listed below ( $n = 8$ ; 2 men) or because they withdrew voluntarily from the study ( $n = 2$ ; both women). This left a total sample of 60 participants (30 men). The participants were aged between 18 and 27 years ( $M = 19.97$ ,  $SD = 1.85$ ).

To determine whether the size of the recruited sample was large enough to observe the hypothesized differences, power analyses were performed based on the effect size ( $r = .331$ ) associated with the differences found by Buchanan and Lovallo (2001). A power analysis for a sample size of 60, with repeated measures on three factors (assuming an average correlation between the repeated measures) at an alpha value of .05, showed a two-group design to have a power that exceeds .90, and a four-group design to have a power of .78 (Faul, Erdfelder, Buchner, & Lang, 2009; Faul, Erdfelder, Lang, & Buchner, 2007).

I attempted to match the experimental and control groups on demographic variables such as age and level of education. Individuals with a history of neurological illness, substance abuse, or psychiatric disorders were excluded from the study. As was the case in Chapter 2, individuals with a prior history of visiting [www.rotten.com](http://www.rotten.com) or [www.charonboat.com](http://www.charonboat.com), or who were familiar with the images displayed on these websites, were also excluded from the study. These participants were excluded because of the chance that people with prior exposure to the 'hot' images would be desensitized to the graphic nature of their content. Any participants who were currently on prescription medication (including oral contraceptives) were also excluded. Finally, any participants who were currently fighting an infection or who had a history of peptic ulcers, osteoporosis, congestive heart failure, diabetes mellitus, chronic renal failure and uraemia, quiescent tuberculosis, glaucoma, hypertension, myasthenia gravis and thromboembolic disorders, were also excluded. It is believed that high levels of cortisol may exacerbate these conditions (Gibbon, 2000).

## Materials

The materials used in the present study were identical to those described in Study A. Specifically, the same stimulus pictures that were rated in Appendix A as being the most defensively arousing, most appetitively arousing, and most neutral in valence and arousal, were again used. The participants also completed the FFST and control manipulations described in Study B. In addition, physiological and self-report measures were collected from the participants.

**Physiological measures.** Heart rate (HR) and galvanic skin response (GSR) measures were collected using the Vrije Universiteit Ambulatory Monitoring System (VU-AMS). In addition, saliva samples were collected via *Salivettes*.

**VU-AMS.** Heart rate/electrocardiography (ECG) data were collected as described in Chapter 3. Galvanic skin response levels were monitored through finger sensors connected to the index and middle fingers of each participant. Time markers were inserted during the measurement process to indicate points of interest in order to assist with data analysis. Heart rate and GSR response were monitored to determine participants' state of physiological arousal during the testing procedure on Day 2. Both HR and GSR levels were compared at three points of interest:

- 4)  $HR_B/GSR_B$ . The average HR/GSR recorded over 2 minutes at the start of the session represented a baseline HR/GSR measure for each participant.
- 5)  $HR_I/GSR_I$ . The average HR/GSR sampled throughout the final 12 minutes of the FFST stress or Control manipulations. The average during this period, which encompassed the speaking and mental arithmetic tasks, as well as the water immersion task, represented HR/GSR during the stress manipulation.
- 6)  $HR_2/GSR_2$ . The average HR sampled for 2 minutes at the end of the testing session (i.e., 35 minutes after the end of the FFST or Control manipulation), taking the average of those 2 minutes as the final representation of HR/GSR.

**Salivettes.** Consistent with Study B, saliva samples were collected using Sarstedt Salivette® Cortisol swabs (Sarstedt, Nümbrecht, Germany) in order to measure cortisol concentrations. Saliva collection and analysis was identical to that described in Study B. Three saliva samples were taken from each participant during the session on Day 2:

- 1)  $CORT_B$ . At the start of the session represented a baseline cortisol measure for each participant.
- 2)  $CORT_I$ . Five minutes after the FFST or Control manipulation ended.

- 3) *CORT*<sub>2</sub>. At the end of the testing session (i.e., 35 minutes after the end of the FFST or Control manipulation).

**Self-report measurements.** I collected data from two self-report questionnaires; the Beck Depression Inventory-Second Edition (BDI-II) and the Spielberger State Anxiety Inventory (STAI-State). These measures are described in Study B. In addition to the STAI-State, I also administered the Spielberger Trait Anxiety Inventory (STAI-Trait).

The STAI-Trait scale consists of a 20-item self-report scale that measures characteristic anxiety. The scale requires the participant to indicate the frequency with which s/he generally experiences anxiety-related symptoms. For the purposes of the present study, the STAI-Trait scale was used to assess participants' general anxiety levels, while the STAI-State scale was used to assess participants' subjective experiences of anxiety throughout the experimental session on Day 2. Three STAI-State measures were taken from each participant during the session on Day 2:

1. *STAI*<sub>B</sub>. At the start of the session represented a baseline self-report anxiety measure for each participant.
2. *STAI*<sub>1</sub>. Five minutes after the FFST or Control manipulation ended.
3. *STAI*<sub>2</sub>. At the end of the testing session (i.e., 35 minutes after the end of the FFST or Control manipulation).

## Apparatus

The apparatus used in the present study was largely the same as that described in Study A. A few changes were, however, made to the CG Arena rooms (to allow for learning and recall sessions) and to the *Object Recognition Task (ORT)*. These changes are discussed below. The *Arena Reconstitution Task (ART)* remained the same as described in Study A (see pg. 60). In addition, a verbal memory test (the *Verbal Paired Associates Test*) was also administered.

**The Computer-Generated Arena.** Five CG Arena rooms, identical to those used in Study A, were created: a waiting room and four experimental rooms (a training room, a Cool experimental room, a Hot Appetitive experimental room, and a Hot Defensive experimental room). The experiment consisted of a learning phase and a recall phase; the sequence of trials differed across these phases. Tables 9 and 10 show the sequence of trials for the learning and recall phases, respectively. As Table 9 shows, the learning phase consisted of 22 CG Arena trials (4 in the training room, and 6 in each of the Cool, Hot Appetitive, and Hot Defensive rooms). The purpose of this phase was to allow the participants to: (a) become familiar with

the CG Arena environment, and (b) encode and consolidate memory for the layouts of the Cool, Hot Appetitive, and Hot Defensive rooms.

The recall phase consisted of 2 trials in each of the Cool, Hot Appetitive, and Hot Defensive rooms (see Table 10). On the first trial (*Recall Trial*), the participants had to move to the place in which the target had been located during the learning phase. The second trial in each room was a probe trial in which the target was absent from the Arena. The purpose of the probe trial was to determine whether the participants were in fact using distal cues to locate the target and not simply locating the target by moving randomly around the room.

**Object Recognition Task (ORT).** This is a yes-no picture recognition test. In the current study, it involved the participant being seated in front of a computer monitor. E-Prime software (Psychological Software Tools, 2002) administered the task. The participants viewed 16 image slides, 8 of which were found on the walls of a previously-seen CG experimental room and 8 of which were distracters. Participants had to press ‘Y’ (yes) or ‘N’ (no) on the keyboard in response to whether they recognize the picture or not.<sup>18</sup> A separate ORT was administered for each of the Cool, Hot Appetitive, and Hot Defensive rooms.

**Verbal Paired Associates Test (VPA).** The VPA (Uttl, Graf, & Richter, 2002) was used to assess explicit verbal episodic memory. I read a list of 15 pairs of words to the participant. Four word pairs were semantically related (e.g., *rose - flower*), while the other 11 were semantically unrelated (e.g., *crush - dark*). After I had read the list once, I read one word of each pair, and the participant was asked to recall the other word, until the list was exhausted. An identical second trial was then conducted. A delayed recall trial was administered during the second test session. Although the inclusion of a verbal memory test does not fall within the specific scope of an examination of visual and spatial cognition, the VPA was administered to relate findings from the current study to previous findings on the effects of stress on verbal memory. Because verbal episodic memory is also dependent on hippocampal activity, one would expect elevated cortisol levels associated with stress to impair this form of memory (e.g., Smeets, 2011). In other words, the inclusion of the VPA allowed for an examination of the effectiveness of the stress manipulation. In addition, it allowed some investigation of whether the effects of stress on memory are material-specific.

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<sup>18</sup>This format of the ORT was changed from that in Study A (see pg. 60). The previous ORT comprised an unwanted learning element. In that version of the task, participants had to make two choices for each Arena picture. Each of those pictures was, however, coupled with a different distracter picture on each choice. Allowing participants to choose between two pictures gives them clues as to further choices that they would have to make. Thus, if a participant recognised the target picture then he/she would know that the other was not in the room; this may have aided their choice next time they saw either of the pictures.

Table 9  
*CG Arena Trial Parameters for the Learning Phase*

Parameter	CG Arena Room			
	Training	Cool	Hot Appetitive	Hot Defensive
Number of trials	4	6	6	6
Start location sequence <sup>a</sup>	N, S, W, E	N, S, W, E	N, S, W, E	N, S, W, E
Target condition	Visible	Invisible	Invisible	Invisible
Time limit (seconds)	120	120	120	120

*Note.* <sup>a</sup>The N (North) starting location was facing the middle of the North wall of the arena, the S (South) starting location was facing the middle of the South wall, and so on. The full sequence of start locations is presented in Appendix D

Table 10  
*CG Arena Trial Parameters for the Recall Phase*

Parameter	CG Arena Room					
	Cool		Hot Appetitive		Hot Defensive	
	Recall Trial	Probe Trial	Recall Trial	Probe Trial	Recall Trial	Probe Trial
Number of trials	1	1	1	1	1	1
Start location <sup>a</sup>	N, W, or E	Random	N, W, or E	Random	N, W, or E	Random
Target condition	Invisible	Absent	Invisible	Absent	Invisible	Absent
Time limit (seconds)	60	30	60	30	60	30

*Note.* <sup>a</sup>The N (North) start location was facing the middle of the North wall of the arena, the W(West) start location was facing the middle of the West wall, and so on. The full sequence of start locations is presented in Appendix D

## Procedure

The study procedures were conducted in the ACSENT Laboratory in the Department of Psychology at the University of Cape Town (UCT). The research described here followed the ethical guidelines for research subjects outlined by the Health Professions Council of South Africa and the UCT Codes for Research. The Research Ethics Committee of the UCT Department of Psychology approved all study procedures.

All testing was performed in the afternoon between 14h00 and 18h00 in order to control for the possible effects of circadian and diurnal rhythms (Lupien et al., 2007; Richter et al., 2012). For each participant, the experimental procedure was split across two sessions, which were run on two consecutive days.

**Day 1.** At the start of the first (learning) session, I asked the participant to read and sign a consent form (Appendix I), and gave him/her the chance to ask any questions concerning that form and the experiment. The participant then completed a socio-demographic questionnaire (Appendix H), followed by the BDI-II and STAI-Trait questionnaires. The participant then completed the immediate recall trials of the VPA.

Following completion of those VPA trials, I read a set of standardised instructions to the participant. These instructions were designed to prepare the participant for the tasks required of him/her in the CG Arena. In addition, these instructions explained the relationship between movements of the joystick and changes in the display of the CG Arena. Finally, the participant was given a chance to ask any additional questions concerning the instructions or the experimental procedure.

The order of presentation of the rooms was counterbalanced across participants for the learning and recall phases. The counterbalancing happened in this way: The order of the three rooms was divided into six sequences (see Table 11). Participants were pseudo-randomly assigned to a group that was uniquely associated with one of the sequences; this assignment was made on the basis of participant numbers (i.e., participant number 1 completed sequence 1, participant number 2 completed sequence 2 ..., participant number 7 completed sequence 1, and so on). This counterbalancing sought to alleviate any influence that the sequence of experimental room tasks might have on the participants and the results.

After the acquisition trials in the CG Arena rooms, I reminded the participant that s/he would have to return for a second session 24 hours later. I also reminded the participant that s/he would have to give a saliva sample at the next session, and instructed him/her not to eat, drink, smoke, chew gum or do physical exercise for two hours before the next session.

Table 11  
*Counterbalanced Sequences of CG Arena Rooms in the Acquisition Phase*

Sequence	Acquisition Phase			
	Trials 1-4	Trials 5-10	Trials 11-16	Trials 17-22
1	Training Room	H+ Room	Cool Room	H- Room
2	Training Room	H+ Room	H- Room	Cool Room
3	Training Room	Cool Room	H+ Room	H- Room
4	Training Room	Cool Room	H- Room	H+ Room
5	Training Room	H- Room	Cool Room	H+ Room
6	Training Room	H- Room	H+ Room	Cool Room

*Note.* H+ = Hot Appetitive; H- = Hot Defensive.

**Day 2.** Figure 16 displays the timeline of events on Day 2. The second session followed 24 hours after the first. On arrival for the second (recall) session, the participant was pseudo-randomly assigned to either a Stress or Control group. I then asked the participant to complete a questionnaire about what he/she had had to eat and drink on that day. Height and weight of the participant was collected for a measure of Body Mass Index (BMI). Thereafter, the participant was connected to the VU-AMS and asked to sit quietly for 5 min in order to acclimatise to the device, after which  $HR_B$  and  $GSR_B$  measurements were taken. An initial saliva sample was then obtained for a measure of cortisol ( $CORT_B$ ) level, and the participant was asked to complete a STAI-State ( $STAI_B$ ) questionnaire. I then read the instructions detailing, depending on the participant's group assignment, either the FFST or the Control condition, and the participant then proceeded to complete the procedures involved with that condition. Heart rate ( $HR_1$ ) and  $GSR_1$  were measured during the performance segment of the FFST or Control manipulation (i.e., following the preparation phase until the conclusion of the manipulation).

Five minutes after the conclusion of the manipulation, a second saliva sample ( $CORT_1$ ) was taken and the participant was asked to complete a second STAI-State ( $STAI_1$ ) questionnaire. Next, the participant was administered the VPA delayed recall trial and then completed the ORTs and ARTs for the CG rooms that they had learned 24 hours before. They were then asked to complete the six CG Arena recall trials (see Table 12).

Following the completion of this part of the experimental protocol, the participant was asked to complete a final STAI-State ( $STAI_2$ ) questionnaire and to provide a final saliva sample ( $CORT_2$ ), along with  $HR_2$  and  $GSR_2$  measurements. The participants were then debriefed and the study concluded. The length of time taken to test each participant was not more than 60 minutes for the first session, and 120 minutes for the second.

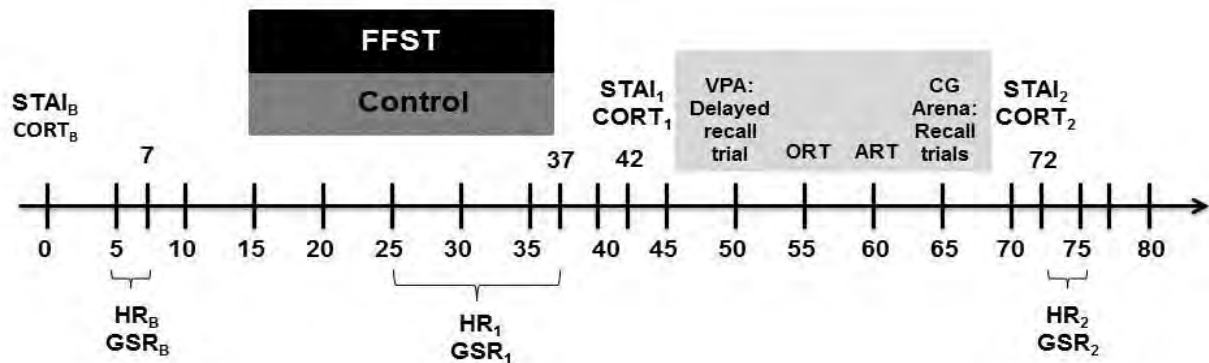


Figure 16. Timeline of events, from 0 minutes to 80 minutes, during the experimental procedures on Day 2. FFST = Fear-Factor Stress Test group; STAI = State-Trait Anxiety Inventory; HR = heart rate (measured in beats per minute); GSR = galvanic skin response; CORT = salivary cortisol (measured in nmol/l). Subscripts represent measurement point (e.g., STAI<sub>B</sub> is the first STAI measurement point, or baseline).

Table 12

*Counterbalanced Sequences of CG Arena Rooms in the Recall Phase*

Sequence	Recall Phase		
	Trials 1 and 2	Trials 3 and 4	Trials 5 and 6
1	H+ Room	Cool Room	H- Room
2	H+ Room	H- Room	Cool Room
3	Cool Room	H+ Room	H- Room
4	Cool Room	H- Room	H+ Room
5	H- Room	Cool Room	H+ Room
6	H- Room	H+ Room	Cool Room

Note. H+ = Hot Appetitive; H- = Hot Defensive.

### Data Analysis

Statistical analyses proceeded using IBM SPSS Statistics version 21. The design of the present study allowed for both within- and between-groups analyses. The threshold for statistical significance was set at  $\alpha = .05$ . Details of the particular analyses used are specified at the start of the presentation of the relevant section of the Results. Unless otherwise stated, all assumptions underlying the inferential statistical tests were upheld.

Overall, two separate sets of analyses were performed. First, the full participant sample was analyzed. Second, consistent with Study B, participants in the Stress groups who showed a marked increase in cortisol following exposure to the FFST were compared to the Control participants. Participants were again classified as responders on a post-hoc basis (i.e., if they showed a 2 nmol/l or more increase over baseline at either cortisol measure following

exposure to the FFST). Comparison of controls against only those participants who showed a cortisol response was done in an attempt to isolate cortisol effects on memory.

## Results

### Sample Characteristics

To ensure that the participants recruited for this study were all sampled from a similar population, characteristics such as age, BMI, BDI-II scores, and STAI-Trait scores were compared across groups. A series of 2 (Experimental Condition: Stress versus Control) x 2 (Sex: male versus female) factorial ANOVAs compared outcomes on these variables. Table 13 presents descriptive statistics for the variables of interest here.

**Age.** The analysis detected no significant main effects for Experimental Condition,  $p = .331$ , or Sex,  $p = .129$ , and no significant Experimental Condition x Sex interaction effect,  $p = .676$ . These results suggest that the cortisol and cognitive data reported below are not confounded by between-group differences in age. This observation is important in light of the fact that, for instance, Harris, Wiener, and Wolbers (2012) showed that navigation strategies change with age. In addition HPA-axis response has also been reported to change with age (Kudielka et al., 2009).

Table 13  
*Descriptive Statistics for Sample Characteristics (N = 60)*

Measure	Group			
	Stress		Control	
	Men $n = 15$	Women $n = 15$	Men $n = 15$	Women $n = 15$
Age	20.20 (1.26)	19.27 (1.39)	20.47 (2.72)	19.93 (1.62)
BMI	23.32 (2.90)	22.43 (2.47)	22.05 (2.21)	22.58 (3.03)
BDI-II	11.00 (5.14)	7.33 (4.89)	8.13 (5.97)	10.40 (6.84)
STAI-Trait	40.87 (8.30)	39.07 (4.62)	36.47 (7.66)	42.00 (10.70)

*Note.* Means are presented with standard deviations in parentheses. BMI = body mass index; BDI-II = Beck Depression Inventory-Second Edition; STAI = State-Trait Anxiety Inventory.

**BMI.** BMI was calculated by dividing the participants weight in kilograms (kg) by his/her height in meters (m) squared (i.e.,  $BMI = kg/(m)^2$ ). The analysis of BMI across the four groups detected no significant main effects for Experimental Condition,  $p = .420$ , or Sex,  $p = .795$ , and no significant Experimental Condition x Sex interaction effect,  $p = .305$ . These results suggest that the cognitive data reported below are not confounded by between-group

differences in BMI. This observation is important in light of the fact that, for instance, diurnal cortisol levels are associated with BMI (Champaneri et al., 2013).

**BDI-II scores.** The analysis of BDI-II scores detected no significant main effects of Experimental Condition,  $p = .947$ , or of Sex,  $p = .640$ , and no significant Experimental Condition x Sex interaction,  $p = .051$ ,  $\eta_p^2 = .07$ . Although this interaction was barely non-significant (with the Stress Male and the Control Female groups showing higher average BDI-II scores; see Table 12), the mean scores for all groups fell in the “minimally depressed” range (i.e., 0-13.99) described by Beck and colleagues (1996).

These results suggest that the cortisol and cognitive data reported below are not confounded by between-group differences in pre-existing depressive symptomatology. This observation is important in light of the fact that patients who experiencing clinical depression show raised cortisol levels and affected cognitive function (Kudielka & Kirschbaum, 2005).

**STAI-Trait scores.** Levene’s test indicated a violation of the assumption of homogeneity of variances. However, due to ANOVA being a robust test and because all the group sizes were equal, I continued with the analysis in the conventional manner. Again, the analysis detected no significant main effect differences for Experimental Condition,  $p = .728$ , or for Sex,  $p = .377$ , and no Experimental Condition x Sex interaction,  $p = .086$ .

To be sure that the groups recruited for the current study were representative of the general population in terms of trait anxiety, a series of one-sample  $t$ -tests compared group averages to normative data for college students presented in the STAI test manual (Spielberg et al., 1983). Male participants ( $n = 30$ ;  $M = 38.66$ ,  $SD = 8.16$ ) did not significantly differ from the normative male population ( $M = 38.30$ ,  $SD = 9.18$ ),  $p = .873$ ). Similarly, female participants ( $n = 30$ ;  $M = 40.53$ ,  $SD = 8.27$ ) did not differ significantly from the normative female population ( $M = 40.40$ ,  $SD = 10.15$ ),  $p = .957$ .

Taken together, these results suggest that the four groups were similar in terms trait anxiety, and were representative of the general population of college students.

### **Experimental Manipulation**

The following series of analyses sought to establish the effectiveness of the experimental manipulation. The intention of the manipulation was to significantly increase the levels of stress of the participants in the Stress groups relative to those of the Control groups. Increased stress levels would be indicated by (relative to baseline) increased self-reported anxiety, cortisol levels, HR, and GSR.

For each of the relevant outcome variables, 2 x 2 x 3 (Experimental Condition [Stress versus Control] x Sex [male versus female] x Time [measure<sub>B</sub> versus measure<sub>1</sub> versus measure<sub>2</sub>]) repeated-measures ANOVAs were conducted, and further within- and between-group analysis was used to explore significant effects. Table 14 provides descriptive statistics for each of the relevant outcome variables.

Table 14  
*Descriptive Statistics for Self-Report and Physiological Measures (N = 60)*

Outcome variable	Group			
	Stress		Control	
	Men (n = 15)	Women (n = 15)	Men (n = 15)	Women (n = 15)
STAI-state				
STAI <sub>B</sub>	29.87 (7.83)	28.40 (7.18)	30.53 (6.13)	32.87 (6.86)
STAI <sub>1</sub>	42.67 (13.10)	47.93 (12.56)	29.53 (6.96)	29.13 (6.05)
STAI <sub>2</sub>	28.80 (6.17)	28.27 (6.65)	27.93 (6.64)	29.20 (6.21)
Cortisol measure				
CORT <sub>B</sub>	3.80 (1.26) <sup>a</sup>	3.63 (1.61)	4.14 (3.07)	4.96 (7.14)
CORT <sub>1</sub>	6.65 (2.40) <sup>a</sup>	5.41 (3.14)	3.48 (2.36)	3.33 (3.38)
CORT <sub>2</sub>	8.41 (6.81) <sup>a</sup>	7.43 (7.75)	2.43 (1.72)	2.50 (2.30)
Heart rate				
HR <sub>B</sub>	73.62 (12.96)	75.95 (10.65)	69.92 (11.89) <sup>a</sup>	81.28 (9.63)
HR <sub>1</sub>	90.52 (13.94)	97.75 (15.72)	80.62 (11.65) <sup>a</sup>	95.72 (13.82)
HR <sub>2</sub>	70.48 (12.99)	73.08 (10.17)	65.49 (8.90) <sup>a</sup>	78.94 (9.64)
Galvanic skin response				
GSR <sub>B</sub>	2.57 (2.28)	1.91 (2.09)	1.56 (1.10) <sup>a</sup>	1.55 (0.87)
GSR <sub>1</sub>	6.09 (3.02)	4.57 (3.10)	2.63 (2.10) <sup>a</sup>	2.45 (1.85)
GSR <sub>2</sub>	4.17 (2.89)	2.50 (2.10)	2.06 (1.40) <sup>a</sup>	2.67 (2.24)

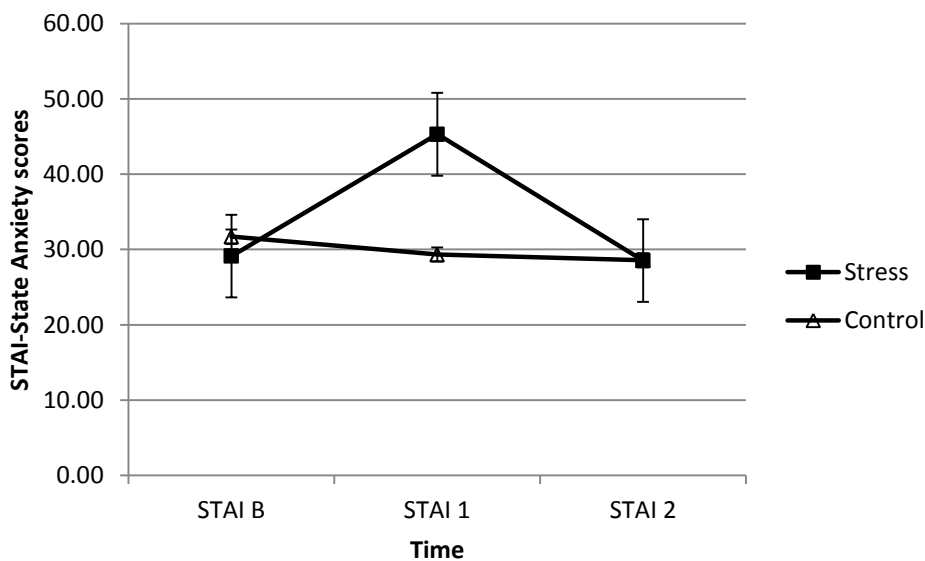
*Note.* Mean scores are provided, with standard deviations in parentheses. Cortisol levels are measured in nanomoles per litre (nmol/l). Where assays determined cortisol levels for a participant to be < 0.50 nmol/l, 0.45 nmol/l was used as an estimate. Heart rate levels are measured in beats per minute (bpm). Galvanic skin response levels are measured in microSiemens (µS). Subscripts represent measurement point (e.g., STAI<sub>B</sub> is the first STAI measurement point, or baseline). <sup>a</sup>n = 14. One Stress Male group salivary cortisol sample was lost due to experimenter error; one Control Male participant's heart rate and skin response data was lost due to hardware malfunction.

**Self-report anxiety measure: STAI – State.** Due to a violation of sphericity (indicated by Mauchly's test),  $\chi^2(2) = 23.48, p < .001$ , it was necessary to use a Greenhouse-Geisser degrees of freedom correction ( $\epsilon = 0.74$ ).

The analysis detected statistically significant main effects of Experimental Condition,  $F(1, 56) = 6.51, p = .014, \eta_p^2 = .10$ , and Time,  $F(1.48, 83.12) = 45.03, p < .001, \eta_p^2 = .45$ , in the absence of a main effect of Sex,  $p = .540$ . The analysis also detected a significant

Experimental Condition x Time interaction,  $F(1.48, 83.12) = 53.32, p < .001, \eta_p^2 = .49$ , in the absence of statistically significant Experimental Condition x Sex,  $p = .995$ , Sex x Time,  $p = .447$ , and Experimental Condition x Sex x Time interaction effects,  $p = .066$ .

These results indicate that only the Experimental Condition and Time had an effect on the subjective anxiety levels of the participants, and that Sex was not a contributing factor in influencing those levels. To investigate the nature of the influence further, I examined each of the contributing factors separately. Figure 17 shows the fluctuations in the Stress and Control groups' anxiety levels across the Day 2 test session.



*Figure 17.* Changes in self-reported state anxiety (STAI) levels on Day 2 for the combined Stress and combined Control groups. Error bars indicate standard error of means. Subscripts represent measurement point (e.g., STAI<sub>B</sub> is the first STAI-State measurement point, or baseline).

Within-group analysis of Time revealed that the Stress group showed a significant increase in reported anxiety levels from STAI<sub>B</sub> ( $M = 29.13, SD = 7.42$ ) to STAI<sub>1</sub> ( $M = 45.30, SD = 12.89; F(1, 29) = 50.46, p < .001, \eta_p^2 = .64$ ). However, by the STAI<sub>2</sub> ( $M = 28.53, SD = 6.31$ ), reported anxiety levels of the Stress group had returned to statistically similar levels to STAI<sub>B</sub>,  $p = .624$ . The Control group, on the other hand, showed a significant decrease in reported anxiety from STAI<sub>B</sub> ( $M = 31.70, SD = 6.50$ ) to STAI<sub>2</sub> ( $M = 29.33, SD = 6.41; F(1, 29) = 5.28, p = .029, \eta_p^2 = .15$ ), and a further decrease by the STAI<sub>2</sub> ( $M = 28.57, SD = 6.35$ ),  $F(1, 29) = 11.68, p = .002, \eta_p^2 = .29$ . Thus, the Stress group showed the intended increase in

reported anxiety after the manipulation. In contrast, the control group showed a decrease in reported anxiety across the Day 2 test session.

Between-group analysis of STAI<sub>B</sub> data detected no significant main effects of Experimental Condition,  $p = .163$ , or of Sex,  $p = .812$ , nor was there a significant Experimental Condition x Sex interaction,  $p = .299$ . This result suggests that there were no between-group differences at the start of Day 2, and that any changes in anxiety levels as the test session progressed could be attributed to the effects of the experimental manipulation.

Between-group analysis of the STAI<sub>1</sub> data detected a significant main effect of Experimental Condition,  $F(1, 59) = 36.92, p < .001, \eta_p^2 = .40$ , no significant main effect of Sex,  $p = .358$ , and no significant Experimental Condition x Sex interaction effect,  $p = .286$ . At this time point, the Stress groups ( $M = 45.30, SD = 12.89$ ) showed significantly raised anxiety levels in comparison to the Control groups ( $M = 29.33, SD = 6.41$ ). As the non-significant interaction effect implies, there were no significant differences between the Stress Male and Stress Female groups,  $p = .162$ , or between the Control Male and Control Female groups,  $p = .915$ .

Between-group analysis of the STAI<sub>2</sub> data detected no significant main effects of Experimental Condition,  $p = .984$ , or of Sex,  $p = .826$ , and no significant Experimental Condition x Sex interaction,  $p = .589$ . Thus, by the STAI<sub>2</sub>, the Stress group's self-reported anxiety levels had returned to slightly below STAI<sub>B</sub> level, and there were no significant between-group differences.

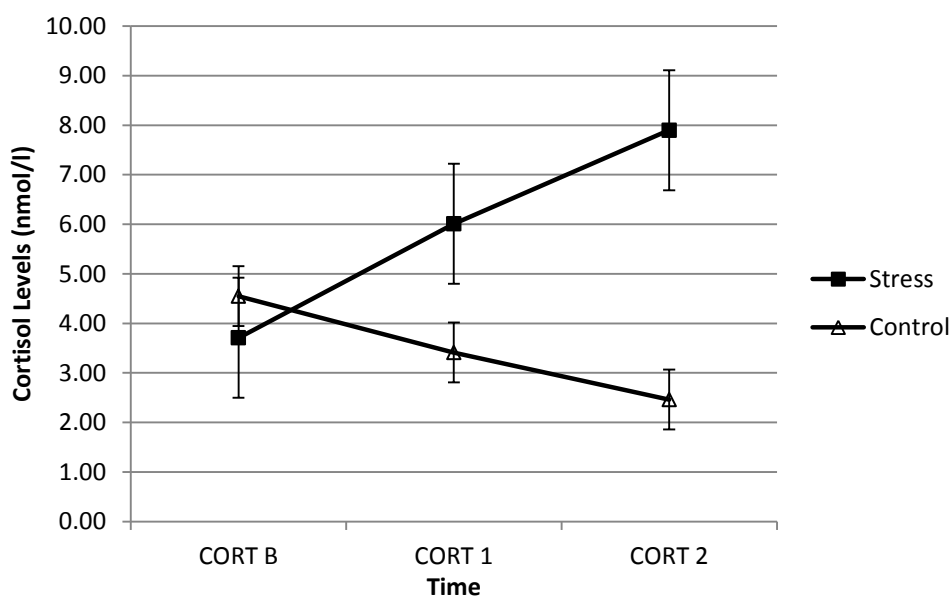
Taken together, this set of results confirms that the manipulation successfully raised subjective anxiety levels in the Stress group, irrespective of sex, and verifies that participants in that group were in a subjectively anxious state following the manipulation. From an ethical perspective, it is important to point out that this heightened stressed state was transient. By the end of the testing session, the STAI-State scores of participants in the Stress group had returned to near-baseline levels, indicating they left the study feeling no more anxious than when they arrived.

The Control group, in contrast, reported a steady decrease in anxiety across the Day 2 test session. Thus, as intended, participants in the Control condition did not find their manipulation to be subjectively stressful.

**Salivary cortisol.** Due to violation of the assumptions of normality, homogeneity of variances, and sphericity, it was necessary to perform transformations on the data. Log transformations corrected for the violations of normality and sphericity. Unfortunately, there still remained a violation of homogeneity of variances for the CORT<sub>B</sub> variable. However, due

to ANOVA being a robust test, I continued with the analyses in the conventional manner, using the log-transformed data.

The analysis detected a significant main effect of Experimental Condition,  $F(1, 55) = 26.66, p < .001, \eta_p^2 = 0.23$ , in the absence of significant main effects of Time,  $p = .214$ , and Sex,  $p = .360$ . In addition, there was a statistically significant Experimental Condition x Time interaction effect,  $F(2, 110) = 20.85, p < .001, \eta_p^2 = .28$ , in the absence of an Experimental Condition x Sex interaction,  $p = .636$ , a Sex x Time interaction,  $p = .610$ , and Experimental Condition x Sex x Time interaction,  $p = 0.781$ . These results suggest that only the Experimental Condition, and its interaction with the Time, had an effect on participants' cortisol levels. Sex, once again, did not appear to be an influencing factor. To investigate the nature of the influence further, I examined each of the contributing factors separately. Figure 18 shows the fluctuations in cortisol levels for each Experimental Condition across Time.



*Figure 18.* Changes in cortisol (CORT) levels on Day 2 for the combined Stress and combined Control groups. Error bars indicate standard error of means. Subscripts represent measurement point (e.g., CORT<sub>B</sub> is the first cortisol measurement point, or baseline).

Within-group analysis of data across Time showed that the Stress group displayed a significant increase in cortisol levels from CORT<sub>B</sub> ( $M = 3.71, SD = 1.43$ ) to CORT<sub>1</sub> ( $M = 6.01, SD = 2.83; F(1, 28) = 14.07, p = .001, \eta_p^2 = .33$ ). Cortisol levels showed a further increase by CORT<sub>2</sub> ( $M = 7.90, SD = 7.20$ ), and Stress-group participants' cortisol levels were still significantly higher at CORT<sub>2</sub> than at CORT<sub>B</sub>,  $F(1, 28) = 15.16, p = .001, \eta_p^2 = .35$ . Control-group participants, on the other hand, showed a non-significant decrease in cortisol

levels from  $CORT_B$  ( $M = 4.55$ ,  $SD = 5.42$ ) to  $CORT_1$  ( $M = 3.41$ ,  $SD = 2.87$ ;  $p = .126$ ). By  $CORT_2$  ( $M = 2.46$ ,  $SD = 1.99$ ), average cortisol levels in the Control group were significantly lower than at  $CORT_B$ ,  $F(1, 28) = 74.50$ ,  $p < .001$ ,  $\eta_p^2 = .73$ . Thus, the two groups showed an opposite pattern in cortisol reaction across Day 2, with the Stress group displaying the intended increase in cortisol levels due to the manipulation, while the Control group displayed a gradual decrease in cortisol levels.

Between-group analysis of the  $CORT_B$  data detected no significant main effects of Experimental Condition,  $p = .606$ , or of Sex,  $p = .643$ , and no significant Experimental Condition x Sex interaction,  $p = .933$ . Thus, there were no significant between-group differences in cortisol levels at the start of the testing process.

Between-group analysis of  $CORT_1$  data detected a significant main effect of Experimental Condition,  $F(1, 58) = 16.91$ ,  $p < .001$ ,  $\eta_p^2 = .24$ , but no significant main effect of Sex,  $p = .155$ , and no significant Experimental Condition x Sex interaction effect,  $p = .638$ . At this time point, the Stress group ( $M = 6.01$ ,  $SD = 2.83$ ) had significantly higher cortisol levels than the Control group ( $M = 3.41$ ,  $SD = 2.87$ ).

Between-group analysis of  $CORT_2$  data detected a significant main effect of Experimental Condition,  $F(1, 58) = 32.41$ ,  $p < .001$ ,  $\eta_p^2 = .37$ , but no significant main effect of Sex,  $p = 0.428$ , and no Experimental Condition x Sex interaction,  $p = 0.521$ . Participants in the Stress group ( $M = 7.90$ ,  $SD = 7.20$ ) continued to show significantly higher cortisol levels than those in the Control group ( $M = 2.46$ ,  $SD = 1.99$ ).

The current results show the intended success of the manipulation. Not only did participants in the Stress group show the intended increase in cortisol levels following the manipulation, but their levels were significantly higher than those in the Control group at both post-manipulation measurement points. In contrast, participants in the Control group did not display an increase in cortisol levels across the Day 2 test session.

**Heart rate.** Due to a violation of assumption of sphericity,  $\chi^2(2) = 22.18$ ,  $p < .001$ , it was necessary to use a Greenhouse-Geisser degrees of freedom correction ( $\epsilon = 0.75$ ).

The analysis detected statistically significant main effects of Sex,  $F(1, 55) = 8.46$ ,  $p = .005$ ,  $\eta_p^2 = .13$ , and of Time,  $F(1.50, 82.29) = 310.56$ ,  $p < .001$ ,  $\eta_p^2 = .85$ , but no significant main effect of Experimental Condition,  $p = .601$ . The analysis also detected significant Experimental Condition x Time,  $F(1.50, 82.92) = 10.70$ ,  $p < .001$ ,  $\eta_p^2 = .16$ , and Sex x Time,  $F(1.50, 82.92) = 3.68$ ,  $p = .042$ ,  $\eta_p^2 = .06$ , interactions. The analysis did not detect statistically significant Experimental Condition x Sex,  $p = .127$ , and Experimental Condition x Sex x Time,  $p = .603$ , interactions. These results suggest that Sex and Time were the main

factors influencing participants' HR. Female participants (irrespective of experimental condition) showed higher HR levels ( $M = 83.79$ ,  $SD = 11.61$ ) than male participants ( $M = 75.11$ ,  $SD = 12.06$ ) across the Day 2 test session. The experimental manipulation, on its own, did not have an influence on participants' HRs, but instead seemed to have an influence only in the interaction with Time. To investigate the exact nature of these influences, I examined each of the contributing factors separately. Figure 19 shows the fluctuations in HR levels for each Experimental Condition across Time.

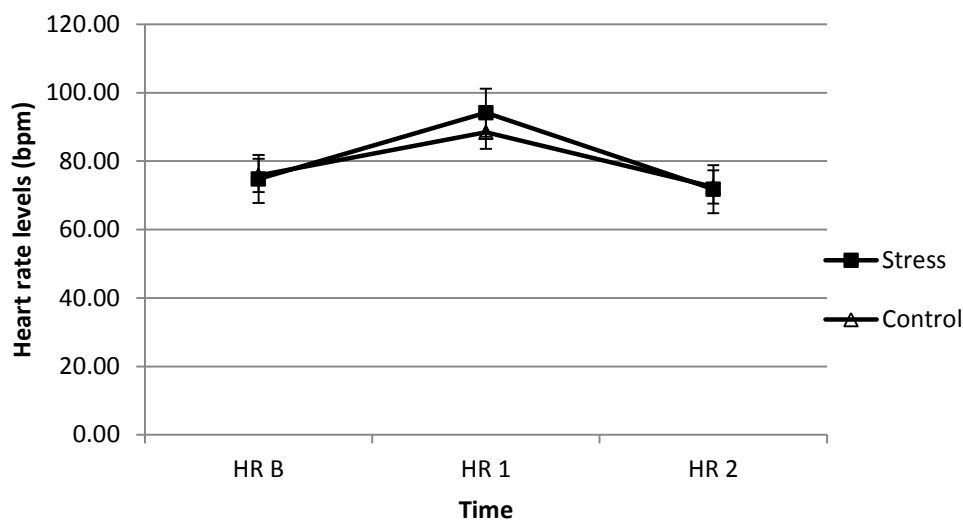


Figure 19. Changes in heart rate (HR) levels on Day 2 for the combined Stress and combined Control groups. Error bars indicate standard error of means. Subscripts represent measurement point (e.g., HR<sub>B</sub> is the first heart rate measurement point, or baseline).

Within-group analysis of HR data across the three measurement points showed that the Stress group displayed a significant increase from HR<sub>B</sub> ( $M = 74.78$ ,  $SD = 11.72$ ) to HR<sub>1</sub> ( $M = 94.13$ ,  $SD = 15.06$ ;  $F(1, 29) = 156.57$ ,  $p < .001$ ,  $\eta_p^2 = .84$ ). However, by HR<sub>2</sub> ( $M = 71.78$ ,  $SD = 11.54$ ), levels of the Stress group had returned to below HR<sub>B</sub>,  $F(1, 29) = 19.28$ ,  $p < .001$ ,  $\eta_p^2 = .40$ . The Control group also displayed a significant increase in heart rate from HR<sub>B</sub> ( $M = 75.80$ ,  $SD = 12.06$ ) to HR<sub>1</sub> ( $M = 88.43$ ,  $SD = 14.75$ ;  $F(1, 29) = 141.95$ ,  $p < .001$ ,  $\eta_p^2 = .84$ ). By HR<sub>2</sub> ( $M = 72.45$ ,  $SD = 11.40$ ), the Control group showed a similar drop to below HR<sub>B</sub> levels,  $F(1, 29) = 16.40$ ,  $p < .001$ ,  $\eta_p^2 = .37$ . These data suggest that participants in both groups showed an increase in HR during the manipulation, and both groups' HR levels returned to significantly below baseline levels by the end of the Day 2 test session.

Between-group analysis of the HR<sub>B</sub> data detected a significant main effect of Sex,  $F(1, 58) = 5.36, p = .024, \eta_p^2 = .09$ , but no significant main effect of Experimental Condition,  $p = .783$ , and no significant Experimental Condition x Sex interaction,  $p = .132$ . At HR<sub>B</sub>, female participants ( $M = 78.61, SD = 10.33$ ) had a higher average HR than male participants ( $M = 71.83, SD = 12.38$ ). This result implies that further sex-based comparisons of HR following the experimental manipulation should be interpreted with caution.

Between-group analysis of HR<sub>1</sub> data also detected a significant main effect of Sex,  $F(1, 58) = 9.51, p = .003, \eta_p^2 = .15$ , but no significant main effect of Experimental Condition,  $p = .105$ , and no Experimental Condition x Sex interaction,  $p = .282$ . Female participants ( $M = 96.73, SD = 14.58$ ), independent of experimental condition, continued to show higher HR levels than their male counterparts ( $M = 85.74, SD = 13.62$ ). The analysis detected no significant difference in average HR between the Stress group ( $M = 94.13, SD = 15.06$ ) and the Control group ( $M = 88.43, SD = 14.75$ ) at HR<sub>1</sub>.

Between-group analysis of the participants' heart rate levels at HR<sub>2</sub> showed similar trends. Again, the analysis detected a significant main effect of Sex,  $F(1, 58) = 8.49, p = .005, \eta_p^2 = .13$ , but no significant main effect of Experimental Condition,  $p = .875$ , and no Experimental Condition x Sex interaction,  $p = .074$ . Female participants ( $M = 76.01, SD = 10.18$ ) continued to show higher heart rate levels than their male counterparts ( $M = 68.07, SD = 11.30$ ), irrespective of Experimental Condition.

These results indicate that participants in both the Stress and Control groups displayed an increase in HR during the experimental manipulation, and all groups returned to similar HR levels by the end of the session. Women, irrespective of experimental condition, showed a higher HR than men across the three measurement points on Day 2.

**Galvanic skin response.** Due to violation of the assumptions of normality and sphericity, it was necessary to perform transformations on the data. Log transformations corrected both violations.

The analysis detected significant main effects of Experimental Condition,  $F(1, 55) = 5.44, p = .023, \eta_p^2 = .09$ , and of Time,  $F(2, 110) = 53.26, p < .001, \eta_p^2 = .49$ , but no significant main effect of Sex,  $p = .207$ . The analysis also detected a statistically significant Experimental Condition x Time interaction,  $F(2, 110) = 14.26, p < .001, \eta_p^2 = .21$ , but no significant Experimental Condition x Sex,  $p = .347$ , Sex x Time interaction,  $p = .885$ , or Experimental Condition x Sex x Time,  $p = .296$ , interactions. These results suggest that only Experimental Condition and Time influenced participants' GSR. To investigate the exact nature of these influences further, I examined each of the contributing factors separately.

Figure 20 shows the fluctuations in skin response for each Experimental Condition across the Time.

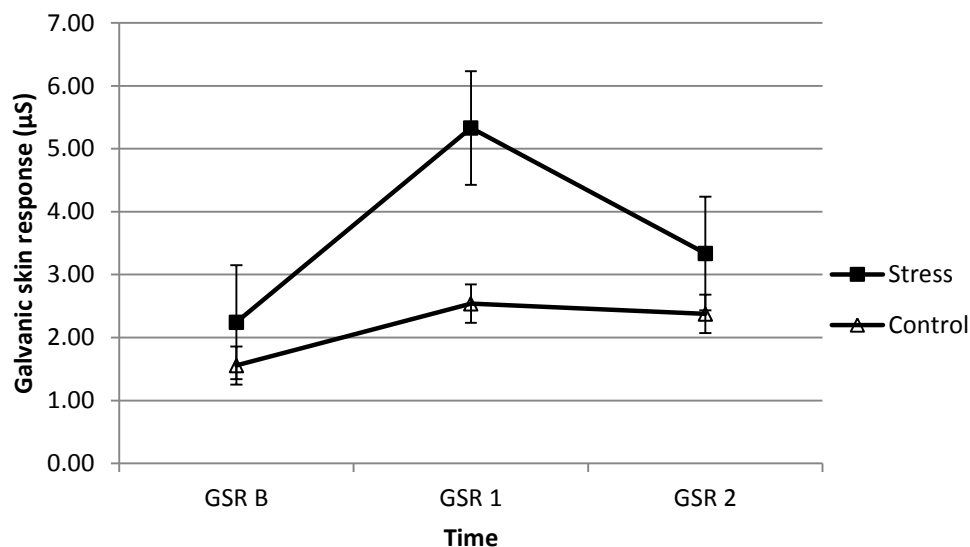


Figure 20. Changes in galvanic skin response (GSR) levels on Day 2 for the combined Stress and combined Control groups. Error bars indicate standard error of means. Subscripts represent measurement point (e.g., GSR<sub>B</sub> is the first GSR measurement point, or baseline).

Within-group analysis of data across the three measurement points revealed that the Stress groups showed a significant increase in skin response from GSR<sub>B</sub> ( $M = 2.24$ ,  $SD = 2.18$ ) to GSR<sub>1</sub> ( $M = 5.33$ ,  $SD = 3.10$ ;  $F(1, 29) = 108.30$ ,  $p < .001$ ,  $\eta_p^2 = .79$ ). By GSR<sub>2</sub> ( $M = 3.34$ ,  $SD = 2.62$ ), levels of the Stress groups were still significantly higher than GSR<sub>B</sub> levels,  $F(1, 29) = 27.11$ ,  $p < .001$ ,  $\eta_p^2 = .48$ . The Control groups showed a similar pattern of data: There was a significant increase in skin response from GSR<sub>B</sub> ( $M = 1.56$ ,  $SD = 0.97$ ) to GSR<sub>1</sub> ( $M = 2.54$ ,  $SD = 1.94$ ;  $F(1, 28) = 23.68$ ,  $p < .001$ ,  $\eta_p^2 = .46$ ). By GSR<sub>2</sub> ( $M = 2.38$ ,  $SD = 1.87$ ), the Control groups' skin response levels were still significantly higher than their GSR<sub>B</sub> levels,  $F(1, 28) = 9.87$ ,  $p = .004$ ,  $\eta_p^2 = .26$ . Hence, both groups showed an increase in skin response during the manipulation, and both groups' GSR levels remained higher than baseline levels for the remainder of the study.

Between-group analysis detected that, at GSR<sub>B</sub> there were no significant main effects of Experimental Condition,  $p = .471$ , or of Sex,  $p = .307$ , and that there was no Experimental Condition x Sex interaction,  $p = .428$ .

Between-group analysis also detected that, at GSR<sub>1</sub> there was a significant main effect of Experimental Condition,  $F(1, 58) = 11.60$ ,  $p < .001$ ,  $\eta_p^2 = .26$ , in the absence of a main

effect of Sex,  $p = .161$ , and of an Experimental Condition x Sex interaction,  $p = 0.706$ . At this time point, the Stress groups ( $M = 5.33$ ,  $SD = 3.10$ ) showed significantly raised GSR levels relative to the Control groups ( $M = 2.54$ ,  $SD = 1.94$ ).

Finally, between-group analysis detected that, at GSR<sub>2</sub>, there were no significant main effects of Experimental Condition,  $p = .142$ , or of Sex,  $p = .281$ , and no significant Experimental Condition x Sex interaction,  $p = .160$ .

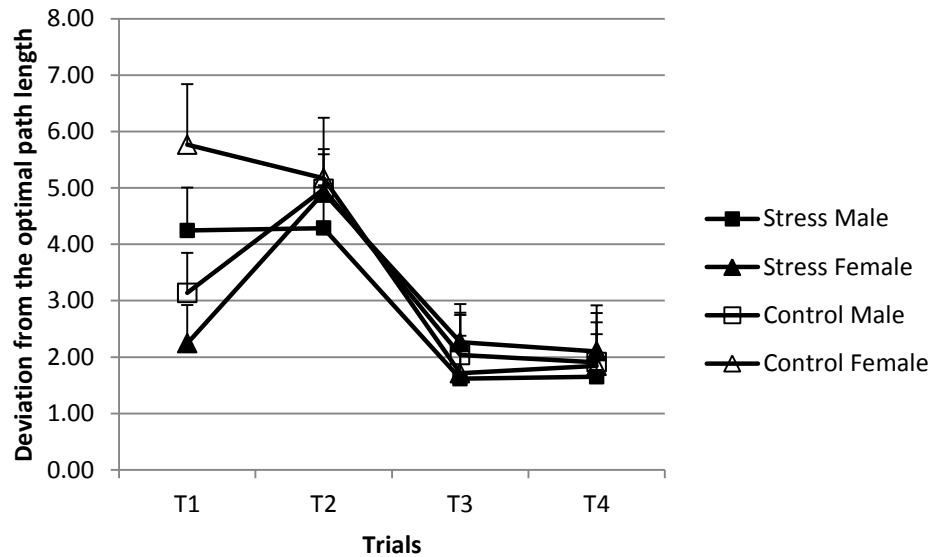
In summary, analysis of the GSR data showed that both the Stress and Control groups displayed an increase in GSR levels during the manipulation (with the Stress groups showing a significantly greater increase than the Control groups). By the end of the testing session on Day 2, there were no significant between-group differences, and GSR levels remained significantly higher than at baseline for both groups.

### CG Arena

The following series of analyses were conducted to: (a) establish that all participant groups showed equal competency in learning the locations of the targets in the CG Arena rooms, and (b) establish the effects of the experimental manipulation on memory retrieval for the locations of those targets, as well as for the pictures and layouts of the pictures in the CG Arena rooms.

**Training Phase: Visible-target training trials.** As was the case in Study A, the prediction here was that there would be no statistically significant between-group differences in path length across the four trials in the training room on Day 1 of testing. A  $2 \times 2 \times 4$  (Experimental Condition [Stress versus Control] x Sex [male versus female] x Trial [training trials 1-4]) repeated-measures ANOVA was used to compare differences in deviation from the optimal path length across trials. Figure 21 depicts the mean deviation from the optimal path length for all groups across the training trials. Visual scrutiny of the figure suggests no between-group differences on any individual trial, but steady improvement of all participants across trials.

Due to violation of the assumption of normality, it was necessary to perform log transformations on the data. Subsequent analyses confirmed the visual impression related above: The analysis detected a significant main effect of Trial,  $F(3, 96) = 9.52$ ,  $p < .001$ ,  $\eta_p^2 = .23$ , in the absence of significant main effects of Experimental Condition,  $p = .876$ , and Sex,  $p = .939$ . The analysis also detected no significant Experimental Condition x Trial,  $p = .073$ , Experimental Condition x Sex,  $p = .939$ , Sex x Trial,  $p = .625$ , and Experimental Condition x Sex x Stage of Trial interactions,  $p = 0.483$ .



*Figure 21.* Mean deviation from the optimal path length for all experimental groups across the Visible target training trials. Error bars indicate standard error of means.

In summary, these data suggest that, on the average, participants in all groups showed learning across the training trials. However, no between-group differences were apparent, signifying that no group was at an advantage or disadvantage leading into the set of acquisition trials.

**Acquisition Phase: Invisible-target acquisition trials.** The following series of analyses sought to establish whether all four experimental groups showed a similar degree of learning across the six acquisition trials in each of the three CG Arena experimental rooms. In addition, the final trial of the acquisition phase (Trial 6) was analysed separately in order to determine whether all groups were performing with relatively equal efficiency by the end of this set of trials.

**Trials 1–6.** Figure 22 shows the mean deviation from the optimal path length for each of the four experimental groups on each of the acquisition trials in CG Arena experimental rooms. To determine if any of the experimental groups showed a distinct performance advantage or disadvantage in any of the CG Arena rooms, three separate 2 x 2 x 6 (Experimental Condition [Stress versus Control] x Sex [male versus female] x Trial [acquisition trials 1-6]), repeated-measures ANOVAs (one for the data from each of the rooms) were used to compare differences in path length deviation from optimal.

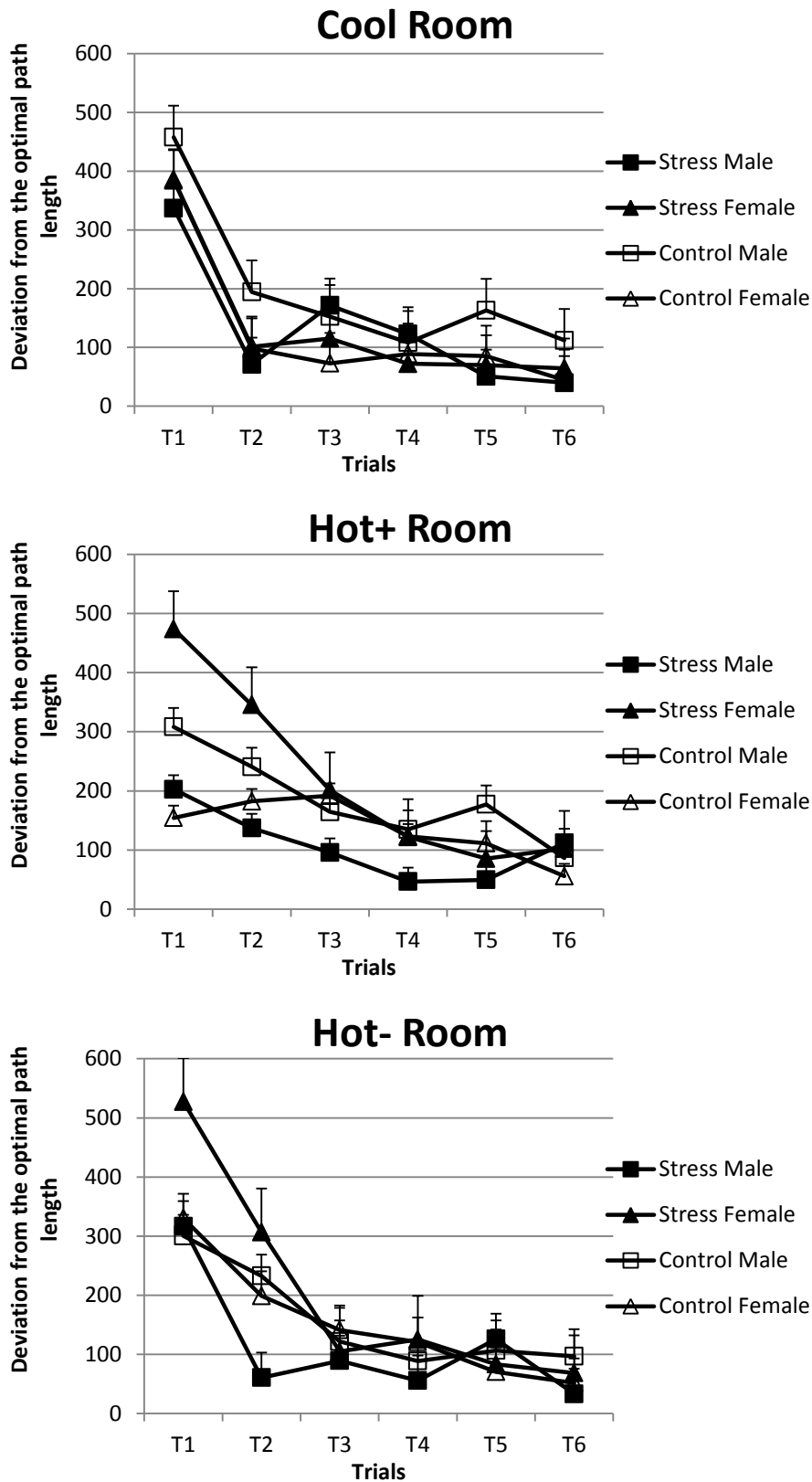


Figure 22. Mean deviation from the optimal path length for the acquisition trials in the Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. Error bars indicate standard error of means.

*Cool room.* Due to violation of the assumption of sphericity,  $\chi^2(14) = 149.01$ ,  $p < .001$ , it was necessary to use a Greenhouse-Geisser degrees of freedom correction ( $\epsilon = 0.50$ ). Subsequent analyses detected a significant main effect of Trial,  $F(2.47, 138.49) = 8.21$ ,  $p < .001$ ,  $\eta_p^2 = .23$ , in the absence of significant main effects of Experimental Condition,  $p = .414$ , and Sex,  $p = .418$ . The analysis also detected no significant Experimental Condition x Trial,  $p = .426$ , Experimental Condition x Sex,  $p = .343$ , Sex x Trial,  $p = .598$ , and Experimental Condition x Sex x Trial interaction effects,  $p = .426$ .

In summary, this analysis showed only the expected change in path length across the six acquisition trials. Decreasing path length across trials, with no between-group differences, indicates that all participants, regardless of experimental condition or sex, were able to find the target more efficiently as the trials proceeded in the Cool room.

*Hot Appetitive room.* Due to violation of the assumption of sphericity,  $\chi^2(14) = 80.51$ ,  $p < .001$ , it was necessary to use a Greenhouse-Geisser degrees of freedom correction ( $\epsilon = 0.64$ ). Subsequent analyses detected a significant main effect of Trial,  $F(3.20, 179.36) = 8.21$ ,  $p < .001$ ,  $\eta_p^2 = .13$ , in the absence of significant main effects of Experimental Condition,  $p = .817$ , and Sex,  $p = .368$ . The analysis also detected a significant Experimental Condition x Sex interaction,  $F(1, 56) = 5.92$ ,  $p = .028$ ,  $\eta_p^2 = .08$ , but no significant Experimental Condition x Trial,  $p = .20$ , Experimental Condition x Sex,  $p = .058$ , Sex x Trial,  $p = .611$ , and Experimental Condition x Sex x Trial interaction effects,  $p = .123$ .

In summary, this analysis showed the expected change in path length, indicating progressively more efficient location of the hidden target, across trials. Interestingly, this time there was a significant Experimental Condition x Sex interaction. Across the six acquisition trials, the Stress Male group ( $M = 104.91$ ,  $SD = 138.21$ ) performed better than the Control Female group ( $M = 136.53$ ,  $SD = 184.83$ ) and the Control Male group ( $M = 186.53$ ,  $SD = 271.66$ ), with the Stress Female group ( $M = 222.19$ ,  $SD = 263.01$ ) performing worst. However, Bonferroni post hoc comparisons failed to confirm significant differences between groups (all  $p$ 's  $> .176$ ). Nevertheless, this superior learning performance of the Stress Male group in comparison to the Stress Female group may have an influence on the recall of the Hot Appetitive room, and thus the results of the recall phase must be interpreted cautiously.

*Hot Defensive Room.* Due to violation of the assumption of sphericity,  $\chi^2(14) = 122.02$ ,  $p < .001$ , it was once again necessary to use a Greenhouse-Geisser degrees of freedom correction ( $\epsilon = 0.46$ ). Subsequent analyses detected a significant main effect of Trial,  $F(2.38, 133.07) = 16.37$ ,  $p < .001$ ,  $\eta_p^2 = .23$ , in the absence of significant main effects of Experimental Condition,  $p = .994$ , or Sex,  $p = .225$ . The analysis detected no significant

Experimental Condition x Trial,  $p = .435$ , Experimental Condition x Sex,  $p = .130$ , Sex x Trial,  $p = .243$ , and Experimental Condition x Sex x Trial interaction effects,  $p = .311$ .

In summary, similar to performance in the other two rooms, all groups showed a significant decrease in deviation from the optimal path length across the trials (see Figure 22), which suggests that they found the hidden target with increasing efficiency. In this room, none of the four groups showed a distinct advantage or disadvantage in terms of learning the location of the hidden target.

**Trial 6.** To determine whether all groups could find the location of the hidden target with relatively equal efficiency by the end of the set of acquisition trials, I analysed the data from the final trial (Trial 6) in each of the CG Arena rooms. First, Trial 6 performance in the three rooms was analyzed using a 2 x 2 x 3 (Experimental Condition [Stress versus Control] x Sex [male versus female] x Room [Cool versus Hot Appetitive versus Hot Defensive]) repeated-measures ANOVA. Second, Trial 6 performance in each room was analysed separately using a 2 x 2 (Experimental Condition [Stress versus Control] x Sex [male versus female]) ANOVA. Table 15 provides descriptive statistics for each group's Trial 6 performance in each of the CG Arena rooms.

Table 15

*Descriptive Statistics for Performance on Trial 6 in Each CG Arena Room (N = 60)*

Room	Group			
	Stress		Control	
	Men (n = 15)	Women (n = 15)	Men (n = 15)	Women (n = 15)
Cool	39.75 (87.68)	64.43 (67.86)	112.06 (226.14)	44.58 (50.14)
Hot Appetitive	111.94 (230.81)	102.24 (137.17)	86.72 (157.00)	55.77 (97.99)
Hot Defensive	33.29 (46.57)	68.50 (127.28)	96.62 (144.27)	51.70 (52.51)

*Note.* Data are  $M (SD)$  for deviation from optimal path length.

Due to violation of the assumption of sphericity,  $\chi^2(2) = 15.84, p < .001$ , it was necessary to use a Greenhouse-Geisser degrees of freedom correction ( $\epsilon = 0.80$ ). The first analysis, comparing performance across the three rooms, did not detect significant main effects of Room,  $p = .292$ , Experimental Condition,  $p = .869$ , or Sex,  $p = .574$ . That analysis also detected no significant Room x Experimental Condition,  $p = .186$ , Room x Sex,  $p = .839$ , Experimental Condition x Sex,  $p = .287$ , and Room x Experimental Condition x Sex interaction effects,  $p = .245$ .

A second set of analyses aimed to determine whether all groups learned the location of the target with relatively equal efficiency in each of three CG Arena rooms. Analysis of the Cool room data did not detect significant main effects of Experimental Condition,  $p = .352$ , or Sex,  $p = .433$ . The analysis also detected no significant Experimental Condition x Sex interaction,  $p = .155$ .

Analysis of the Hot Appetitive room data did not detect significant main effects of Experimental Condition,  $p = .417$ , or Sex,  $p = .598$ . The analysis also detected no significant Experimental Condition x Sex interaction,  $p = .708$ . Importantly, the significant across-trials difference between the Stress Male and Stress Female groups in the Hot Appetitive room was not apparent on the final trial in the room.

Finally, analysis of the Hot Defensive room data detected no significant main effects of Experimental Condition,  $p = .384$ , or Sex,  $p = .856$ . The analysis also detected no significant Experimental Condition x Sex interaction,  $p = .137$ .

In summary, these analyses suggest that all groups learned the location of the target with relatively equal efficiency by the final trial in each of the three CG Arena rooms.

**Recall Phase.** The following series of analyses were conducted in order to establish the effects of the experimental manipulation on recall for the visual and spatial elements of the CG Arena rooms to which the participants had been exposed on the previous day. First, I compared recall performance for the three rooms using a 2 x 2 x 3 (Experimental Condition [Stress versus Control] x Sex [male versus female] x Room [Cool versus Hot Defensive versus Hot Appetitive]) repeated-measures ANOVA. Second, I analyzed the data from each room separately using a 2 x 2 (Experimental Condition [Stress versus Control] x Sex [male versus female]) ANOVA. Bonferroni pairwise comparisons further analyzed significant main effects. Table 16 provides descriptive statistics for all the relevant measures here.

**Recall trial.** Figure 23 depicts each group's performance on the first recall trial in each of the CG Arena rooms. The repeated-measures ANOVA analysis detected no significant main effects of Room,  $p = .829$ , Experimental Condition,  $p = .320$ , or Sex,  $p = .720$ . That analysis also detected no significant Room x Sex,  $p = .278$ , Room x Experimental Condition,  $p = .426$ , Experimental Condition x Sex,  $p = .737$ , or Room x Experimental Condition x Sex interaction effects,  $p = .793$ .

Table 16  
*Descriptive Statistics for Recall Performance in each of the CG Arena rooms (N = 60)*

Room / Outcome variable	Group			
	Stress		Control	
	Men (n = 15)	Women (n = 15)	Men (n = 15)	Women (n = 15)
<b>Cool Room</b>				
Recall trial	143.13 (199.16)	176.78 (206.43)	253.57 (258.80)	269.89 (247.95)
Dwell time	60.01 (20.74)	65.76 (25.81)	65.32 (25.96)	70.19 (24.35)
ART score	22.60 (5.64)	19.73 (7.09)	20.47 (7.72)	22.53 (5.82)
ORT <i>d'</i> score	1.26 (0.72)	1.31 (0.66)	1.33 (0.65)	1.15 (0.88)
<b>Hot Appetitive Room</b>				
Recall trial	221.62 (300.13)	231.69 (240.61)	218.89 (231.44)	244.36 (225.76)
Dwell time	60.95 (15.50)	63.10 (23.96)	61.90 (20.20)	61.80 (23.37)
ART score	17.93 (5.75)	20.93 (5.42)	22.40 (4.98)	22.80 (5.93)
ORT <i>d'</i> score	1.62 (0.77)	1.64 (0.66)	1.90 (0.62)	1.67 (0.70)
<b>Hot Defensive Room</b>				
Recall trial	261.99 (297.93)	129.34 (149.09)	239.13 (266.62)	194.48 (233.28)
Dwell time	60.94 (29.14)	63.62 (27.39)	59.32 (21.41)	62.99 (29.53)
ART score	21.93 (6.36)	21.47 (4.78)	21.80 (5.00)	17.73 (7.23)
ORT <i>d'</i> score	1.76 (0.77)	1.74 (0.59)	2.02 (0.61)	1.75 (0.69)

Note. Data are *M* (*SD*). The variable Recall trial represents deviations from the optimal path length.

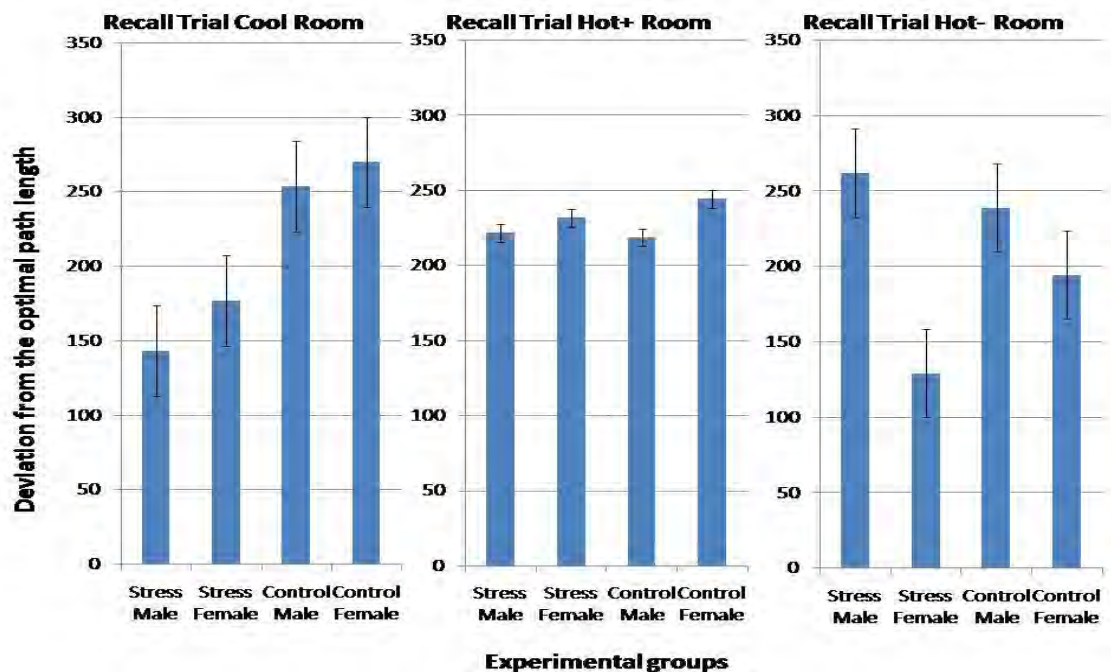


Figure 23. Mean deviation from the optimal path length for recall trials in the Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. Error bars indicate standard error of means.

A second set of analyses aimed to look more closely at between-group differences in each of the three CG Arena rooms separately. Analysis of the Cool room data detected no significant main effects of Experimental Condition,  $p = .091$ ,  $\eta_p^2 = .05$ , or Sex,  $p = .675$ , and no significant Experimental Condition x Sex interaction,  $p = .884$ .<sup>19</sup>

Analysis of the Hot Appetitive room data also detected no significant main effects of Experimental Condition,  $p = .939$ , or Sex,  $p = .785$ , and no significant Experimental Condition x Sex interaction,  $p = .906$ .

The data from the Hot Defensive room violated the assumption of homogeneity of variances. However, I continued with analysis in conventional fashion because ANOVA is a robust test and because all group sizes were equal. The analysis here also detected no significant main effects of Experimental Condition,  $p = .738$ , or Sex,  $p = .163$ , and no significant Experimental Condition x Sex interaction,  $p = .486$ .

In summary, there were no significant within- or between-group differences in performance on the Day 2 recall trial, in any of the three CG arena rooms. In all three rooms, all participants, regardless of experimental condition or sex, re-located with equal efficiency the location at which the target had been hidden in the Day 1 acquisition trials.

**Probe Trial.** The series of analyses described in this section sought to describe the effects of the experimental manipulation on recall of the hidden target's location in the CG Arena rooms during the second recall trial. This trial was a probe trial where the target (unknown to participants) was absent from the room. The key outcome variable, *dwelt time*, was calculated as the proportion of time that the participants spent searching for the hidden target in the quadrant of the room where it had been located (in this case, the southwest quadrant).

Figure 24 depicts each group's performance on the probe trial in each of the three CG Arena rooms. A repeated-measures ANOVA detected no significant main effects of Room,  $p = .574$ , Experimental Condition,  $p = .789$ , or Sex,  $p = .479$ . The analysis also detected no significant Room x Experimental Condition,  $p = .702$ , Room x Sex,  $p = .854$ , Experimental Condition x Sex,  $p = .936$ , or Room x Experimental Condition x Sex interactions,  $p = .978$ .

To examine between-group differences in dwell time more closely, I analyzed performance in each of the three CG Arena rooms separately. Analysis of the Cool room data detected no significant main effects of Experimental Condition,  $p = .441$ , or Sex,  $p = .401$ , and no significant Experimental Condition x Sex interaction,  $p = .945$ .

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<sup>19</sup>Cortisol responders versus control participants analyses (presented below and in Appendix J) detected a borderline significant main effect of Experimental Condition.

Analysis of the Hot Appetitive room data also detected no significant main effects of Experimental Condition,  $p = .974$ , or Sex,  $p = .852$ , and no significant Experimental Condition x Sex interaction,  $p = .836$ .

Similarly, analysis of the Hot Defensive room data detected no significant main effects of Experimental Condition,  $p = .873$ , or Sex,  $p = .651$ , and no significant Experimental Condition x Sex interaction,  $p = .944$ .

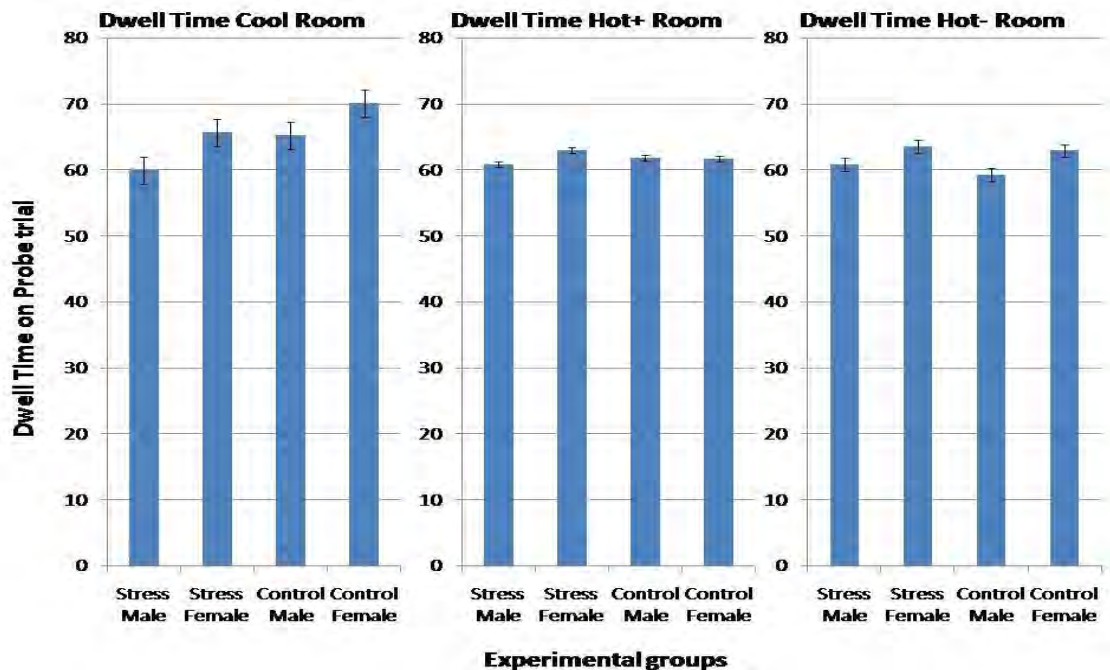


Figure 24. Mean proportion of dwell time in the target (SW) quadrant on the probe trial in the Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. Error bars indicate standard error of means.

**ORT Score.**<sup>20</sup> The series of analyses described in this section sought to describe the effects of the experimental manipulation on recognition memory for the pictures that hung on the walls of the three CG Arena rooms.

Recognition performance was assessed, primarily, by converting raw ORT scores to  $d'$  prime ( $d'$ ) scores. The latter were calculated by subtracting the number of “hits” (H; pictures correctly identified as having been in the CG Arena rooms) from the number of “false alarms” (FA; pictures incorrectly identified as having been in the CG Arena rooms). The formula was  $d' = z(\text{FA}) - z(\text{H})$ , with bigger  $d'$  values indicating greater discrimination between the original and distracter stimuli, and therefore better recognition performance. For perfect hit or false positive rates (1 or 0 respectively), the formula  $1 - 1/(2N)$  was used to

<sup>20</sup>Although the ORT data is presented under the title, “Recall phase”, it is a recognition (not a recall) test.

calculate adjusted hit rates, and the formula  $1/(2N)$  was used to calculate adjusted FA rates. Figure 25 depicts each group's mean ORT  $d'$  score for each of the CG Arena rooms.

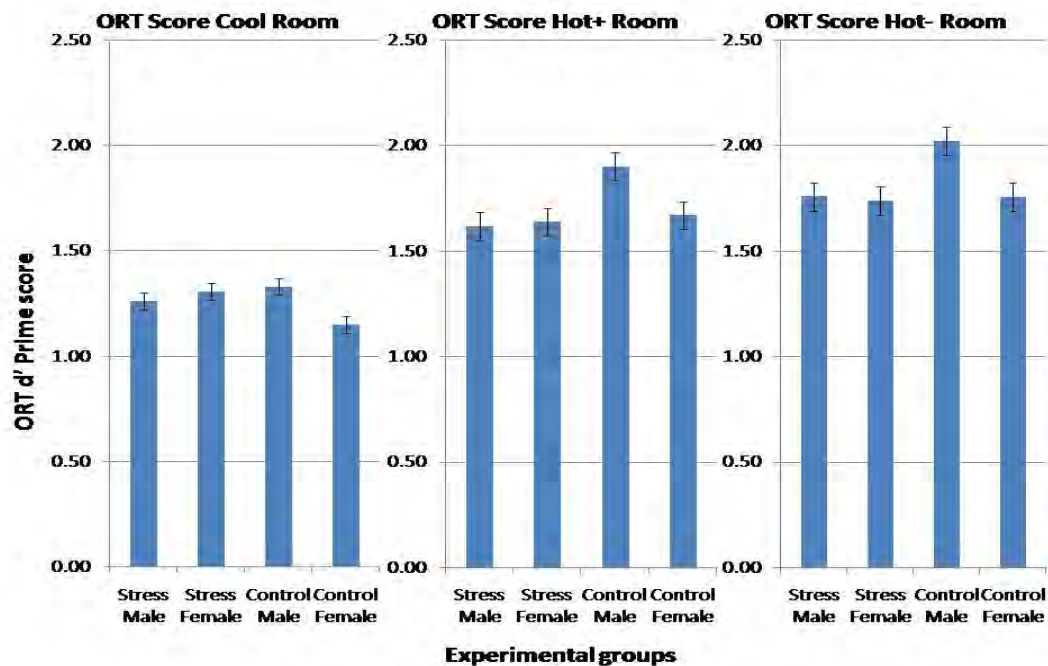


Figure 25. Mean ORT  $d'$  scores for the Cool, Hot Appetitive (Hot+), and Hot Defensive (Hot-) CG Arena rooms. Error bars indicate standard error of means.

A repeated-measures ANOVA, similar to that described in the previous section, detected a significant main effect of Room,  $F(2, 112) = 18.31, p < .001, \eta_p^2 = .25$ , but no significant main effects of Experimental Condition,  $p = .552$ , or Sex,  $p = .462$ . The analysis also detected no significant Room x Experimental Condition,  $p = .518$ , Room x Sex,  $p = .928$ , Experimental Condition x Sex,  $p = .399$ , or Room x Experimental Condition x Sex interactions,  $p = .998$ .

This pattern of data, and the means depicted in Table 16 and Figure 25, suggests that participants, regardless of their sex or the experimental condition to which they were exposed, showed the best recognition for the pictures that had been in the Hot Defensive room ( $M = 1.81, SD = 0.66$ ), followed by those that had been in the Hot Appetitive room ( $M = 1.71, SD = 0.68$ ), and then followed by those that had been in the Cool room ( $M = 1.26, SD = 0.72$ ). A series of Bonferroni pairwise comparisons detected significant differences between ORT  $d'$  scores for the Hot Defensive room and the Cool room ( $p < .001$ ), and between the Hot Appetitive room and the Cool room ( $p < .001$ ). The analysis did not detect a significant difference between ORT  $d'$  scores for the Hot Defensive room and those for the Hot Appetitive room ( $p = .563$ ).

To examine between-group differences in recognition more closely, I analysed  $d'$  scores in each of the three CG Arena rooms separately. Analysis of the Cool room data detected no significant main effect of Experimental Condition,  $p = .819$ , or of Sex,  $p = .724$ , and no significant Experimental Condition x Sex interaction,  $p = .550$ .

Similarly, analysis of the Hot Appetitive room data detected no significant main effect of Experimental Condition,  $p = .381$ , or of Sex,  $p = .561$ , and no significant Experimental Condition x Sex interaction,  $p = .482$ .

Again similarly, analysis of the Hot Defensive room data detected no significant main effect of Experimental Condition,  $p = .421$ , or of Sex,  $p = .412$ , and no significant Experimental Condition x Sex interaction,  $p = .487$ .

In summary, analyses of ORT  $d'$  scores indicated that all participants' recognition of pictures previously seen in the CG Arena was better for arousing stimuli (irrespective of the valence of the picture) than for neutral stimuli.

**ART Score.** The series of analyses described in this section sought to describe the effects of the experimental manipulation on cued-recall for the spatial layout of the pictures that had hung on the walls of each of the three CG Arena rooms. Figure 26 depicts each group's mean ART displacement score for each of the CG Arena rooms. Lower scores indicate better performance in reconstructing the spatial layout of the rooms.<sup>21</sup>

A repeated-measures ANOVA detected no significant main effects of Room,  $p = .859$ , Experimental Condition,  $p = .575$ , or Sex,  $p = .729$ . The analysis also detected no significant Room x Experimental Condition,  $p = .068$ , Room x Sex,  $p = .194$ , Experimental Condition x Sex,  $p = .820$ , or Room x Experimental Condition x Sex interactions,  $p = .105$ .

Analysis of the Cool room data detected no significant main effect of Experimental Condition,  $p = .846$ , or of Sex,  $p = .816$ , and no significant Experimental Condition x Sex interaction,  $p = .155$ .

A similar analysis of the Hot Appetitive room data detected a significant main effect of Experimental Condition,  $F(1, 56) = 4.92$ ,  $p = .031$ ,  $\eta_p^2 = .08$ , but no significant main effect of Sex,  $p = .239$ , and no significant Experimental Condition x Sex interaction,  $p = .367$ . These analyses suggested that participants in the Stress group ( $M = 19.43$ ,  $SD = 5.70$ ) showed a significantly better recall for the spatial layout of the pictures in this room than the Control group ( $M = 22.60$ ,  $SD = 5.39$ ).

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<sup>21</sup>The ART displacement score is introduced in Study A (pg. 62) and a worked example is presented in Appendix F.

Finally, analysis of the Hot Defensive room data detected no significant main effect of Experimental Condition,  $p = .212$ , or of Sex,  $p = .144$ , and no significant Experimental Condition x Sex interaction,  $p = .245$ .

In summary, the only significant performance difference in ART scores was detected in the Hot Appetitive room. In that room, participants in the Stress group showed better recognition memory for the spatial layout of the room than did their counterparts in the Control group.

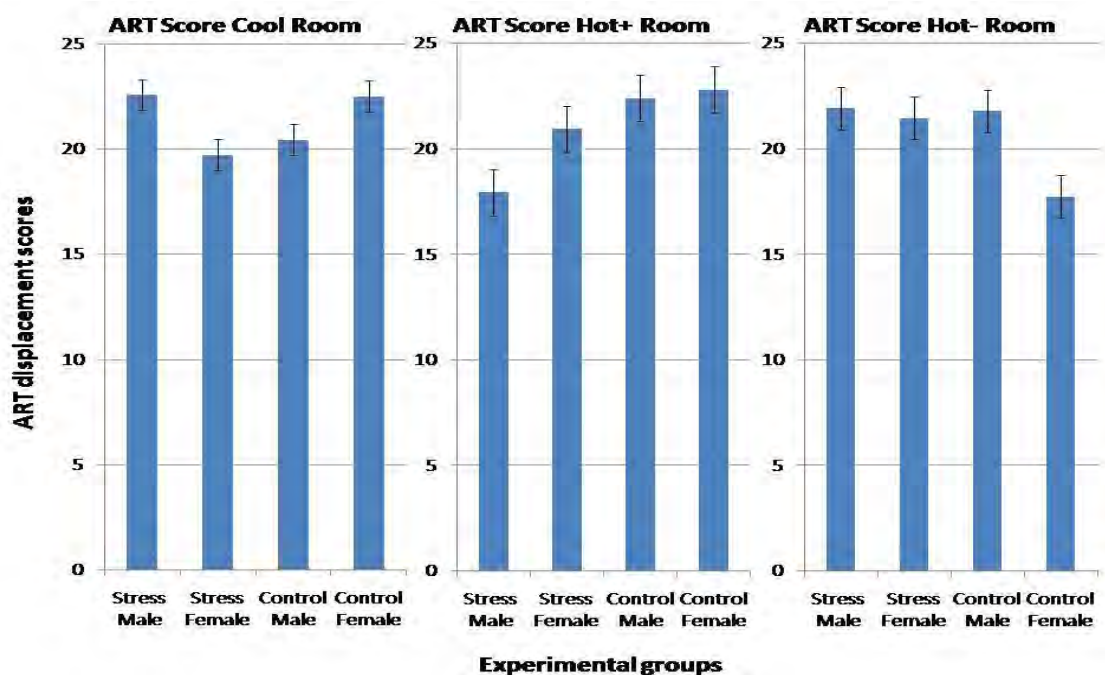


Figure 26. Mean ART displacement scores for the Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. Error bars indicate standard error of means.

### Verbal Paired Associates Test

Score on each of the cued recall trials of the VPA task was calculated as the number of word pairs recalled correctly. Slight variations of the original words were scored as correct (e.g., “cry” for “cries”). To account for possible within- and between-subject variance in initial learning of the word pairs, the score on the cued recall task on Day 2 was expressed as the percentage of words remembered in relation to the second (and last) learning trial on Day 1 (Kuhlmann et al., 2005). The final score from this calculation was labelled as the “percentage retained” score for cued-recall.

**Day 1: Immediate recall trials.** To investigate whether there were between-group differences with regard to recall of the word list across the two Day 1 trials, I first used a 2 x 2 x 2 (Experimental Condition [Stress versus Control] x Sex [male versus female] x Trial [VPA recall trials 1 and 2]) repeated-measures ANOVA. Second, I analyzed performance on each trial separately using a 2 x 2 (Experimental Condition [Stress versus Control] x Sex [male versus female]) factorial ANOVA. Table 17 presents descriptive data for the VPA; Figure 27 displays these data graphically.

Table 17

*Descriptive Statistics for Verbal Paired Associates Test Recall and Percentage Retained scores (N = 60)*

Outcome variable	Group			
	Stress		Control	
	Men (n = 15)	Women (n = 15)	Men (n = 15)	Women (n = 15)
Recall trial 1	7.07 (2.99)	7.07 (3.71)	6.13 (2.85)	6.53 (3.50)
Recall trial 2	10.60 (2.59)	10.60 (3.36)	9.93 (2.94)	11.27 (2.71)
Delayed recall trial	7.67 (2.29)	9.00 (3.02)	7.53 (2.36)	8.80 (3.30)
Percentage retained	71.49 (9.36)	86.55 (14.40)	76.85 (15.48)	76.68 (17.21)

*Note.* Data presented are means, with standard deviations in parentheses.

The repeated-measures ANOVA detected a significant main effect of Trial,  $F(1, 56) = 219.53, p < .001, \eta_p^2 = .80$ , in the absence of significant main effects of Experimental Condition,  $p = .630$ , and of Sex,  $p = .569$ . The analysis also detected no significant Trial x Experimental Condition,  $p = .169$ , Trial x Sex,  $p = .379$ , Experimental Condition x Sex,  $p = .569$ , or Trial x Experimental Condition x Sex interactions,  $p = .377$ .

Comparison across the first two trials therefore detected a significant effect of Trial, indicating that all participants, regardless of experimental group, recalled significantly more words on the second recall trial than on the first.

The factorial ANOVA scrutinizing data from the first recall trial detected no significant main effects of Experimental Condition,  $p = .391$ , or of Sex,  $p = .814$ , and no significant Experimental Condition x Sex interaction,  $p = .814$ .

The factorial ANOVA scrutinizing data from the second recall trial also detected no significant main effects of Experimental Condition,  $p = 1.000$ , or of Sex,  $p = .379$ , and no significant Experimental Condition x Sex interaction,  $p = .380$ .

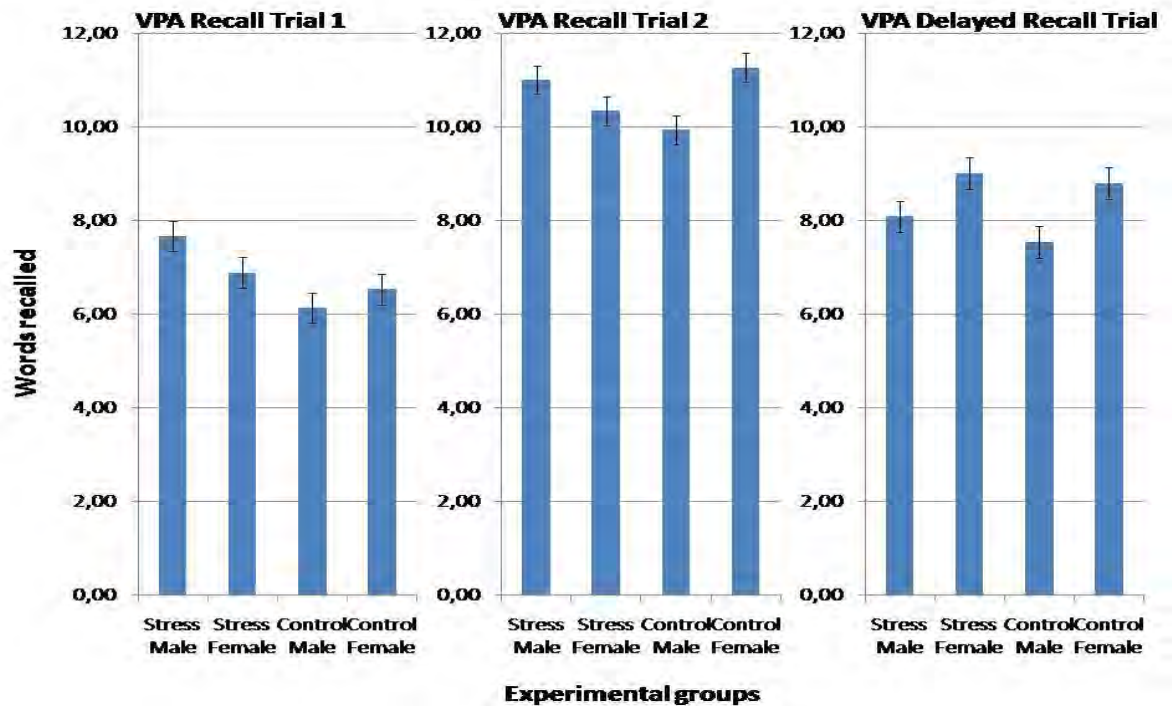


Figure 27. Mean number of words recalled on each trial of the Verbal Paired Associates Test (VPA). Error bars indicate standard error of means.

In summary, analysis of the first two learning trials showed that all participants, regardless of experimental group, benefitted from the second presentation of the word list. On average, participants in all groups recalled a greater number of word pairs after the second presentation of the pairs than after the first. Additionally, there were no other within- or between-group differences detected on either recall trial, suggesting that no group showed a distinct advantage or disadvantage in recalling the previously-presented word pairs.

**Day 2: Recall trial.** To investigate whether there were between-group differences with regard to recall of the word list on the delayed recall trial, I first compared performance on the delayed recall trial (Trial 3) with that on the final Day 1 trial (Trial 2) using a 2 x 2 x 2 (Experimental Condition [Stress versus Control] x Sex [male versus female] x Trial [VPA Trial 2 versus Trial 3]) repeated-measures ANOVA. Second, I analysed performance on Trial 3 only using a 2 x 2 (Experimental Condition [Stress versus Control] x Sex [male versus female]) factorial ANOVA. Table 17 presents the descriptive data for the VPA; Figure 27 displays these data graphically.

The repeated-measures ANOVA detected a significant main effect of Trial,  $F(1, 56) = 128.98, p < .001, \eta_p^2 = .70$ , in the absence of significant main effects of Experimental Condition,  $p = .906$ , and of Sex,  $p = .168$ . The analysis also detected no significant Trial x Experimental Condition,  $p = .689$ , Trial and Sex,  $p = .132$ , Experimental Condition x Sex,  $p =$

.655, or Trial x Experimental Condition x Sex interactions,  $p = .096$ . Taken together with the data presented in Table 17, these analyses suggest that all participants, regardless of Experimental Condition or Sex, recalled significantly fewer word pairs on the final recall trial compared to the second recall trial. Apparently, the 24-hour delay in recall of the word list resulted in all participants recalling fewer words on Trial 3 than on Trial 2.

The second set of analyses investigated whether between-group differences were apparent on Trial 3. The factorial ANOVA detected no significant main effect of Experimental Condition,  $p = .817$ , or of Sex  $p = .075$ , and no significant Experimental Condition x Sex interaction,  $p = .963$ .

In summary, analysis of the delayed recall trial (Trial 3) revealed that participants in all groups showed a decrease in the number of words recalled compared to Trial 2. This result indicates that the 24-hour delay in recall had a detrimental effect on cued-recall memory for the word list; this effect held constant regardless of the participant's sex or the experimental condition. There were no significant within- or between-groups comparisons on recall Trial 2 and on recall Trial 3.

**Percentage retained.** To determine whether between-group differences were apparent after taking into account possible within- and between-subject variance in initial learning of the word pairs, I analysed percentage retained scores using a 2 x 2 (Experimental Condition [Stress versus Control] x Sex [male versus female]) ANOVA. Table 17 presents the relevant descriptive statistics; Figure 28 displays these data graphically.

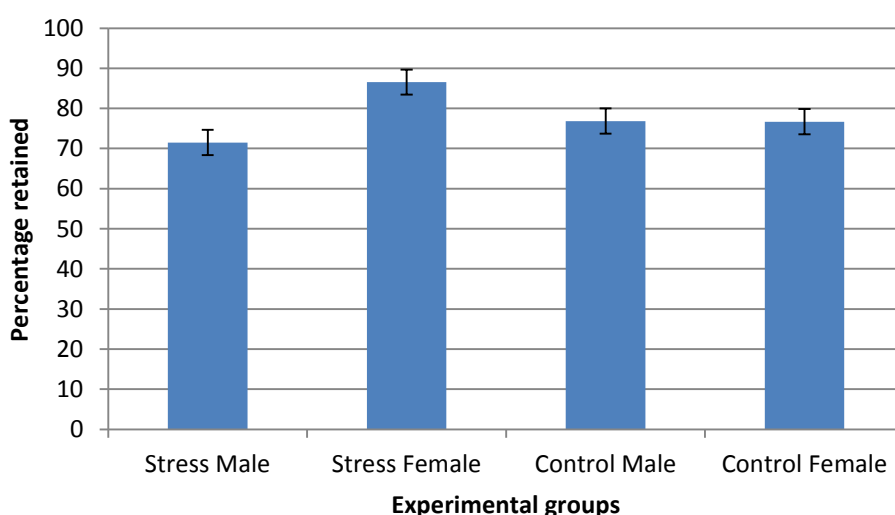


Figure 28. Mean percentage retained scores for the delayed recall trial of the Verbal Paired Associates Test. Error bars indicate standard error of means.

The analysis detected a significant main effect of Sex,  $F(1, 56) = 4.00, p = .050, \eta_p^2 = .07$ , in the absence of a significant main effect of Experimental Condition,  $p = .548$ . The analysis also detected a significant Experimental Condition x Sex interaction,  $F(1, 56) = 4.18, p = .045, \eta_p^2 = .07$ .

Thus, comparison of percentage retained scores revealed that the male groups ( $M = 74.17, SD = 12.86$ ) showed significantly lower scores in comparison to the female groups ( $M = 81.62, SD = 16.38$ ). The female participants therefore retained a greater number of words than the males, regardless of the experimental manipulation.

To explore the significant interaction effect further, I ran a set of Bonferroni post-hoc comparisons. These pairwise analyses detected a significant difference in performance between the Stress Female and Stress Male groups,  $p = .036$ , but no other significant between-group differences ( $ps > .390$ ). Further contrast analyses detected a significant difference between the Stress Female group and the other three groups taken together,  $t(56) = 2.69, p = .010, d = 0.72$ , but not between the Stress Male group and the other three groups taken together,  $p = .052, d = 0.53$ .

In summary, analysis of percentage retained scores revealed that, in general, female participants, irrespective of the experimental condition to which they were assigned, retained and recalled a greater number of words than the male participants. However, this significant effect of sex seems to be driven by the significant interaction effect between stress and sex. That is, the Stress Male and Stress Female groups showed opposing percentage retained scores, with the Stress Female group recalling significantly more word pairs than the Stress Male group. In fact, participants in the Stress Female group recalled, on average, significantly more words than participants in the other three groups taken together. This result suggests that stress may have had an enhancing effect on the recall of word pairs in women exposed to the stressor.

### **Cortisol Responders vs. Control Participants**

This series of analyses compared those participants in the Stress groups who could be classified as cortisol responders (that is, the participants who showed a 2 nmol/l increase, relative to their individual baseline, in cortisol levels either 5 or 35 minutes after the manipulation ended) to control participants. The final size of the responder groups were 11 in the Stress Male group, and 9 in the Stress Female group. The subset of analyses examined group differences in cortisol response, CG Arena performance, and VPA performance.

Statistical analysis of the responder groups versus the control groups mirrored the whole-group analysis presented above.

However, the cortisol responders versus control participants analyses did not uncover any further significant differences from those detected in the whole-group analyses. Therefore, these analyses are presented in full in Appendix J, while three notable results are briefly described below.

First, between-group analysis of the recall trial in the CG Arena Cool room detected a borderline significant main effect of Experimental Condition,  $F(1, 47) = 3.93, p = .053, \eta_p^2 = .08$ , but no significant main effect of Sex,  $p = .312$ , or significant Experimental Condition  $\times$  Sex interaction,  $p = .452$ . On the recall trial in the Cool room, the Stress groups ( $M = 130.93, SD = 152.97$ ) displayed a near-significantly shorter path length than the Control groups ( $M = 261.73, SD = 249.16$ ).

Second, analysis of the ART scores for Hot Appetitive room detected an increase in the difference between the Stress and Control groups seen in the whole-group analysis. Consistent with the previous result, analysis detected a main effect of Experimental Condition,  $F(1, 47) = 5.99, p = .018, \eta_p^2 = .11$ , in the absence of a main effect of Sex,  $p = .146$ , or a significant Experimental Condition  $\times$  Sex interaction,  $p = .227$ . The Stress group ( $M = 18.46, SD = 5.71$ ) showed a better recall of the spatial layout of the pictures in the Hot Appetitive room than the Control group ( $M = 22.60, SD = 5.39$ ). However, the effect size for the difference was greater for the responder group ( $\eta_p^2 = .11$ ) in comparison to whole-group ( $\eta_p^2 = .08$ ).

Finally, analysis of the percentage retained VPA data detected a slightly different pattern to that seen in the whole-group results. Responder analysis showed only a significant interaction effect between Experimental Condition and Sex,  $F(1, 47) = 4.09, p = .049, \eta_p^2 = .08$ , in the absence of a significant main effects of Sex,  $p = .053, \eta_p^2 = .07$ , or Experimental Condition,  $p = .247$ . Therefore, responder analysis did not detect the significant Sex difference that was seen in the whole-group analysis. In addition, contrast analyses detected an increase in the significant differences between the Stress Female group and the other three groups,  $t(47) = 2.69, p = .010, d = 0.78$  and between the Stress Female and Control Female groups,  $t(47) = 2.17, p = .035, d = 0.63$ . These latter differences suggest that the significant difference seen between the Stress Female group and the other three groups may have strengthened in the cortisol responder analysis (signified by a slightly greater effect size,  $d = 0.78$ ), in comparison to the whole-group analysis ( $d = 0.72$ ).

## Discussion

The present study aimed to determine the effects of stress on retrieval of previously learned visual and spatial information. In addition, it also aimed to determine what influence emotion arousal, of varying valence, had on the quality of the retrieved memory. In specific, I tested the following hypotheses:

- 1) Overall, elevated cortisol levels will have an impairing effect on memory retrieval.
- 2) Memory for the different rooms will be influenced by the arousal content of the pictures used as landmarks in the CG Arena.
- 3) Women will, relative to men, display inferior spatial memory.

To explore these questions, 60 participants learned the location of a target in the three CG Arena rooms that had been created and validated in an earlier study (see Study A). The navigational landmarks used in these rooms (i.e., the pictures on the walls of the rooms) had all been rated by a separate participant sample as being significantly different in terms of valence and arousal qualities (see Appendix A).

Twenty-four hours after having been exposed to the CG Arena rooms through a series of acquisition trials, the participants returned to the lab and were randomly assigned to either a Stress or Control group. Participants in the Stress group were exposed to the Fear Factor Stress Test (FFST), a method developed in the course of this dissertation (see Study B); participants in the Control group were exposed to the FFST's control condition. After the experimental manipulations, participants were asked, for each of the three Arena rooms, to locate the hidden target they had found the day before. They were then administered a test of recognition for landmarks encountered in the Arena rooms (the Object Recognition Test, or ORT), and a test of recall for the spatial layout of the Arena rooms (the Arena Reconstitution Test, or ART). In summary, this study aimed to explore the effects of acute stress on visual and spatial memory retrieval for three previously learned 3-dimensional virtual environments that varied in arousal and valence qualities.

In the present study, each Stress and Control group contained equal numbers of men and women. Thus, there were four experimental groups of 15 participants each: a male and a female Stress group, and a male and female Control group. A comparison of the sample characteristics across these four groups showed no between-group differences in terms of age, BMI, depressive symptomatology, and trait anxiety. Hence, participants in the four groups were sampled from the same population and were in a similar (neutral) emotional state when entering the experimental environment.

## Summary of Results

On the first day, all participants completed the training and acquisition trials in the CG Arena rooms. As noted in Study A, the purpose of the training trials was to ensure that participants were familiar with the movements of the joystick within the CG Arena, and with the tasks required of them. I was also able to gauge whether the participants were capable of performing the tasks in the CG Arena. Analysis of path lengths across the training trials confirmed that there were no between-group performance differences. Thus, participants in all groups entered the acquisition trials displaying a similar degree of competency in manipulating the joystick in order to navigate to a target in the CG Arena.

After the training trials, the participants proceeded to locate and learn the location of an invisible target in the three experimental CG Arena rooms. To determine whether participants in the four groups showed a similar performance in terms of learning the location of the target during the learning phase, I analyzed their path lengths to the target on each of the six acquisition trials. I predicted that there would be no significant between-group differences at this stage (the experimental manipulations would only be administered on the next day). Analysis of data from the acquisition trials revealed that the four groups showed similar path lengths across the acquisition trials in both the Cool and Hot Defensive CG Arena rooms. In these two rooms, no one group took a significantly shorter or longer path length to the target across the acquisition trials.

In contrast, analyses of path length to the target across trials in the Hot Appetitive room detected a significant Experimental Condition x Sex interaction. Specifically, participants in the Stress Male group showed significantly shorter path lengths across trials than participants in the Stress Female group. This effect, however, did not hold overall for Sex: Participants in the Control Male and Control Female groups showed statistically similar path lengths across the acquisition trials.

I conducted a second set of analyses on the final acquisition trial in order to determine whether participants in all groups were performing with relatively equal efficiency by the end of the set of acquisition trials. Again, because the stress/control manipulations were only to occur the following day, I predicted there would be no significant between-group differences in terms of path length to the target on acquisition Trial 6. The analyses confirmed the prediction. Of note is that the significant interaction effect detected across trials in the earlier analysis was not present here. Thus, it appears that the advantage that Stress Male participants had over Stress Female participants in finding the target across earlier acquisition

trials in the Hot Appetitive room had disappeared by the time participants undertook the final trial in the room.

In addition to the CG Arena and related visual-spatial tasks, the participants were also administered a verbal memory task, the Verbal Paired Associates Test (VPA). I included a verbal memory task so that the current visual-spatial findings could be compared to previous findings on the effects of stress on verbal memory. As discussed previously, most studies investigating the effects of stress on memory have focused on verbal material. Therefore, the inclusion of a verbal memory test was one way to check on the effectiveness of the stress manipulation; furthermore, it allowed some investigation of whether the effects of stress on memory are material-specific. Regarding Day 1 performance on the VPA, I predicted (in a manner consistent with the predictions made before) that there would be no significant between-group differences in terms of learning the list of word pairs. Analyses of data from the two Day 1 VPA recall trials confirmed this prediction.

In summary, analysis of the Day 1 data suggested that participants in the four groups were of a similar age and BMI, and had similar levels of depressive symptomatology and trait anxiety. The groups also showed a similar pattern of learning across the training and acquisition trials in the CG Arena, with exception of the difference that was observed between the Stress Male and Stress Female groups across the six acquisition trials in the Hot Appetitive room. Importantly, this difference had disappeared by the final trial, as there were no between-group differences in performance on Trial 6 in each of the CG experimental rooms. In addition, the groups displayed similar performance on the two recall trials of the VPA. Hence, given that the analyses of Day 1 suggested that participants in all groups (a) had similar biographical, clinical, and emotional characteristics, and (b) performed equally on both the CG Arena tasks and the VPA, any differences in performance on Day 2 can be attributed to the effects of the experimental manipulation.

Twenty-four hours after the first session, the participants returned to the lab and were pseudo-randomly assigned to an experimental group. After physiological and self-report baseline measures were taken, each participant was exposed to either the FFST or the FFST control condition. The present study examined cortisol, heart rate, and galvanic skin response levels in each participant as the experimental manipulation unfolded. Analysis of the effects of the FFST on the Stress Male and Stress Female groups showed that the manipulation successfully increased (relative to baseline) cortisol, heart rate, and galvanic skin response levels, as well as self-rated anxiety. Therefore, it appears that both the autonomic and HPA axis stress systems, in conjunction with a subjective experience of stress, were activated in

participants in the stress condition. Of critical importance was that the cortisol levels of participants in the Stress groups remained elevated throughout the memory testing phase of Day 2. In comparison, participants in the Control groups showed an increase in heart rate and in galvanic skin response (although the latter increase was significantly lower than that in the Stress groups) in the absence of an increase in cortisol levels or self-reported anxiety. Thus, the Control groups showed only nominal activation of the autonomic system, without activation of the HPA axis or any subjective experience of stress. The autonomic increase that was seen in the control condition can be associated with the increased cardiovascular activity associated with the control task. As discussed in Chapter 3, the participants' baseline heart rates and skin responses were measured while they sat quietly at a table. In the control manipulation, the participants were asked to stand and read out aloud while heart rate and skin responses were measured. The increase in the two measures might therefore be attributed to the physical exertion associated with the task. This autonomic increase was noted in Control group in Study B and has also been reported for a control condition of the TSST (Het et al., 2009).

After the experimental manipulation, the participants completed the recognition and recall tests for each of the CG Arena rooms, and the delayed recall trial of the VPA. The results of these tests are discussed below, in relation to the stated hypotheses.

***Summary of results in relation to tested hypotheses.*** The first hypothesis, regarding memory performance, was that stress would have an overall impairing effect on memory retrieval of previously learned information. Hence, participants in the Stress groups were expected to perform more poorly than those in the Control groups on all memory tests. This hypothesis was not confirmed on any of the visual, spatial, or the verbal recall memory measures. Specifically, those in the Stress groups did not perform more poorly than those in the Control groups on the Day 2 recall or probe trials in the CG Arena, nor did they show relatively impaired performance on the ORT or the ART. Furthermore, there were no between-group differences in terms of memory for the VPA word pairs.

With specific regard to only the neutral memory material, the prediction was that participants in the Stress groups would show impaired retrieval for details of the Cool CG Arena room (i.e., the room containing images neutral in valence and arousal) and for the word pairs on the VPA. Failure to confirm these hypotheses is a surprising result. As reviewed earlier in this chapter, and in Chapter 1, the literature surrounding this topic points strongly toward the impairing effects that stress has on memory retrieval (see, e.g., de Quervain et al., 2009; Roozendaal et al., 2009; Schwabe et al., 2012; Wolf, 2009). Although

previous studies have, for the most part, used verbal stimulus material, some studies have also demonstrated the retrieval impairment when using visual and spatial material (see, e.g., Buchanan & Tranel, 2008; Quesada et al., 2012; Schönfeld et al., 2014; Schwabe & Wolf, 2009). Thus, failure to confirm the first hypothesis is inconsistent with the general literature surrounding this topic. It should be noted, however, that some other studies have also failed to find stress-induced retrieval impairments (Schoofs & Wolf, 2009<sup>22</sup>; Wolf et al., 2002).

In stark contrast to the negative findings regarding retrieval *impairments*, exposure to the stressor may have had an *enhancing* effect on memory retrieval for word pairs of the VPA in women. Although, overall, the women in the study displayed significantly better retention for the word pairs than the men did, this difference was strongly influenced by the performance of participants in the Stress Female group. Those participants retained significantly more word pairs than participants in the Stress Male group, and significantly more than participants in the other three groups as a whole. In addition, when comparing cortisol responders to controls, the overall significant sex difference disappeared, and the effect size associated with the comparison between the Stress Female and the other three groups taken together increased slightly.

This finding that stress might have an enhancing effect on memory stands in direct contrast to numerous studies reporting impairing effects of stress on verbal memory (e.g., Buchanan et al., 2006; Dome et al., 2004; Kuhlmann et al., 2005; Smeets, 2011; Smeets et al., 2008; Tollenaar et al., 2008). However, it is not an isolated finding in this literature. For instance, Schwabe et al. (2009) reported that participants (all men) who underwent a stress manipulation (SECPT) showed selectively enhanced retrieval of emotionally arousing words. The authors subsequently demonstrated that treatment with propranolol (a beta-blocker) negated the stress-induced enhancement of memory for emotional words. Schwabe et al. attributed the positive effects of stress on memory retrieval to an inverted-U relationship between stress and memory, which was most prominent for the emotional material. Further discussion of the current findings in relation to the inverted-U hypotheses is presented in Chapter 6.

It is interesting that exposure to the stressor had a positive effect on verbal memory in women but not in men. Previous research suggests that interactions between sex hormones and glucocorticoids during memory processing are complex and not well understood

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<sup>22</sup>Although, as mentioned in Chapter 1, Schoofs and Wolf (2009) only tested female participants in the luteal phase of their menstrual cycle. The luteal phase is characterized by elevated gonadal steroids, which is associated with reduced glucocorticoid sensitivity in women.

(Andreano & Cahill, 2006, 2009; Kudielka et al., 2009). Previous research also suggests that stress effects on memory may be different in men and women (Andreano & Cahill, 2006; Cahill, 2005; Wolf et al., 2001). Explanations for these different effects include reference to influential factors such as endogenous sex steroids and phase of the menstrual cycle (Kudielka et al., 2009). In this present study, phase of the menstrual cycle was not controlled for, given that the purpose was to examine the effects of stress on a more broad population rather than on a specific population group. Unfortunately, the use of a diverse female sample makes it difficult to isolate the possible reasons for the positive stress-induced effects observed in women. However, one might speculate that because women are generally reported to outperform men on verbal memory tests (Andreano & Cahill, 2009); it is possible that the interaction between stress hormones and endogenous sex steroids may have elicited this verbal memory advantage in the Stress Female group.

The second hypothesis predicted that memory for the three CG Arena rooms would be influenced by the arousal content of the pictures that were used as landmarks. The Stress groups were predicted to show an even greater retrieval impairment (over and above the general stress impairment predicted in the first hypothesis) for the arousing stimuli versus the neutral stimuli. The Control groups, on the other hand, were predicted to show enhanced retrieval for the picture stimuli that contained the arousing content versus the neutral content. This second hypothesis was confirmed only partially: That is to say, participants in the Stress groups did not perform in the predicted manner, whereas those in the Control groups did (but only for the recognition task).

Participants in the Control groups showed better recognition for the pictures in the arousing CG Arena rooms (irrespective of valence) than for those in the Cool room. However, this superior recognition performance was not isolated to the Control groups: Participants in the Stress groups also showed a similarly enhanced recognition for the arousing stimuli. Thus, all participants, on average and regardless of the experimental manipulation, showed enhanced recognition memory for the arousing stimuli relative to the neutral stimuli. The arousing stimuli did not seem to influence the Stress and Control groups' wayfinding or dwell time performance in the CG Arena.

Interestingly, recall of the spatial layout of the CG Arena rooms seemed to be influenced by exposure to the stressor and by the arousing qualities of the landmark pictures in the room. Analysis of ART scores showed that participants in the Stress Male and Stress Female groups had superior recall for the spatial layout of the Hot Appetitive room than did participants in the Control Male and Control Female groups. This result is in the opposite

direction to that hypothesized: Instead of seeing the exaggerated memory-impairing effect of stress for arousing material, I observed an enhancing effect of stress for arousing material.

Furthermore, in an observation similar to that described above regarding positive effects of stress on verbal memory performance, the effect size of this significant between-group difference on the ART was slightly stronger when the cortisol responders were analyzed in isolation. In other words, those Stress-group participants who showed a markedly increased cortisol response following exposure to the stressor recalled the spatial layout of the Hot Appetitive room with an even greater accuracy than both Control-group participants and Stress-group participants without such marked cortisol elevations. Thus, similar to Schwabe et al.'s (2009) study discussed above, these findings also demonstrate that stress can have a positive effect on the retrieval of emotional information.

It is possible, however, that the significantly better Stress-group performance on the ART is related to the significant differences observed between the Stress Male and the Stress Female groups on the acquisition trials in the Hot Appetitive room. As discussed above, the Stress Male group located the target in a significantly shorter path length than the Stress Female group. In the CG Arena, participants who find a hidden target more directly are likely to have a better idea of the location of the target than participants who find it less directly. This also means, however, that those former participants spend less time in the room, and thus spend less time exploring and becoming more familiar with it. In other words, if Stress Male participants find the target more directly than Stress Female participants, this might mean that the Stress Male participants had better memory for the location of the target; although, that knowledge may come at the expense of becoming familiar with the full set of images (and the layout of those images) on the walls of the room. However, given that the Stress Male and Stress Female groups showed opposite performances across acquisition trials, and that neither of the groups differed from the Control groups, it is unlikely that the retrieval differences reflect a difference in learning, as there were no such Stress versus Control differences on Day 1.

The third hypothesis was that women would, on average and regardless of experimental group, display inferior spatial learning and memory than men. Congruent with the findings presented in Study A, this hypothesis was largely disconfirmed in the present study. In terms of spatial learning, men and women performed similarly on the CG Arena training and acquisition trials (Day 1 of the protocol). In fact, the only significant sex difference noted was that mentioned previously (i.e., the difference between the Stress Male and Stress Female groups across the acquisition trials in the Hot Appetitive room). However,

this difference did not extend overall for sex, as there were no between-group differences when comparing performance in the Hot Appetitive room of control women to control men.

In terms of spatial memory (i.e., memory for the contents and spatial layout of the CG Arena rooms), the current data analyses also detected no significant sex differences. That is, there were no significant differences between men and women in terms of wayfinding performance on the recall trial, dwell time on the probe trial, recognition of the landmarks, or reconstruction of the CG Arena rooms.

Chapter 6 (the General Discussion) presents further discussion of, and explanations for, the findings of the present study. That chapter provides discussion in the context of (a) previous studies in this literature, (b) theories attempting to explain the effects of stress on memory, and (c) a functional perspective on memory.

***Summary of results for cortisol responders versus control participants comparisons.***

Subsequent analysis of the data from participants in the Stress group who had displayed a marked cortisol elevation (cortisol responders) revealed no pattern of significant differences other than those already detected by the whole-group analysis (Hot Appetitive ART score and percentage retained VPA score). However, the effect sizes associated with the previously detected between-group differences increased marginally in these subsequent analyses. In addition, responder analysis revealed a borderline significant difference ( $p = .053$ ) in wayfinding performance between the Stress and Control groups on the recall trial in the Cool room: Participants in the Stress groups located the hidden target more efficiently.

The observed increase in effect sizes from the whole-group analyses to the cortisol responder analyses is consistent with the notion that cortisol is the primary modulator of possible stress-induced between-group differences. To test this notion further, one might question whether artificially increasing cortisol levels through cortisol administration would induce the same pattern of memory performance as that was described above. Administration of cortisol would concentrate the focus on the stress hormone, and exclude confounding factors (e.g., autonomic increases of catecholamines (such as epinephrine, norepinephrine),  $\alpha$ -amylase, heart rate, blood pressure, and galvanic skin response) that are associated with a stressful experience. In addition, experimental administration of cortisol would reduce the inter-individual variability in cortisol response seen after a stress manipulation. Thus, administering cortisol should result in a larger number of cortisol responders in the sample. Furthermore, depending on the dose quantity, administering cortisol could also raise cortisol to higher levels than those seen following a stress manipulation. It is possible that such further increases in cortisol levels might amplify the differences seen in this study.

Consequently, the administration of cortisol, as opposed to a laboratory-based stress induction procedure, may help determine whether cortisol is a primary modulator of the observed differences between the Stress and Control groups. This question is explored in Study 2.

### **Conclusion**

The data obtained in the present study failed to confirm any of the three hypotheses that were tested. First, stress did not impair retrieval of visual, spatial, or verbal information. Instead, exposure to the stressor had a positive effect on the recall of verbal information in female participants. Second, there was no exaggerated stress-induced memory impairment observed for the arousing visual or spatial information. However, participants in both the Stress (not predicted) and Control (predicted) groups showed enhanced recognition for the arousing stimuli. Third, women did not display inferior spatial learning and memory in comparison to the men. They did, however, show superior verbal memory performance relative to the men, although this superior performance may have been driven by a stress-induced memory enhancement in the Stress Female group.

**CHAPTER FIVE:**  
**STUDY 2 – THE EFFECTS OF CORTISOL ADMINISTRATION ON**  
**RETRIEVAL OF VISUAL AND SPATIAL MATERIAL**

Chapter 1 described the body's stress response, characterizing it as an adaptive response to a threatening situation, and noting that it is marked by the release of stress hormones. Two separate, yet interacting, response systems are active in the body during a stressful experience. The first is a rapid response of the noradrenergic system that involves the release of catecholamines and, to a lesser extent, glucocorticoids (GCs) via the hypothalamic-pituitary-adrenal (HPA) axis. The second response system is slower, and is initiated solely by the activation of the HPA axis. This latter response results in the release of glucocorticoids (corticosterone in animals and cortisol in humans) from the adrenal cortex (Roozendaal et al., 2006, 2009).

From a cognitive perspective, catecholamines do not directly influence brain function, as they cannot cross the blood-brain barrier easily. However, they can exert some influence through the stimulation of the vagus nerve in the brainstem (Roozendaal et al., 2006). In contrast, GCs can cross the blood-brain barrier easily. They then bind to receptors in both subcortical and cortical regions (de Kloet et al., 2005; Herbert et al., 2006; McEwen, 1998). It is this second, slower, stress response system, and its effects on memory retrieval, that is the focus of the study presented in this chapter.

### **Effects of Cortisol on Memory Retrieval**

As reviewed in Chapter 1, the reported effects of cortisol administration on memory mimic those of exposure to an acute stressor. That is, the direction of the effects depends on timing. An acute increase of cortisol is generally reported to have an enhancing effect on memory consolidation, but an impairing effect on memory retrieval. Reports regarding effects on encoding are inconsistent, largely attributed to the confounding influence of the other memory phases (de Quervain et al., 2009; Het et al., 2005; Smeets et al., 2012; Wolf, 2008, 2009).

In a manner consistent with research into the effects of psychosocial/physiological stress, the effects of pharmacologically elevated GCs on memory retrieval have been investigated in both human and animal studies. As noted earlier, de Quervain et al. (1998) first demonstrated that the administration of GCs to non-stressed rats resulted in similar memory retrieval impairments to those seen in the Morris Water Maze (MWM) with stressed

rats. Subsequent rodent studies have reported similar spatial and contextual memory retrieval impairments (Atsak et al., 2012; Rashidy-Pour, Sadeghi, Taherain, Vafaei, & Fathollahi, 2004; Roozendaal et al., 2003; 2004; Sajadi, Samaei, & Rashidy-Pour, 2007).

Following that seminal 1998 study, de Quervain et al. (2000) demonstrated in humans that the administration of a single dose of 25mg of cortisone impaired memory for words that had been learned 24 hours earlier. Subsequent human studies have confirmed this impairing effect of elevated cortisol on retrieval of verbal material (Buss et al., 2004; Coluccia et al., 2008; de Quervain et al., 2007; Domes et al., 2005; Het et al., 2005; Kuhlmann et al., 2005; Kuhlmann & Wolf, 2005; Smeets et al., 2008; Tollenaar et al., 2009; Wingenfeld et al., 2012; Wolf et al., 2001). Some of these studies have reported that emotionally arousing information is especially sensitive to the impairing effects of elevated GCs on memory retrieval (de Quervain et al., 2007; Kuhlmann et al., 2005; Kuhlmann & Wolf, 2005; Smeets et al., 2008).<sup>23</sup> In addition, emotional arousal during the testing situation has also been shown to facilitate the impairing effects of elevated GCs on memory retrieval (Kuhlmann & Wolf, 2006).

Despite the numerous studies that report impairing effects of pharmacologically elevated cortisol on verbal memory retrieval, there is a surprising absence of studies investigating these effects on visual and spatial memory in humans. To my knowledge, only one published study has reported investigating the effects of cortisol administration on retrieval of visual and spatial material. Domes et al. (2005) investigated the effects of administering a 25mg dose of hydrocortisone on retrieval of verbal and nonverbal material that had been learnt roughly an hour earlier.<sup>24</sup> The authors reported no global effect of elevated cortisol on either verbal or nonverbal memory. However, participants who displayed a high cortisol response showed a verbal memory impairment, but not a visual and spatial impairment. The authors attributed this memory impairment to cortisol having an inverted-U effect on memory retrieval that was more pronounced for verbal material.

In fact, Domes et al. (2005) are not alone in reporting an inverted-U relationship between cortisol and memory retrieval performance. Recently, Schilling et al. (2013) investigated the effects of varying doses of cortisol (0, 3, 6, 12, 24mg) on retrieval of verbal descriptions of neutral faces learnt one week earlier. Although the authors did not examine

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<sup>23</sup>Although Tollenaar et al. (2009) reported retrieval impairment for both neutral and emotional words that had been learned 1 week earlier.

<sup>24</sup>The nonverbal memory tests used by Domes et al. (2005) were: (i) memory for a marked route drawn on a city map; (ii) memory for pictures of various objects; and (iii) memory for associations between figural patterns.

visual and spatial memory of the type under investigation here, they reported that moderate doses of cortisol had an enhancing effect on retrieval for the descriptions of those faces

In summary, although the impairing effects of cortisol administration on memory retrieval are well documented for verbal material, these effects are yet to be confirmed for visual and spatial material. The present study aims to explore this gap in the literature.

### **Aims, Rationale, and Hypotheses**

As noted earlier, the aim of the major studies presented here (i.e., those documented in Chapters 4 and 5) is to systematically replicate de Quervain et al.'s (1998) study in humans. To recap briefly, de Quervain and colleagues first demonstrated that stress (in the form of foot-shocks) impaired performance in a Morris Water Maze that had been learned 24 hours prior. They reported subsequently that administration of GCs resulted in similarly impaired performance.

The study described below, then, follows on from that presented in Chapter 4. In Study 1, participants learned (a) the location of a hidden target in three different CG Arena rooms, and (b) the word pairs constituting the Verbal Paired Associates test (VPA). Twenty-four hours later, the participants returned and completed either the Fear Factor Stress Test (FFST) or a control manipulation. Thereafter, they completed tests of retrieval for various aspects of the CG Arena rooms to which they had been exposed, along with a delayed recall trial of the VPA.

Study 1's results suggested that exposure to the acute stressor did not impair memory retrieval performance on either the visual and spatial tasks or the verbal tasks. Instead, in a manner similar to that seen in control participants, Stress-group participants showed enhanced recognition of the arousing stimuli, irrespective of valence. In addition, exposure to the stressor may have had positive effects on retrieval of spatial and verbal material. Specifically, both men and women who were exposed to the stress manipulation displayed more accurate memory for the spatial layout of the landmarks in the Hot Appetitive room than the control participants did. Additionally, women who had been exposed to the stressor recalled more correct word pairs of the VPA than the other participants.

The subsequent comparison of cortisol responders in the Stress group with the Control group participants showed a slight increase of effect sizes for the differences previously detected in the full-sample analysis. Of particular note was the strengthening of the positive differences mentioned above. Thus, the increases in these positive differences

between the cortisol responders and the control participants hinted at the likelihood of cortisol being the primary modulator of these retrieval differences.

Following de Quervain et al. (1998), the present study aims to substitute the stress manipulation with a dose of cortisol, and to then repeat the rest of the study unchanged. Therefore, the aim of the following comparative study is to examine the effects of an acute elevation of cortisol on visual and spatial memory retrieval. In addition, this study aims to examine the effects of emotional arousal on the quality of visual-spatial memory retrieval following cortisol administration.

As in Study 1, I tested the following hypotheses:

1) Cortisol will have, overall, an impairing effect on memory retrieval. Thus, participants who are administered cortisol (Stress group<sup>25</sup>) should perform worse on all tests of memory retrieval than participants who are not administered cortisol (Control group).

2) Memory for the different rooms will be influenced by the arousal content of the pictures used as landmarks in the CG Arena. The Stress and Control groups will show contrasting patterns of retrieval for the arousing versus the neutral stimuli. That is, even though participants in the Stress group should show an overall retrieval impairment, they should show a greater retrieval impairment for the arousing stimuli versus the neutral stimuli. Participants in the Control group, on the other hand, should show enhanced retrieval for the stimuli that contain the arousing content versus the neutral content.

Despite not being confirmed in Study A or Study 1, I continued with the hypotheses regarding sex differences:

3) Women will display inferior spatial memory compared to men.

## Methods

### Participants

Seventy-two undergraduate students (33 men) were recruited through the University of Cape Town (UCT) Department of Psychology's Student Research Participation Program (SRPP). Twelve participants were excluded from the study because they either did not meet the eligibility criteria<sup>26</sup> ( $n = 9$ ; 3 men) or because they voluntarily withdrew from the study before completing the experimental procedures ( $n = 3$ ; all women). Hence, a final sample of

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<sup>25</sup> Although participants in the "Stress" group in Study 2 were not physically stressed, the group label was retained in order to be consistent with the primary question examined in the dissertation.

<sup>26</sup> The eligibility criteria were identical to those used in Study 1. Hence, a full description of them is provided in Chapter 4.

$N = 60$  (30 men) participants provided data for analysis. The age range of this sample was 18-31 years ( $M = 21.26$ ,  $SD = 3.22$ ). As noted in the Procedure section below, each participant was pseudo-randomly assigned to either a Stress or a Control condition.

### **Materials and Apparatus**

The materials and apparatus used here were virtually identical to those described in Study 1. Specifically, the self-report measures (the Beck Depression Inventory-Second Edition [BDI-II] and the Spielberger State Anxiety Inventory [STAI]), the CG Arena rooms (Cool, Hot Appetitive, and Hot Defensive rooms), the CG Arena-related tasks (probe trial, Object Recognition Task [ORT], and Arena Reconstitution Task [ART]), and the VPA, were all identical to those described in the previous study.

However, in contrast to Study 1, I did not collect measures of heart rate and galvanic skin response. I took this decision because cortisol administration does not, reportedly, activate the autonomic nervous system (e.g., see Cornelisse et al., 2011). In addition, I initially attempted to use an alternative saliva collection apparatus to the salivettes that were used in Study 1. In the present study, I initially used Salimetrics Eyespear Sorbettes (Salimetrics LLC, Pennsylvania, USA) because a comparison of three saliva collection methods (passive, salivettes and eyespears) showed that the eyespear produced less reduction in concentration of cortisol. Eyespears were also reported to offer methodological advantages for the collection of saliva, as they have acquired positive ratings for their comfort and acceptability to research participants (Strazdins et al., 2005). However, preliminary cortisol analysis from the first 28 participants revealed that the eyespear was not suitable because 8 cortisol samples were lost due to insufficient saliva. I subsequently ceased using the eyespear and reverted back to using salivettes.

Of course, the most prominent change in the present study relative to Study 1 was the substitution of the FFST-Stress and FFST-Control conditions by Prednisone (cortisol) and placebo, respectively.

**Prednisone.** Participants in the Stress group were each orally administered 25mg of Prednisone. This is the minimum dose of cortisol that is equivalent to stress-level cortisol (de Quervain et al., 2000), and is the median dose reported in a meta-analytic review on the effects of cortisol on memory (Het et al., 2005). Prednisone has a biological half-life of between 18 and 36 hours, with acute effects experienced 1-2 hours after administration (Gibbon, 2000).

Participants in the Control group were given a sugar capsule that looked identical to the Prednisone capsule. The Prednisone and the placebo were both repackaged into identical capsules by Professor Reinhardt Uebel (Pharmaceutics Discipline, School of Pharmacy, University of the Western Cape). The capsules were stored in airtight containers in a cool, dry environment until administration.

## **Procedure**

The study procedures were conducted in the ACSENT Laboratory in the Department of Psychology at the University of Cape Town. The research described here followed the ethical guidelines for research subjects outlined by the Health Professions Council of South Africa and the UCT Codes for Research. The Research Ethics Committee of the UCT Department of Psychology approved all study procedures. As was the case in Study 1, all testing was performed between 14h00 and 18h00 to control for the possible effects of cortisol's diurnal cycle.

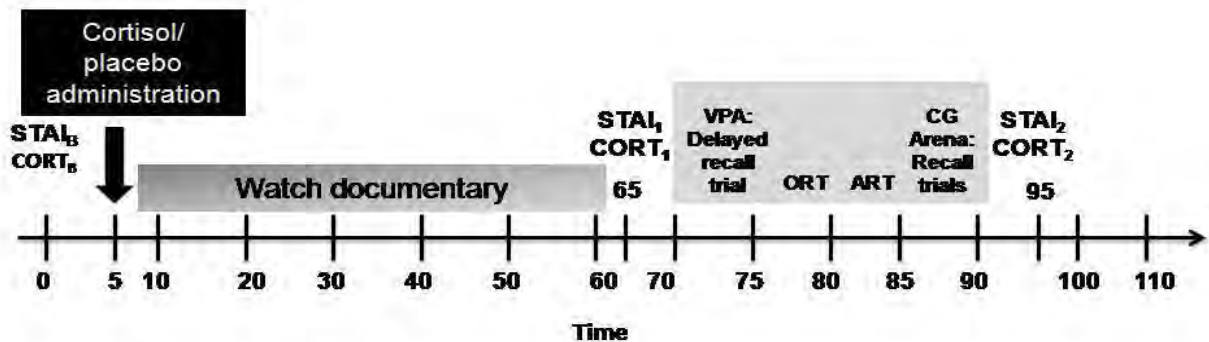
Furthermore, the two-day procedure used for the present study was almost identical to that used in Study 1. On Day 1, each participant was asked to read and sign a consent form (Appendix K), and was also given a chance to ask any questions concerning that form and the experiment. The participant then completed the BDI-II, the STAI-Trait and learnt the VPA along with the same CG Arena rooms that were described in Study 1. After the acquisition trials in the CG Arena rooms, the participants were reminded that they would have to return for a second session 24 hours later. They were also reminded that they would have to give a saliva sample at that session, and were given the same instructions as in Study 1 to ensure that their saliva and cortisol levels would not be negatively affected.

The second testing session followed 24 hours after the first. Figure 29 illustrates the timeline of events on Day 2. On arrival, each participant was pseudo-randomly assigned to either a Stress or Control group. Each participant was then asked to complete a questionnaire about what s/he had eaten and drank on that day. An initial saliva sample was then obtained as a measure of baseline cortisol ( $CORT_B$ ), and the participant was asked to complete a baseline STAI-State ( $STAI_B$ ) questionnaire. I then administered the cortisol or placebo capsule<sup>27</sup>, after which I asked the participant to sit and watch a documentary video for an hour. S/he was allowed to choose one of three videos to watch: a documentary on the history

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<sup>27</sup>This study utilized a double-blind experimental design. Thus, neither the participant nor I knew what dose (prednisone or placebo) was being administered.

of the classical guitar, a documentary on the history of the electric car, or a documentary on memory.



*Figure 29.* Timeline of events, from 0 minutes to 110 minutes, depicting the experimental procedures on Day 2. STAI = Spielberger State-Trait Anxiety Inventory; CORT = salivary cortisol (measured in nmol/l). Subscripts represent measurement point (e.g., STAI<sub>B</sub> is the first STAI measurement point, or baseline).

After an hour, the participant was asked to provide a second saliva sample (CORT<sub>1</sub>), and to complete a second STAI-State (STAI<sub>1</sub>) questionnaire. Next, the participant completed the same VPA, ORTs, ARTs, and recall trials in the CG Arena rooms that were described in Study 1. Finally, the participant was asked to complete a final STAI-State (STAI<sub>2</sub>) questionnaire and provide a final saliva sample (CORT<sub>2</sub>).

Following completion of this part of the experimental protocol, the participant was debriefed and the study concluded. The length of time for testing each participant was not more than 60 minutes for the first session and not more than 120 minutes for the second session.

### Data Analysis

Statistical analyses were calculated using IBM SPSS Statistics version 21. The design of the present study allowed for both within- and between-group analyses. The statistical significance level was set at  $\alpha = .05$ . Details of the particular analyses used for each section of results are specified at the start of the presentation of the relevant section. Unless otherwise stated, all assumptions underlying the relevant inferential statistical analyses were upheld.

Given that increases in cortisol concentrations following cortisol administration are more consistent than those following acute stressors (Lupien et al., 2007), it was not necessary to compare the cortisol responders with the control participants (as was the case in

Study 1).<sup>28</sup> Therefore, only one set of analyses, exploring differences in the full participant sample, is presented below.

## Results

### Sample Characteristics

To ensure that the participants recruited for this study were all sampled from a similar population, characteristics such as age, BDI-II scores, and STAI-Trait scores, were compared across groups. A series of 2 (Experimental Condition: Stress versus Control) x 2 (Sex: male versus female) factorial ANOVAs compared outcomes on these variables. Table 18 shows the descriptive statistics for these outcome variables. Due to experimenter error, depression and trait anxiety data are only available for 32 participants in the present sample.<sup>29</sup>

Table 18  
*Descriptive Statistics for Sample Characteristics (N = 60)*

Measure	Group			
	Stress		Control	
	Men (n = 15)	Women (n = 15)	Men (n = 15)	Women (n = 15)
Age	22.47 (3.54)	20.13 (1.36)	20.80 (3.49)	21.20 (3.03)
BDI-II	9.86 (6.77) <sup>a</sup>	9.11 (5.53) <sup>b</sup>	10.57 (5.91) <sup>a</sup>	10.89 (5.33) <sup>b</sup>
STAI – Trait	39.00 (12.23) <sup>a</sup>	41.56 (9.85) <sup>b</sup>	43.86 (8.27) <sup>a</sup>	40.44 (9.26) <sup>b</sup>

*Note.* Means are presented with standard deviations in parentheses. BDI-II = Beck Depression Inventory-Second Edition; STAI = State-Trait Anxiety Inventory. <sup>a</sup>n = 7. <sup>b</sup>n = 9.

**Age.** The analysis detected no significant main effects for Experimental Condition,  $p = .699$ , or for Sex,  $p = .216$ , and no significant Experimental Condition x Sex interaction effect,  $p = .082$ . These results suggest that the cortisol and cognitive data reported below are not confounded by between-group differences in age.

**BDI-II scores.** The analysis detected no significant main effects of Experimental Condition,  $p = .554$ , or of Sex,  $p = .919$ , and no significant Experimental Condition x Sex interaction,  $p = .800$ . All groups fell in the “minimally depressed” range (a score between 0 - 13.99) described by Beck et al. (1996). These results suggest that the cortisol and cognitive data reported below are not confounded by between-group differences in pre-existing depressive symptomatology.

<sup>28</sup>In the present study, all participants in the Stress groups showed increases over baseline cortisol concentrations greater than 2 nmol/l.

<sup>29</sup>Experimenter error (which entailed not expeditiously capturing the data) was unfortunately coupled with the loss (theft) of a bag containing, amongst other things, the uncaptured hard copies of 28 participants' BDI-II, STAI and CORT<sub>2</sub> data.

**STAI-Trait scores.** Analysis of the STAI-Trait scores detected no significant main effect differences for Experimental Condition,  $p = .601$ , or Sex,  $p = .905$ , and no Experimental Condition x Sex interaction,  $p = .407$ .

To be sure that the groups recruited for the current study were representative of the general population in terms of trait anxiety, a series of one-sample  $t$ -tests compared group averages to normative data for college students presented in the STAI test manual (Spielberg et al., 1983). Male participants ( $n = 14$ ;  $M = 41.43$ ,  $SD = 10.35$ ) did not significantly differ from the normative male population ( $M = 38.30$ ,  $SD = 9.18$ ;  $p = .278$ ). Similarly, female participants ( $n = 18$ ;  $M = 41.00$ ,  $SD = 9.29$ ) did not differ significantly from the normative female population ( $M = 40.40$ ,  $SD = 10.15$ ;  $p = .787$ ).

Taken together, these results suggest that the four groups were similar in terms trait anxiety, and were representative of the general population of college students.

### **Experimental Manipulation**

The following series of analyses sought to establish the effectiveness of the experimental manipulation. The intention of the manipulation was to significantly raise the cortisol levels of the participants in the Stress group (relative to the Control group), without increasing participants' subjective anxiety levels, and to then examine the effects of raised cortisol levels on memory retrieval.

For both cortisol levels and STAI-State scores,  $2 \times 2 \times 3$  (Experimental Condition [Stress versus Control] x Sex [male versus female] x Time [measure<sub>B</sub> versus measure<sub>1</sub> versus measure<sub>2</sub>]) repeated-measures ANOVAs were conducted, and further within- and between-group analysis was used to explore significant effects. Table 19 provides descriptive statistics for each of the relevant outcome variables.

As previously mentioned, several salivary cortisol samples could not be analysed due to insufficient saliva (a problem attributed to the Sorbett eyespear). For this reason, eight salivary cortisol samples were lost (four in the Stress Male group, two in the Stress Female group, and one in each of the Control groups) from CORT<sub>B</sub> and CORT<sub>1</sub> measures. In addition, due to experimenter error, CORT<sub>2</sub> and STAI-state data are only available for 32 participants (seven in both the Stress Male and Control Male groups, and nine in both the Stress Female and Control Female groups).

Table 19  
*Descriptive Statistics for Salivary Cortisol and STAI-State Data (N = 60)*

Outcome Variable	Group			
	Stress		Control	
	Men ( <i>n</i> = 15)	Women ( <i>n</i> = 15)	Men ( <i>n</i> = 15)	Women ( <i>n</i> = 15)
Cortisol measure				
CORT <sub>B</sub>	1.98 (1.08) <sup>a</sup>	2.14 (1.42) <sup>a</sup>	2.56 (1.41)	2.90 (1.90)
CORT <sub>1</sub>	36.11 (30.65) <sup>b</sup>	64.64 (43.49) <sup>a</sup>	1.74 (0.71) <sup>a</sup>	2.82 (2.00) <sup>a</sup>
CORT <sub>2</sub>	47.00 (39.65) <sup>c</sup>	58.33 (39.18) <sup>d</sup>	1.85 (0.95) <sup>c</sup>	3.07 (1.75) <sup>d</sup>
STAI-state				
STAI <sub>B</sub>	30.71 (9.74) <sup>c</sup>	31.67 (10.44) <sup>d</sup>	33.43 (6.37) <sup>c</sup>	31.33 (5.63) <sup>d</sup>
STAI <sub>1</sub>	31.71 (13.92) <sup>c</sup>	34.11 (6.43) <sup>d</sup>	32.00 (6.35) <sup>c</sup>	30.89 (12.76) <sup>d</sup>
STAI <sub>2</sub>	36.00 (13.83) <sup>c</sup>	32.22 (5.40) <sup>d</sup>	38.71 (8.42) <sup>c</sup>	33.78 (9.68) <sup>d</sup>

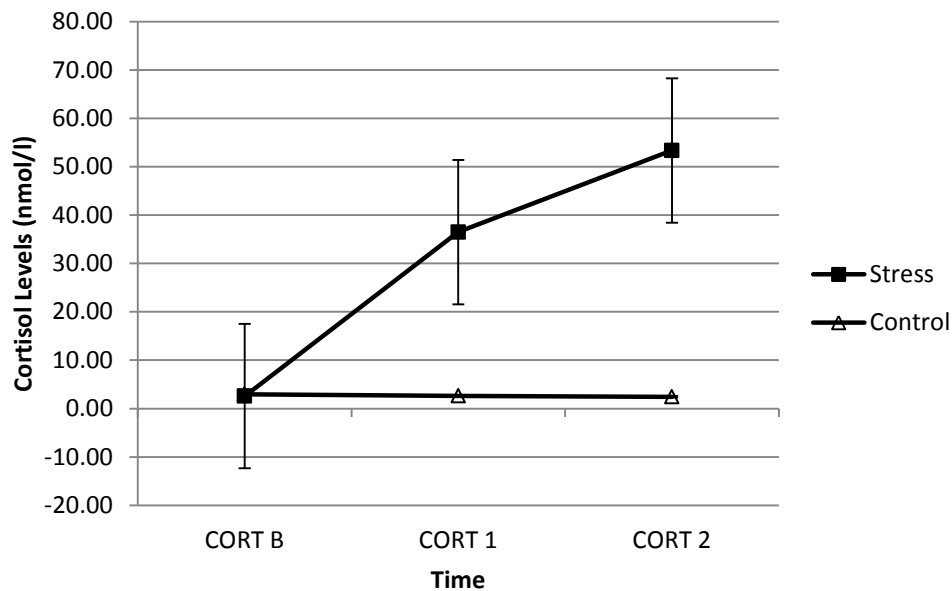
*Note.* Data shown are means, with standard deviations in parentheses. Cortisol levels are measured in nanomoles per litre (nmol/l). Where cortisol levels for a participant were indicated to be < 0.50 nmol/l, 0.45 nmol/l was used as an estimate. Subscripts represent measurement point (e.g., STAI<sub>B</sub> is the first STAI measurement point, or baseline). <sup>a</sup>*n* = 14; <sup>b</sup>*n* = 12; <sup>c</sup>*n* = 7; <sup>d</sup>*n* = 9.

**Salivary cortisol levels.** Due to violations of the assumptions of normality and sphericity, it was necessary to transform the data. Log transformations were used to correct the violation of normality. To correct the violation of sphericity,  $\chi^2(2) = 18.70$ ,  $p < .001$ , it was necessary to use a Greenhouse-Geisser degrees of freedom correction ( $\epsilon = 0.66$ ).

The analysis detected statistically significant main effects of Time,  $F(1.31, 34.06) = 30.69$ ,  $p < .001$ ,  $\eta_p^2 = .54$  and Experimental Condition,  $F(1, 26) = 43.50$ ,  $p < .001$ ,  $\eta_p^2 = .63$ , in the absence of a significant main effect of Sex,  $p = .229$ . The analysis also detected a significant Time x Experimental Condition interaction,  $F(1.31, 34.01) = 42.50$ ,  $p < .001$ ,  $\eta_p^2 = .62$ , in the absence of statistically significant Experimental Condition x Sex,  $p = .777$ , Time x Sex,  $p = .484$ , or Time x Experimental Condition x Sex,  $p = .577$ , interactions. These results suggest that only Experimental Condition and Time had an effect on the participants' cortisol levels. To investigate the nature of the influence further, I examined each of the contributing factors separately. Figure 30 shows the fluctuations in cortisol levels for each experimental group across the testing session.

Within-group analysis across Time showed that the Stress groups displayed a significant increase in cortisol levels from CORT<sub>B</sub> ( $M = 2.58$ ,  $SD = 1.25$ ) to CORT<sub>1</sub> ( $M = 36.49$ ,  $SD = 38.97$ ;  $F(1, 14) = 12.37$ ,  $p = .003$ ,  $\eta_p^2 = .47$ ). Cortisol levels showed a further increase by the CORT<sub>2</sub> measure ( $M = 53.37$ ,  $SD = 38.54$ ), and the participants' cortisol levels were still significantly higher at that point relative to CORT<sub>B</sub>,  $F(1, 14) = 25.37$ ,  $p < .001$ ,  $\eta_p^2 = .64$ . The Control group, on the other hand, showed stable cortisol levels from CORT<sub>B</sub> ( $M =$

2.97,  $SD = 1.49$ ) to  $CORT_1$  ( $M = 2.62$ ,  $SD = 1.65$ ;  $p = .356$ ). By  $CORT_2$  ( $M = 2.45$ ,  $SD = 1.59$ ), Control participants' cortisol levels were non-significantly lower than at  $CORT_B$  ( $p = .133$ ). Thus, the two groups showed an opposite pattern in cortisol reaction across Day 2, with the Stress group displaying the predicted increase in cortisol levels due to the manipulation, while the Control group displayed a gradual decrease in cortisol levels.



*Figure 30.* Changes in cortisol (CORT) levels on Day 2 for the combined Stress and combined Control groups. Error bars indicate standard error of means. Subscripts represent measurement point (e.g.,  $CORT_B$  is the first cortisol measurement point, or baseline).

Between-group analysis of the  $CORT_B$  data detected no significant main effects of Experimental Condition,  $p = .096$ , or of Sex,  $p = .529$ , and no significant Experimental Condition x Sex,  $p = .827$ , interaction. Thus, there were no significant between-group differences in cortisol levels at the start of the testing process.

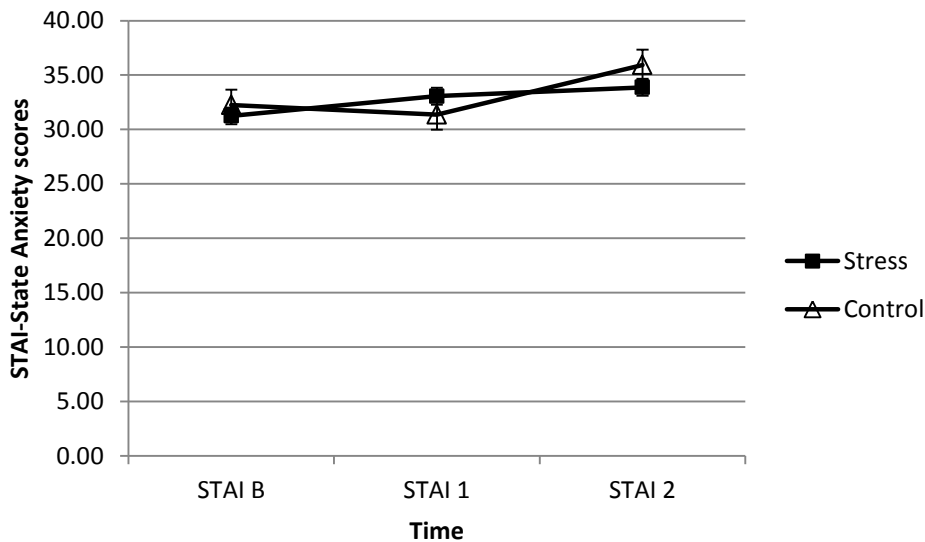
Between-group analysis of the  $CORT_1$  data detected a significant main effect of Experimental Condition,  $F(1, 54) = 44.44$ ,  $p < .001$ ,  $\eta_p^2 = .47$ , and Sex,  $F(1, 54) = 4.21$ ,  $p = .045$ ,  $\eta_p^2 = .08$ , in the absence of a significant Experimental Condition x Sex interaction,  $p = .063$ . At this measurement point, the Stress groups ( $M = 51.47$ ,  $SD = 40.09$ ) showed significantly raised cortisol levels in comparison to the Control groups ( $M = 2.28$ ,  $SD = 1.57$ ). In addition to the significant Experimental Condition effect, there was also a significant sex difference: Female participants ( $M = 33.73$ ,  $SD = 43.63$ ), irrespective of experimental condition, showed higher cortisol levels than the male participants ( $M = 17.60$ ,  $SD = 26.81$ ). Closer inspection of the means (see Table 19) suggested that this difference was driven by the

higher cortisol levels present in the Stress Female group. Bonferroni post-hoc comparisons confirmed this impression, as there was a significant difference between the Stress Female and Control Female groups,  $p < .001$ , while differences between the Stress Female and Stress Male groups were (barely) non-significant,  $p = .051$ . There were no significant differences between the Control Female and Control Male groups,  $p = 1.000$ .

Between-group analysis of the  $CORT_2$  data detected a significant main effect of Experimental Condition,  $F(1, 32) = 25.48, p < .001, \eta_p^2 = .48$ , but no significant main effect of Sex,  $p = .533$ , and no Experimental Condition x Sex interaction,  $p = .615$ . The Stress groups ( $M = 53.37, SD = 38.54$ ) continued to show significantly higher cortisol levels than the Control groups ( $M = 2.54, SD = 1.55$ ). In addition, the significant Sex difference seen at the  $CORT_1$  stage had disappeared by  $CORT_2$ . Thus, it is important to note that the participants in the Stress groups showed consistently higher cortisol levels following the manipulation on Day 2.

**STAI-State.** Figure 31 depicts the fluctuations in anxiety levels for the two experimental groups across the Day 2 testing session. Analysis detected no significant main effects of Time,  $p = .055$ , Experimental Condition,  $p = .833$ , and Sex,  $p = .627$ . The analysis also detected no significant Time x Experimental Condition,  $p = .459$ , Experimental Condition x Sex,  $p = .662$ , Time x Sex,  $p = .223$ , or Time x Experimental Condition x Sex,  $p = .916$ , interaction effects. These results suggest that all participants, regardless of sex or group assignment, showed similar levels of self-reported anxiety across the testing session on Day 2. Most importantly, the experimental manipulation did not have an effect on the subjective anxiety levels of the participants.

In conclusion, analysis of both cortisol levels and self-reported anxiety levels shows the data trending in the predicted directions. Specifically, participants in the Stress groups showed, relative to those in the Control groups, an increase in cortisol levels, and there were no between-group differences in subjective anxiety levels (i.e., neither group showed, on average, any increases from baseline across subsequent measurement points).



*Figure 31.* Changes in self-reported state anxiety (STAI) levels on Day 2 for the combined Stress and combined Control groups. Error bars indicate standard error of means. Subscripts represent measurement point (e.g., STAI<sub>B</sub> is the first STAI measurement point, or baseline).

### CG Arena

The following series of analyses sought to (a) establish that participants in all groups showed equal competency in learning the locations of the targets in the CG Arena rooms, and (b) establish the effects of the experimental manipulation on memory retrieval for the locations of those targets, as well as for the contents and spatial layout of the pictures in the CG Arena rooms.

**Training phase: Visible-target trials.** As was the case in Study A and Study 1, the prediction here was that there would be no statistically significant between-group differences in path length across the four trials in the training room on Day 1 of testing. A 2 x 2 x 4 (Experimental Condition [Stress versus Control] x Sex [male versus female] x Trial [training trials 1-4]) repeated-measures ANOVA compared group differences in path length deviation from optimal across trials.

Due to a violation of the assumption of sphericity,  $\chi^2(5) = 25.46, p < .001$ , it was necessary to use a Greenhouse-Geisser degrees of freedom correction ( $\epsilon = 0.78$ ). The subsequent analysis detected no significant main effects of Experimental Condition,  $p = .794$ , Sex,  $p = .939$ , and of Trial,  $p = .069$ . There were no significant interaction effects between Experimental Condition x Trial,  $p = .441$ , Experimental Condition x Sex,  $p = .807$ , Sex x Trial,  $p = .075$ , and Experimental Condition x Sex x Trial,  $p = .060$ . Thus, the analysis suggested (a) there were no significant between-group or between-sex differences in

deviation from optimal path length across the four training trials, and (b) performance on the four training trials was, in all participants, equally efficient.

**Acquisition phase: Invisible-target trials.** The following series of analyses sought to establish whether all experimental groups showed a similar degree of learning across the six acquisition trials in each of the three CG Arena experimental rooms. In addition, I analyzed data from the final trial of the acquisition phase (Trial 6) separately in order to determine whether all groups were performing with relatively equal efficiency by the end of the set of trials.

**Trials 1–6.** Figure 32 shows the mean deviation from the optimal path length for each of the experimental groups on each of the acquisition trials in CG Arena experimental rooms. To determine if any of the groups showed a distinct performance advantage or disadvantage in any of the CG Arena rooms, three separate 2 x 2 x 6 (Experimental Condition [Stress versus Control] x Sex [male versus female] x Trial [acquisition trials 1-6]) repeated-measures ANOVAs (one for the data from each of the rooms) were used to compare differences in path length deviation from optimal.

*Cool room.* Due to a violation of the assumption of sphericity,  $\chi^2(14) = 108.17, p < .001$ , it was necessary to use a Greenhouse-Geisser degrees of freedom correction ( $\epsilon = 0.54$ ). Subsequent analyses detected significant main effects of both Trial,  $F(2.68, 150.32) = 10.31, p < .001, \eta_p^2 = .16$ , and Sex,  $F(1, 56) = 4.46, p = .039, \eta_p^2 = .07$ , in the absence of a significant main effect of Experimental Condition,  $p = .817$ . The analysis detected no significant Experimental Condition x Trial,  $p = .076$ , Experimental Condition x Sex,  $p = .765$ , Sex x Trial,  $p = .145$ , and Experimental Condition x Sex x Trial,  $p = .419$ , interaction effects.

Thus, this analysis suggested there was a change in path length across the six acquisition trials. As depicted in Figure 32, the mean deviation from the optimal path length decreased, for all groups, across the trials. The decrease indicates that the participants were able to find the target more efficiently as the trials proceeded in the Cool room. In addition, there was a significant main effect of Sex across the acquisition trials. On average across the six acquisition trials, male participants ( $M = 166.44, SD = 269.90$ ) took significantly longer path lengths to the target than female participants ( $M = 95.88, SD = 152.96$ ).

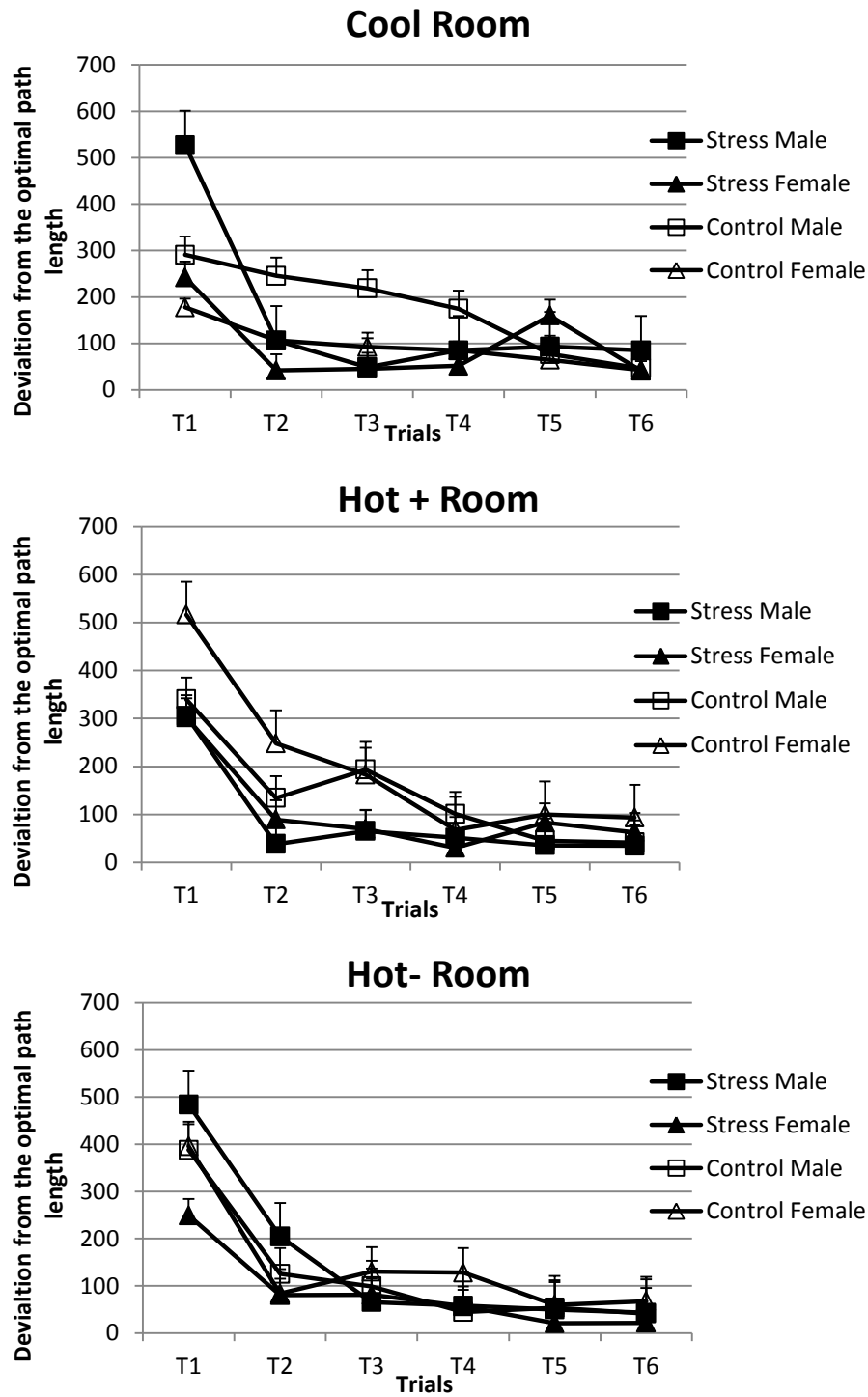


Figure 32. Mean deviation from the optimal path length across the acquisition trials in the Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. Error bars indicate standard error of means.

*Hot Appetitive room.* Due to a violation of the assumption of sphericity,  $\chi^2(14) = 144.11, p < .001$ , it was necessary to use a Greenhouse-Geisser degrees of freedom correction ( $\epsilon = 0.46$ ). Subsequent analyses detected significant main effects of Trial,  $F(2.31, 129.38) = 18.55, p < .001, \eta_p^2 = .25$ , and Experimental Condition,  $F(1, 56) = 5.09, p = .028, \eta_p^2 = .08$ , in the absence of a significant main effect of Sex,  $p = .142$ . There were no significant Experimental Condition x Trial,  $p = .301$ , Experimental Condition x Sex,  $p = .580$ , Sex x Trial,  $p = .407$ , and Experimental Condition x Sex x Trial,  $p = .625$ , interaction effects.

The analysis here therefore showed the expected change in path length, indicating progressively more efficient location of the hidden target, across trials. Interestingly this time, Experimental Condition was a significant factor across trials. Specifically, participants in the Stress groups ( $M = 103.21, SD = 137.47$ ) took a significantly shorter path length to the target than those in the Control groups ( $M = 175.12, SD = 236.21$ ).

*Hot Defensive Room.* Due to a violation of the assumption of sphericity,  $\chi^2(14) = 220.37, p < .001$ , it was once again necessary to use a Greenhouse-Geisser degrees of freedom correction ( $\epsilon = 0.39$ ). Subsequent analyses detected a significant main effect of Trial,  $F(1.97, 110.10) = 32.08, p < .001, \eta_p^2 = .36$ , in the absence of significant main effects of Experimental Condition,  $p = .428$ , or of Sex,  $p = .597$ . There were no significant Experimental Condition x Trial,  $p = .615$ , Experimental Condition x Sex,  $p = .117$ , Sex x Trial,  $p = .141$ , and Experimental Condition x Sex x Trial,  $p = .436$ , interaction effects.

Thus, similar to performance in the other two rooms, participants in all groups showed, on average, a significant decrease in deviation from the optimal path length across the trials (see Figure 32), suggesting they found the hidden target with increasing efficiency. In this room, none of the groups showed a distinct advantage or disadvantage in terms of learning the location of the hidden target.

**Trial 6.** To determine whether participants in all groups could find the location of the hidden target with relatively equal efficiency by the end of the set of acquisition trials, I analysed the data from the final trial (Trial 6) in each of the CG Arena rooms. First, Trial 6 performance in the three rooms was compared using a 2 x 2 x 3 (Experimental Condition [Stress versus Control] x Sex [male versus female] x Room [Cool Appetitive versus Hot Appetitive versus Hot Defensive]) repeated-measures ANOVA. Second, Trial 6 performance in each room was analysed separately using a 2 x 2 (Experimental Condition [Stress versus Control] x Sex [male versus female]) ANOVA. Table 20 provides descriptive statistics for

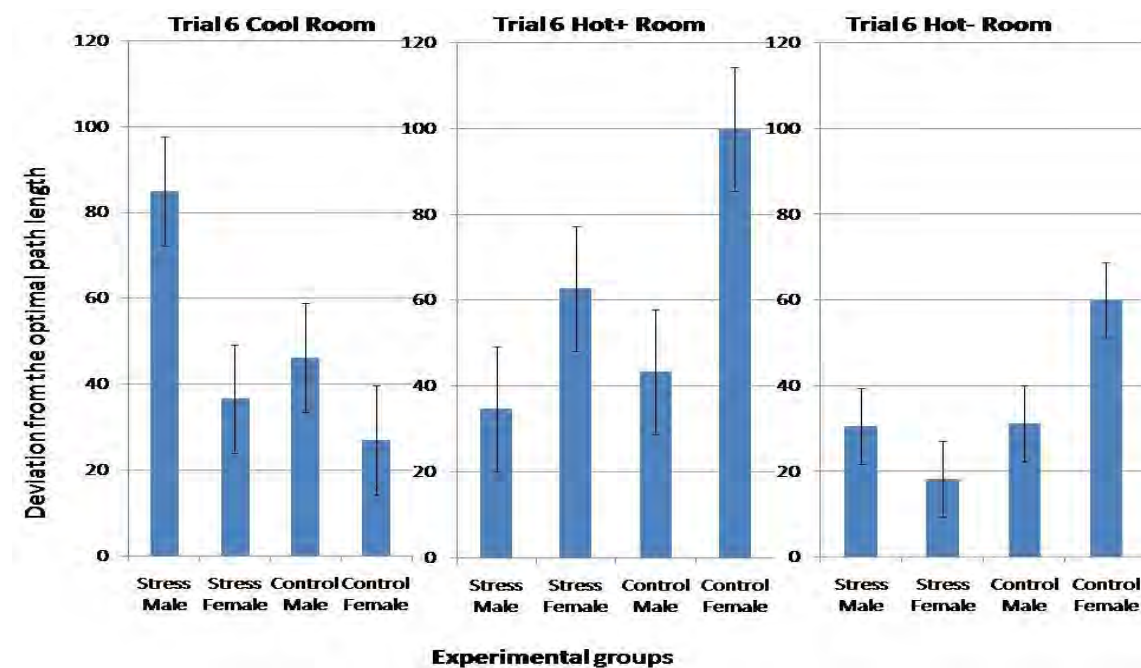
the experimental groups on Trial 6 in each of the CG Arena rooms; Figure 33 depicts these data graphically.

Table 20

*Descriptive Statistics for Trial 6 in each CG Arena room (N = 60)*

Room	Group			
	Stress		Control	
	Men ( <i>n</i> = 15)	Women ( <i>n</i> = 15)	Men ( <i>n</i> = 15)	Women ( <i>n</i> = 15)
Cool room	84.90 (133.82)	36.55 (53.75)	46.12 (67.34)	26.98 (28.43)
Hot Appetitive room	34.64 (44.85)	62.60 (157.13)	43.21 (53.81)	99.79 (119.50)
Hot Defensive room	30.65 (42.78)	18.28 (14.84)	31.30 (41.08)	59.99 (60.01)

*Note.* Data are *M* (*SD*) for deviation from optimal path length.



*Figure 33.* Mean deviation from the optimal path length on Trial 6 in the Cool, Hot Appetitive (Hot+), and Hot Defensive (Hot-) CG Arena rooms. Error bars indicate standard error of means.

Repeated measures analysis did not detect significant main effects of Room,  $p = .166$ , Experimental Condition,  $p = .667$ , or Sex,  $p = .718$ . However, analysis detected a significant Room x Sex interaction,  $F(2, 104) = 4.23$ ,  $p = .017$ ,  $\eta_p^2 = .08$ , in the absence of significant Experimental Condition x Room,  $p = .130$ , Experimental Condition x Sex,  $p = .287$ , and Experimental Condition x Sex x Room,  $p = .965$ , interaction effects.

To describe the significant interaction between Room and Sex further, I conducted a follow-up within-sex analysis of performance across the three rooms. This analysis showed that the female participants took a longer path length in the Hot Appetitive room ( $M = 80.51$ ,

$SD = 138.91$ ) than in either the Cool room ( $M = 31.94$ ,  $SD = 42.91$ ) or the Hot Defensive room ( $M = 38.36$ ,  $SD = 47.15$ ). The analysis confirmed a significant difference between the female participants' path length in the Cool and Hot Appetitive rooms,  $F(1, 26) = 5.03$ ,  $p = .034$ ,  $\eta_p^2 = .16$ , but not between that in the Hot Appetitive and Hot Defensive rooms,  $p = .121$ . In contrast, male participants took a longer path length in the Cool room ( $M = 66.18$ ,  $SD = 106.99$ ) than in the Hot Appetitive room ( $M = 38.78$ ,  $SD = 48.67$ ) and in the Hot Defensive room ( $M = 30.96$ ,  $SD = 41.21$ ). However, there was no significant difference in path length between the Cool room and the Hot Appetitive room,  $p = .153$ , or between the Cool room and the Hot Defensive room,  $p = .079$  for the male participants. Therefore, the significant Sex x Room interaction appears to be driven by female, but not male, participants taking a significantly longer path length in the Hot Appetitive room than in the Cool room.

A second set of analyses aimed to determine whether all groups learned the location of the target with relatively equal efficiency in each of three CG Arena rooms. Analysis of the Cool room data did not detect significant main effects of Experimental Condition,  $p = .388$ , or Sex,  $p = .276$ . The analysis also detected no significant Experimental Condition x Sex interaction,  $p = .352$ .

Analysis of the Hot Appetitive room data did not detect significant main effects of Experimental Condition,  $p = .489$ , or Sex,  $p = .144$ . The analysis also detected no significant Experimental Condition x Sex interaction,  $p = .660$ .

Finally, analysis of the Hot Defensive room data detected no significant main effects of Experimental Condition,  $p = .053$ ,  $\eta_p^2 = .07$ , or Sex,  $p = .222$ . The analysis also detected no significant Experimental Condition x Sex interaction,  $p = .060$ ,  $\eta_p^2 = .06$ . Despite not being significantly different, several of the above effects bordered on significance. Notably, the Stress groups ( $M = 26.52$ ,  $SD = 33.50$ ) showed a non-significantly shorter path length than the Control groups ( $M = 50.28$ ,  $SD = 58.00$ ) on the final trial in the Hot Defensive room. This difference seems to be driven by the differing performances in the Stress Female and Control Female groups (see Table 20).

In summary, analysis of data from the acquisition trials revealed that, for the most part, the experimental groups showed a similar degree of learning across the six acquisition trials in the CG Arena. However, three distinct significant effects were prominent in analyses of performance on the acquisition trials. First, there was significant sex difference across the acquisition trials in the Cool room: In this room, female participants took a significantly shorter path length across trials than male participants. Second, there was a significant effect of Experimental Condition across trials in the Hot Appetitive room: In this room, participants

in the Stress groups took, on average, a more direct route to the location of the target than the Control groups did. Third, analysis of Trial 6 showed a significant Sex x Room interaction effect, which could be isolated to the fact that female participants took a significantly shorter path length in the Cool room than in the Hot Appetitive room. These significant results suggest that some participants performed better than others on the acquisition trials; hence, interpretation of recall performance should be viewed with the caution appropriate to consideration of these differences.

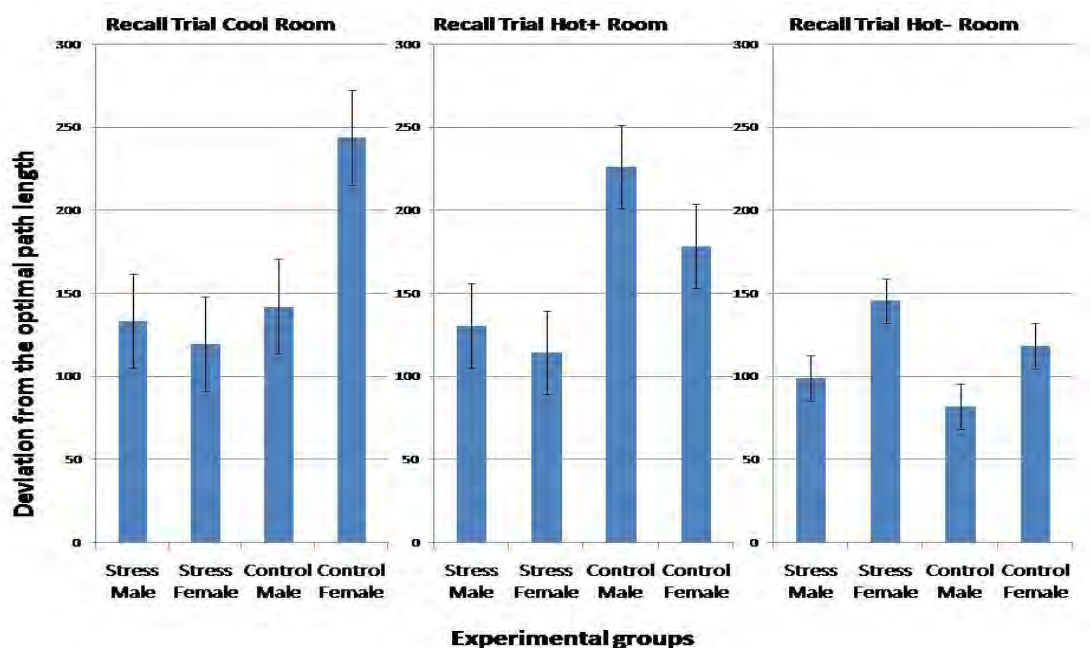
**Recall phase.** The following series of analyses sought to establish the effects of the experimental manipulation on recall for the visual and spatial elements of the CG Arena rooms to which the participant had been exposed on the previous day. First, I compared recall performance for the three rooms using a 2 x 2 x 3 (Experimental Condition [Stress versus Control] x Sex [male versus female] x Room [Cool versus Hot Defensive versus Hot Appetitive]) repeated-measures ANOVA. Second, I analyzed the data from each room separately using a 2 x 2 (Experimental Condition [Stress versus Control] x Sex [male versus female]) ANOVA. Bonferroni post-hoc pairwise comparisons further analyzed significant main effects. Table 21 provides the descriptive statistics for each CG Arena recall task on Day 2.

Table 21  
*Descriptive Statistics for Recall Performance in each of the CG Arena rooms (N = 60)*

Room /Outcome variable	Group			
	Stress		Control	
	Men (n = 15)	Women (n = 15)	Men (n = 15)	Women (n = 15)
<b>Cool Room</b>				
Recall trial	133.47 (186.43)	119.61 (142.96)	142.29 (199.50)	243.97 (254.83)
Dwell time	73.43 (20.37)	77.20 (13.76)	55.80 (27.86)	69.12 (26.85)
ART score	22.60 (3.66)	20.53 (6.72)	20.87 (5.84)	18.73 (5.08)
ORT <i>d'</i> score	1.02 (0.65)	1.23 (0.40)	1.40 (0.58)	1.27 (0.72)
<b>Hot Appetitive Room</b>				
Recall trial	243.97 (254.83)	114.52 (152.06)	226.18 (255.72)	178.53 (194.76)
Dwell time	72.81 (22.78)	74.98 (11.45)	59.97 (20.60)	66.87 (23.87)
ART score	19.87 (5.48)	21.33(4.01)	21.60 (5.87)	20.07 (7.03)
ORT <i>d'</i> score	1.35 (0.70)	1.96 (0.67)	1.56 (0.70)	1.73 (0.76)
<b>Hot Defensive Room</b>				
Recall trial	98.91 (169.69)	145.49 (162.78)	81.96 (99.01)	118.27 (145.43)
Dwell time	71.39 (22.32)	75.81 (16.50)	68.74 (19.72)	67.71 (27.05)
ART score	17.07 (5.76)	17.87 (5.74)	17.80 (6.43)	19.93 (4.88)
ORT <i>d'</i> score	1.99 (0.55)	2.02 (0.68)	1.92 (0.50)	1.79 (0.63)

*Note.* Data are *M* (*SD*). Data for the variable labeled *Recall trial* are deviations from the optimal path length.

**Recall trial.** Figure 34 depicts each group's performance on the recall trial in each of the CG Arena rooms. Due to a violation of the assumption of normality, it was necessary to perform log transformations on the data. The repeated-measures ANOVA analysis detected no significant main effects of Room,  $p = .569$ , Experimental Condition,  $p = .775$ , or Sex,  $p = .199$ . There were also no significant Room x Sex,  $p = .392$ , Room x Experimental Condition,  $p = .313$ , Experimental Condition x Sex,  $p = .964$ , and Room x Experimental Condition x Sex,  $p = .558$ , interactions.



*Figure 34.* Mean deviation from the optimal path length for recall trial in the Cool, Hot Appetitive (Hot+), and Hot Defensive (Hot-) CG Arena rooms. Error bars indicate standard error of means.

A second set of analyses aimed to look more closely at between-group differences in each of the three CG Arena rooms separately. Analysis of the Cool room data did not detect significant main effects of Experimental Condition,  $p = .678$ , or Sex,  $p = .404$ , and detected no significant Experimental Condition x Sex interaction,  $p = .410$ .

Analysis of the Hot Appetitive room data also detected no significant main effects of Experimental Condition,  $p = .205$ , or Sex,  $p = .822$ , and no significant Experimental Condition x Sex interaction,  $p = .961$ .

Finally, analysis of the Hot Defensive room data detected no significant main effects of Experimental Condition,  $p = .967$ , or Sex,  $p = .188$ , and no significant Experimental Condition x Sex interaction,  $p = .768$ .

In summary, there were no significant within- or between-group differences in performance on the Day 2 recall trial, in any of the three CG arena rooms. In all three rooms, all participants, regardless of experimental condition or sex, re-located with equal efficiency the location at which the target had been hidden in the Day 1 acquisition trials.

**Probe Trial.** The series of analyses described in this section sought to describe the effects of the experimental manipulation on recall of the hidden target's location in the CG Arena rooms during the second recall (probe) trial. Figure 35 depicts each group's performance on the probe trial in each of the CG Arena rooms. Consistent with the analyses presented in Study 1, dwell time was calculated as the proportion of time the participant spent searching for the hidden target in the quadrant of the room where it had been located.

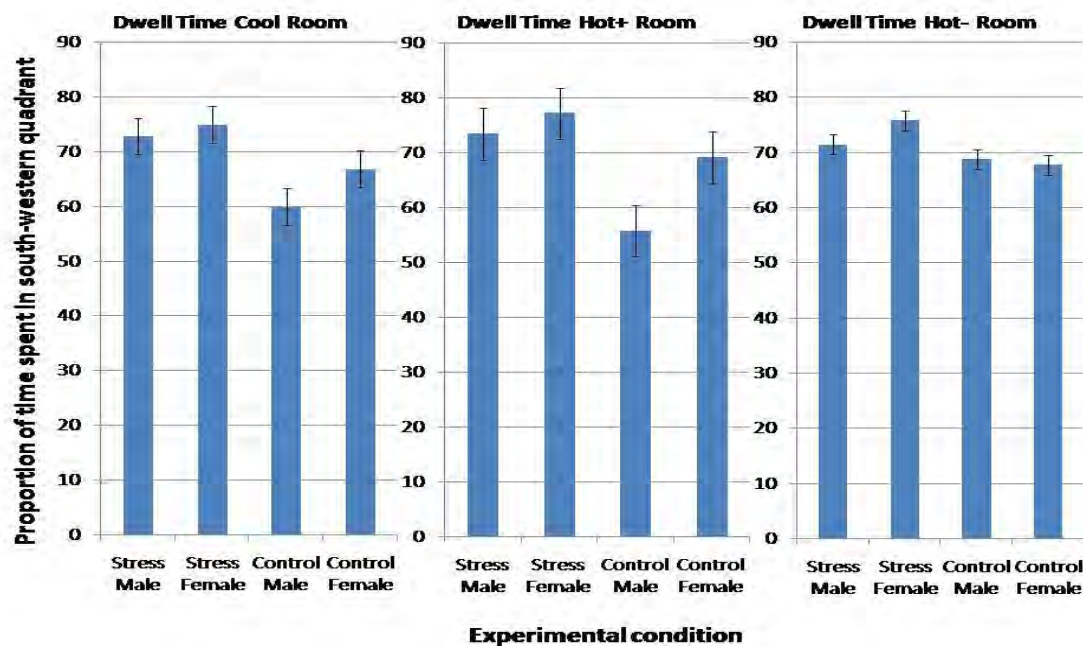


Figure 35. Mean proportion of dwell time in the Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. Error bars indicate standard error of means.

A repeated-measures ANOVA detected a significant main effect of Experimental Condition,  $F(1, 56) = 4.65$ ,  $p = .035$ ,  $\eta_p^2 = .07$ , in the absence of significant main effects of Room,  $p = .703$ , and Sex,  $p = .272$ . The analysis detected no significant Room x Sex,  $p = .509$ , Room x Experimental Condition,  $p = .435$ , Experimental Condition x Sex,  $p = .741$ , or Room x Experimental Condition x Sex,  $p = .435$ , interactions.

Regarding the significant main effect of Experimental Condition across all three rooms on the probe trial, participants in the Stress groups ( $M = 74.27$ ,  $SD = 18.11$ ) had a longer dwell time than those in the Control group ( $M = 64.70$ ,  $SD = 24.39$ ).

To determine whether this Experimental Condition effect was consistent across the three CG Arena rooms, I analyzed dwell time in each of the CG rooms separately. Analysis of the Cool room data detected a significant main effect of Experimental Condition,  $F(1, 56) = 4.00$ ,  $p = .050$ ,  $\eta_p^2 = .07$ , in the absence of a significant Sex effect,  $p = .390$ , or a significant Experimental Condition x Sex interaction,  $p = .653$ . Thus, in the Cool room, participants in the Stress groups ( $M = 73.89$ ,  $SD = 17.75$ ) spent, on average, a longer time searching in the quadrant where the target had been located than did participants in the Control groups ( $M = 63.41$ ,  $SD = 22.19$ ).

Analysis of data from the Hot Appetitive room detected the same pattern as observed in Cool room. That is, the analysis detected a significant main effect of Experimental Condition,  $F(1, 56) = 4.72$ ,  $p = .034$ ,  $\eta_p^2 = .08$ , in the absence of a significant Sex effect,  $p = .154$ , or a significant Experimental Condition x Sex interaction,  $p = .423$ . Once again, participants in the Stress groups ( $M = 75.31$ ,  $SD = 17.19$ ) spent, on average, more time searching in the quadrant where the target had been than did participants in the Control groups ( $M = 62.46$ ,  $SD = 27.72$ ).

Finally, analysis of data from the Hot Defensive room detected no significant main effect of Experimental Condition,  $p = .342$ , or of Sex,  $p = .764$ , and no significant Experimental Condition x Sex interaction,  $p = .630$ .

In summary, analysis of probe-trial dwell time data revealed that, on average and in the Cool and Hot Appetitive rooms only, participants in the Stress groups spent longer in the quadrant where the targets had been than did participants in the Control group.

**ORT  $d'$  score.** The series of analyses described in this section sought to describe the effects of the experimental manipulation on recognition memory for the pictures that hung on the walls of the three CG Arena rooms. Figure 36 depicts each group's mean ORT  $d'$  scores for each of the CG Arena rooms.

A repeated-measures ANOVA detected a significant main effect of Room,  $F(2, 112) = 18.54$ ,  $p < .001$ ,  $\eta_p^2 = .25$ , but no significant main effect of Experimental Condition,  $p = .858$ , or of Sex,  $p = .188$ . The analysis also detected no significant Room x Sex,  $p = .140$ , Room x Experimental Condition,  $p = .298$ , Experimental Condition x Sex,  $p = .105$ , or Room x Experimental Condition x Sex,  $p = .830$ , interactions.

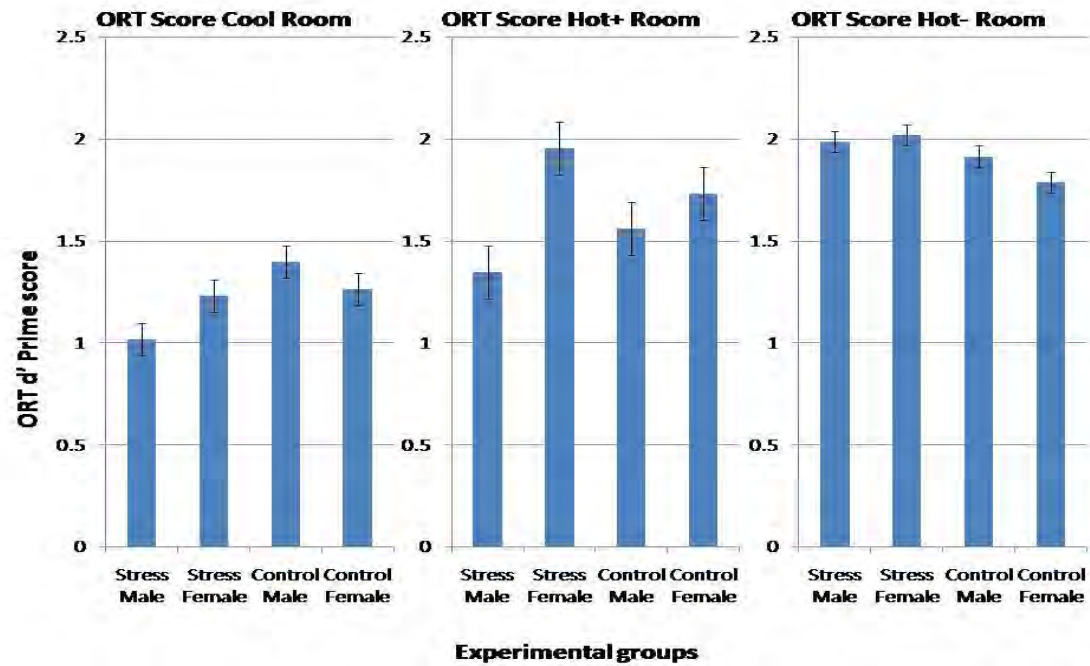


Figure 36. Mean ORT  $d'$  scores for the Cool, Hot Appetitive (Hot+), and Hot Defensive (Hot-) CG Arena rooms. Error bars indicate standard error of means.

This pattern of data, and the means depicted in Figure 36 and in Table 21, suggests that participants, regardless of their sex or the experimental condition to which they were exposed, showed the best recognition for the pictures that had been in the Hot Defensive room ( $M = 1.93$ ,  $SD = 0.59$ ) followed by those that had been in the Hot Appetitive room ( $M = 1.65$ ,  $SD = 0.71$ ), and then followed by those that had been in the Cool room ( $M = 1.23$ ,  $SD = 0.59$ ). A series of Bonferroni pairwise comparisons detected a significant difference in ORT  $d'$  scores between the Hot Defensive room and those from the Cool room,  $p < .001$ , and between those from the Hot Appetitive room and those from the Cool room,  $p = .002$ . The analysis did not detect a significant difference between ORT  $d'$  scores from the Hot Defensive room and those from the Hot Appetitive room,  $p = .111$ .

To examine between-group differences in recognition memory more closely, I analyzed  $d'$  scores in each of the three CG Arena rooms separately. Analysis of the Cool room data detected no significant main effect of Experimental Condition,  $p = .185$ , or Sex,  $p = .800$ , and no significant Experimental x Condition and Sex interaction,  $p = .270$ .

Analysis of the Hot Appetitive room data detected a significant main effect of Sex,  $F(1, 56) = 4.55$ ,  $p = .037$ ,  $\eta_p^2 = .08$ , in the absence of a significant Experimental Condition effect,  $p = .980$ , or a significant Experimental Condition x Sex interaction,  $p = .237$ . Female participants ( $M = 1.85$ ,  $SD = 0.71$ ), irrespective of assigned experimental condition, displayed

better recognition memory for the pictures in the Hot Appetitive room than male participants ( $M = 1.46, SD = 0.69$ ).

Finally, analysis of the Hot Defensive room data detected no significant main effect of Experimental Condition,  $p = .324$ , or of Sex,  $p = .754$ , and no significant Experimental Condition x Sex interaction,  $p = .605$ .

In summary, analyses of the ORT  $d'$  scores indicates that, on average, participants' recognition memory was better for the arousing stimuli, irrespective of the valence of the pictures. In addition, female participants (irrespective of the experimental condition to which they had been assigned) displayed better recognition than male participants for the pictures that had been in the Hot Appetitive room.

**ART score.** The series of analyses described in this section sought to describe the effects of the experimental manipulation on cued recall for the spatial layout of the pictures that had hung on the walls of each of the three CG Arena rooms. Figure 37 depicts each group's mean ART displacement score for each of the CG Arena rooms. Lower scores indicate better performance in reconstructing the spatial layout of the rooms.<sup>30</sup>

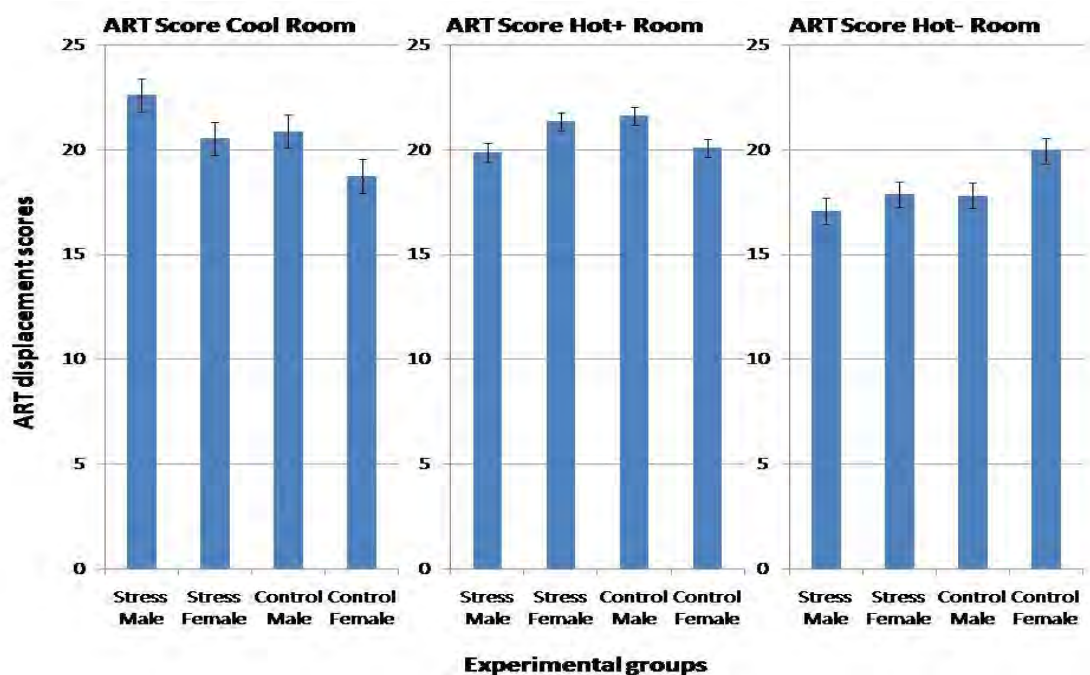


Figure 37. Mean ART displacement scores for the Cool, Hot Appetitive (Hot+), and Hot (Hot-) Defensive CG Arena rooms. Error bars indicate standard error of means.

<sup>30</sup>The ART displacement score is introduced in Study A (pg. 62) and a worked example is presented in Appendix F.

A repeated-measures ANOVA detected a significant main effect of Room  $F(2, 112) = 4.70, p = .011, \eta_p^2 = .08$ , in the absence of significant main effects of Experimental Condition,  $p = .963$ , and Sex,  $p = .815$ . The analysis also detected no significant Room x Sex,  $p = .177$ , Room x Experimental Condition,  $p = .249$ , Experimental Condition x Sex,  $p = .761$ , or Room x Experimental Condition x Sex,  $p = .513$ , interactions. This analysis reflects that participants, on average and regardless of their sex or the experimental condition to which they had been exposed, showed better memory for the spatial layout of the pictures in the Hot Defensive room ( $M = 18.17, SD = 5.68$ ) than for that in the Hot Appetitive room ( $M = 20.72, SD = 5.60$ ) and for that in the Cool room ( $M = 20.68, SD = 5.49$ ). Regarding those ART scores, a series of Bonferroni pairwise comparisons detected (a) a significant difference between performance for the Hot Defensive room stimuli and that for the Cool room stimuli,  $p = .016$ , (b) no significant difference between performance for the Hot Defensive room stimuli and that for the Hot Appetitive room stimuli,  $p = .056$ , and (c) no significant difference between performance for the Cool room stimuli and that the Hot Appetitive room stimuli,  $p = 1.000$ .

Analysis of the Cool room data (similar to that described in the previous section) detected no significant main effect of Experimental Condition,  $p = .214$ , or of Sex,  $p = .141$ , and no significant Experimental Condition x Sex interaction,  $p = .981$ .

Analysis of the Hot Appetitive room data detected no significant main effect of Experimental Condition,  $p = .875$ , or of Sex,  $p = .982$ , and no significant Experimental Condition x Sex interaction,  $p = .312$ .

Finally, analysis of the Hot Defensive room data detected no significant main effect of Experimental Condition,  $p = .348$ , or of Sex,  $p = .326$ , and no significant Experimental Condition x Sex interaction,  $p = .654$ .

In summary, analysis of the ART displacement scores showed that, on average, all participants (regardless of assigned experimental condition or sex) recalled the spatial layout of the pictures in the Hot Defensive room better than that for the pictures in the other two rooms. The analyses detected no between-group differences for recall of the spatial layout of the pictures in any of the three CG Arena rooms.

### **Verbal Paired Associates Test**

**Day 1: Immediate recall trials.** To investigate whether there were between-group differences with regard to recall of the word list across the two Day 1 trials, I first used a  $2 \times 2 \times 2$  (Experimental Condition [Stress versus Control] x Sex [male versus female] x Trial

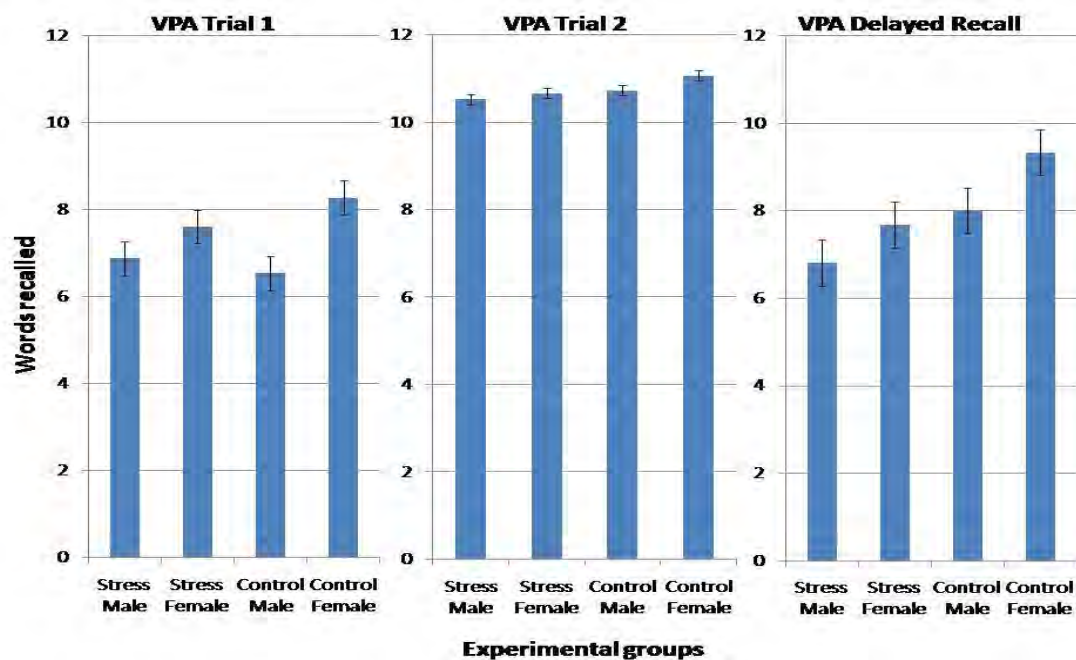
[VPA recall trials 1 and 2]) repeated-measures ANOVA. Second, I analyzed performance on each trial separately using 2 x 2 (Experimental Condition [Stress versus Control] x Sex [male versus female]) factorial ANOVAs. Table 22 presents descriptive data for the VPA; Figure 38 displays these data graphically.

Table 22

*Descriptive Statistics for Verbal Paired Associates Test Recall and Percentage Retained scores (N = 60)*

Outcome variable	Group			
	Stress		Control	
	Men (n = 15)	Women (n = 15)	Men (n = 15)	Women (n = 15)
VPA trial 1	6.87 (2.50)	7.60 (3.48)	6.53 (3.07)	8.27 (3.63)
VPA trial 2	10.53 (2.97)	10.67 (3.18)	10.73 (3.26)	11.07 (3.51)
VPA delayed recall	6.80 (3.19)	7.67 (3.15)	8.00 (3.64)	9.33 (3.74)
Percentage retained	63.10 (20.63)	70.18 (19.18)	74.19 (20.77)	83.87 (19.16)

*Note.* Data presented are means, with standard deviations in parentheses.



*Figure 38.* Mean number of words recalled on each trial of the Verbal Paired Associates Test (VPA). Error bars indicate standard error of means.

The repeated-measures analysis detected a significant main effect of Trial,  $F(1, 56) = 356.61, p < .001, \eta_p^2 = .86$ , in the absence of significant main effects of Experimental Condition,  $p = .775$ , and Sex,  $p = .370$ . The analysis also detected a significant Trial x Sex interaction,  $F(1, 56) = 7.50, p = .008, \eta_p^2 = .12$ , in the absence of Trial x Experimental

Condition,  $p = .715$ , Experimental Condition x Sex,  $p = .713$ , or Trial x Experimental Condition x Sex,  $p = .276$ , interactions.

These results suggest that all participants, regardless of experimental group, recalled significantly more words on the second recall trial than on the first. Regarding the significant Sex x Trials interaction, male participants displayed a mean increase of 3.93 words from the first recall ( $M = 6.70$ ,  $SD = 2.50$ ) to the second recall ( $M = 10.63$ ,  $SD = 3.07$ ). Female participants, on the other hand, displayed a smaller mean increase of 2.94 words from first ( $M = 7.93$ ,  $SD = 3.19$ ) to second recall ( $M = 10.87$ ,  $SD = 3.30$ ).

The factorial ANOVA examining data from the first recall trial detected no significant main effect of Experimental Condition,  $p = .814$ , or of Sex,  $p = .141$ , and no significant Experimental Condition x Sex interaction,  $p = .548$ .

The factorial ANOVA examining data from the second recall trial also detected no significant main effect of Experimental Condition,  $p = .721$ , or of Sex,  $p = .781$ , and no significant Experimental Condition x Sex interaction,  $p = .905$ .

In summary, analysis of the two immediate recall trials showed that all participants, regardless of experimental group, benefitted from the second presentation of the word list. On the average, participants in all groups recalled a greater number of word pairs after the second presentation of the pairs than after the first. In particular, male participants showed a noticeable improvement in the number of words recalled after the second presentation. There were no between-group differences in performance on either immediate recall trial, suggesting that no group showed a distinct advantage or disadvantage in recalling previously-presented verbal information.

**Day 2: Delayed recall.** To investigate whether there were between-group differences with regard to recall of the word list on the delayed recall trial, I first compared performance on the delayed recall trial (Trial 3) with that on the final Day 1 trial (Trial 2) using a 2 x 2 x 2 (Experimental Condition [Stress versus Control] x Sex [male versus female] x Trial [VPA Trial 2 versus Trial 3]) repeated-measures ANOVA. Second, I analyzed performance on Trial 3 only using a 2 x 2 (Experimental Condition [Stress versus Control] x Sex [male versus female]) factorial ANOVA. Table 22 and Figure 38 present the data of relevance here.

The repeated-measures analysis detected a significant main effect of Trial,  $F(1, 56) = 116.15$ ,  $p < .001$ ,  $\eta_p^2 = .68$ , in the absence of significant main effects of Experimental Condition,  $p = .297$ , and Sex,  $p = .421$ . The analysis also detected a significant Trial x Experimental Condition interaction,  $F(1, 56) = 4.76$ ,  $p = .033$ ,  $\eta_p^2 = .08$ , in the absence of

Trial x Sex,  $p = .101$ , Experimental Condition x Sex,  $p = .840$ , and Trial x Experimental Condition x Sex,  $p = .798$ , interactions.

Taken together with the data presented in Table 22, these analyses suggest that all participants, regardless of Experimental Condition or Sex, recalled significantly fewer word pairs on the delayed recall trial than on the second immediate recall trial. In particular, participants in the Stress groups showed, on average, a marked decrease in the number of words (3.37 words) recalled on the delayed recall trial ( $M = 7.23$ ,  $SD = 3.19$ ) from that recalled on the second immediate recall trial ( $M = 10.60$ ,  $SD = 3.02$ ). Control participants, showed, on average, a smaller decrease (2.23 words) from Trial 2 ( $M = 10.90$ ,  $SD = 3.34$ ) to Trial 3 ( $M = 8.67$ ,  $SD = 3.67$ ).

The second set of analyses investigated whether between-group differences were apparent on the delayed recall trial. The factorial ANOVA detected no significant main effect of Experimental Condition,  $p = .112$ , or of Sex,  $p = .221$ , and no significant Experimental Condition x Sex interaction,  $p = .794$ .

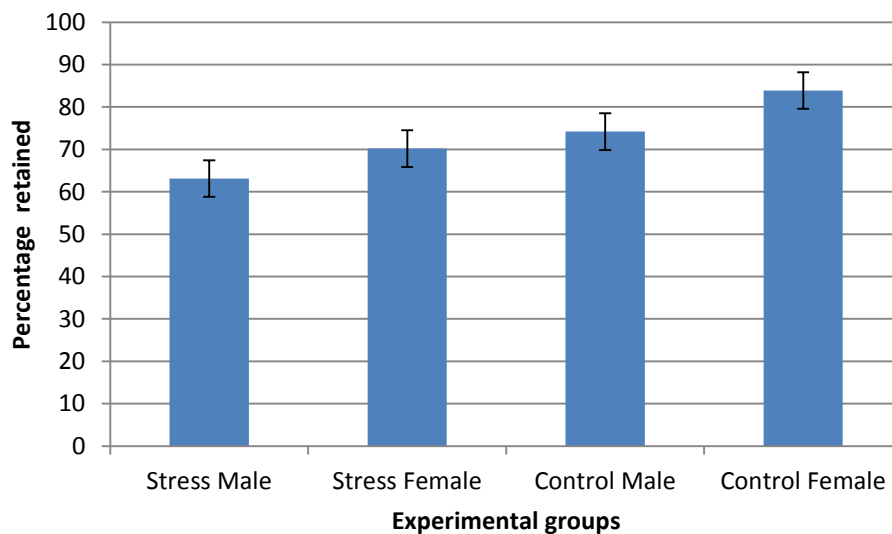
In summary, analysis of performance on the delayed recall trial revealed that participants in all groups showed a decline from the second immediate recall trial. This result suggests that the 24-hour delay in recall had a detrimental effect on cued-recall memory for the word list. Furthermore, this effect held constant regardless of the participant's sex or the experimental condition to which s/he had been exposed. However, participants in the Stress groups displayed, on average, a more pronounced decline in performance than participants in the Control groups. This result suggests that the experimental manipulation may have had a detrimental effect on the Stress-group participants' ability to retrieve previously-learned verbal information.

**Percentage retained.** To determine whether between-group differences were apparent after taking into account possible within- and between-subject variance in initial learning of the word pairs, I analyzed percentage retained scores using a 2 x 2 (Experimental Condition [Stress versus Control] x Sex [male versus female]) ANOVA. Table 22 presents the relevant descriptive statistics; Figure 39 displays these data graphically.

The analysis detected a significant main effect of Experimental Condition,  $F(1, 56) = 5.79$ ,  $p = .019$ ,  $\eta_p^2 = .09$ , in the absence of a significant main effect of Sex effect,  $p = .109$ , and of a significant Experimental Condition x Sex interaction,  $p = .802$ .

Thus, the comparison of the percentage retained scores revealed that the Stress groups ( $M = 66.64$ ,  $SD = 19.90$ ) showed significantly lower percentage retained scores in comparison to the Control groups ( $M = 79.04$ ,  $SD = 20.24$ ). This result is consistent with that

presented above in suggesting that cortisol administration had an impairing effect on Stress-groups participants' retrieval of the word pairs.



*Figure 39.* Mean percentage retained scores for the delayed recall trial of the Verbal Paired Associates Test. Error bars indicate standard error of means.

### Discussion

This study aimed to examine the effects of an acute increase in cortisol on visual and spatial memory retrieval. In addition, it sought to examine what influence emotional arousal, of varying valence, would have on that retrieval. As discussed in Chapter 1, cortisol is the primary stress hormone released following activation of the HPA axis, and is believed to be a primary modulator of stress-induced memory effects.

To replicate the design of de Quervain et al. (1998), the present study continued on from Study 1, which examined the effects of an acute stressor on visual and spatial memory retrieval. The data from Study 1 suggested that acute stress did not have an impairing effect on either verbal, visual, or spatial memory retrieval. Participants exposed to the FFST stress manipulation showed equivalent and, in some cases, better memory retrieval performance compared to controls. Subsequent comparison of performance by the cortisol responders in the Stress groups with that of the Control participants revealed that the effect sizes of the enhancing effects of stress were slightly increased. The present study also aimed to examine, then, whether elevated cortisol levels were responsible for these observed selective enhancements in memory retrieval performance.

This study, then, tested the following hypotheses:

- 1) Overall, elevated cortisol levels will have an impairing effect on memory retrieval.
- 2) Memory for the different rooms will be influenced by the arousal content of the pictures used as landmarks in the CG Arena.
- 3) Women will, relative to men, display inferior spatial memory.

As was the case in Study 1, 60 participants learned the location of a hidden target in the same three CG Arena rooms that had been created and verified earlier (see Chapter 2, Study A). Twenty-four hours after having learnt the locations of those hidden targets, the participants returned to the laboratory and were randomly assigned to either an experimental (Stress) or placebo (Control) condition. Those in the Female and Male Stress groups received 25mg of Prednisone; those in the Female and Male Control groups received a placebo capsule. One hour after taking the cortisol/placebo capsule, the participants completed tests of recognition (ORT), spatial recall (ART), and wayfinding in the CG Arena rooms that had been learnt the previous day. They also completed a delayed recall trial of the Verbal Paired Associates (VPA) test.

Analysis of the sample characteristics indicated there were no significant between-group differences in age, current depressive symptomatology, or trait anxiety. Hence, participants in the four groups were sampled from the same population and were in a similar (viz., neutral) emotional state when entering the experimental environment.

### **Summary of Results**

In the first session, participants completed training and acquisition trials in the CG Arena rooms. Analysis of path lengths on the training trials showed that there were no between-group differences in performance. Therefore, all participants, regardless of sex or the experimental condition to which they had been assigned, entered the acquisition trials showing a similar degree of competency in manipulating the joystick for the purpose of navigating to a specific location in the CG Arena.

After completing the training trials, participants proceeded to learn the location of a hidden target in each of the three CG Arena rooms (Cool, Hot Defensive, and Hot Appetitive). To determine whether there were between-group performance differences during the acquisition phase, I analyzed path lengths across the six acquisition trials. Given that the experimental manipulation was only to occur the following day, I predicted that there would be no significant between-group differences. This prediction was only partially confirmed, however. Although there were largely similar learning patterns across trials in the groups,

there were some significant between-group differences in learning performance in both the Cool and Hot Appetitive rooms.

In the Cool room, there was a significant sex difference across the six acquisition trials. In comparison to male participants, female participants displayed a significantly shorter average path length (i.e., they took a more direct route to the location of the target). Similarly, in the Hot Appetitive room, Stress-group participants took a more direct route to the target than Control-group participants did. As discussed in Chapter 4, a significantly shorter path length across trials could be interpreted as being either an advantage or a disadvantage for later retrieval of information about the room. On the one hand, finding the target more directly may indicate that the participants had a better idea of the location of the target, and therefore had a better idea of the spatial relations among different elements of the room. On the other hand, however, taking a more direct route to the target means that the participant spends less time in the room, and therefore has less time to become familiar with images on the walls, and with the spatial layout of the room.

Analysis of data from the final acquisition trial (Trial 6) revealed that the above-mentioned between-group differences, although present on the average across trials, were not present on the final trial. However, the analysis also showed that the female, but not male, participants took a more direct route to the target in the Cool room than in the Hot Appetitive room. It is possible, of course, that this result might be a residual effect of the significantly shorter path length displayed by the women (in comparison to the men) across the acquisition trials in the Cool room. Taken together, their superior performance across the trials in the Cool room might indicate that women had learnt the location of the target in that room better than they did in the Hot Appetitive room. Overall, interpretation of recall performance on Day 2 should, consequently, be viewed with appropriate caution in light of these Day 1 learning differences in the CG Arena.

In addition to learning the location of the hidden targets in the CG Arena rooms, the participants also learned the 15 word pairs that constituted the VPA. Again, given that the experimental manipulation was to take place the following day, I predicted that there would be no significant between-group differences on the Day 1 immediate recall trials of the VPA. Statistical analyses confirmed this prediction.

In summary, initial statistical analyses confirmed that, on average, participants in the four groups (Stress Female, Stress Male, Control Female, and Control Male) were of a similar age and in a similar emotional state when entering the experiment. On Day 1 in the CG Arena rooms, the groups demonstrated a similar learning pattern, with the only

exceptions being the main effects of Sex and of Experimental Condition across the six acquisition trials in the Cool and Hot Appetitive rooms, respectively. Analysis of Trial 6 performance confirmed that the groups were performing equally efficiently at that point and equally efficiently across rooms, although it did appear that women found the target in the Cool room more directly than they did in the Hot Appetitive room. In terms of VPA performance, there were no significant between-group differences, although the men derived greater benefit from the second presentation of the word list.

Twenty-four hours after the first testing session, the participants returned to the laboratory and were assigned randomly to an experimental condition. After physiological and self-report baseline measures were taken, participants were administered either the cortisol or placebo dose. The purpose of the experimental manipulation in this study was to isolate the effects of cortisol on memory (i.e., to significantly raise the cortisol levels, but not the subjective anxiety levels) of the participants in the Stress groups. Analysis of the cortisol and self-report data confirmed the manipulation's success: Across groups and on average, participants started the Day 2 session with comparable cortisol and subjective anxiety levels. Following administration of the drug manipulation, however, those who had received prednisone showed significantly elevated cortisol levels relative to those who had received the placebo. Interestingly, women in the Stress group showed borderline significantly higher cortisol levels one hour following administration in comparison to the men in the Stress group. This result indicates that the administration of Prednisone increases salivary cortisol levels in women more rapidly than it does in men. To my knowledge, there is no previous literature supporting sex differences in Prednisone synthesis and, thus, this result warrants further exploration in a larger sample. This cortisol increase was not, however, associated with an increase in self-reported anxiety: On average, participants in the Stress and Control groups showed similar subjective anxiety levels throughout the Day 2 testing session.

An hour after cortisol or placebo administration, the participants completed the same set of recall and recognition tests that were administered in Study 1. Analyses of performance on those tests are discussed below, in relation to the stated hypotheses.

**Summary of results in relation to tested hypotheses.** As in Study 1, the first hypothesis tested was that, overall, stress/elevated cortisol levels would have an impairing effect on memory retrieval. This hypothesis was confirmed for the VPA. In comparison to the Control groups, the Stress groups retrieved significantly fewer word pairs on the delayed recall trial, even after taking into account relative performance on the immediate recall trials. This finding is consistent with previous studies demonstrating that an acute increase in

cortisol has an impairing effect on memory for verbal material (Buss et al., 2004; Coluccia et al., 2008; de Quervain et al., 2007; Domes et al., 2005; Het et al., 2005; Kuhlmann et al., 2005; Kuhlmann & Wolf, 2005; Smeets et al., 2008; Tollenaar et al., 2009; Wingefeld et al., 2012; Wolf et al., 2001). Of interest here, however, is that this impairing effect was not present in Study 1. Hence, it is possible that this impairment is due to a threshold effect: Cortisol levels were raised more markedly in Study 2 than in Study 1 (i.e., by the prednisone administration compared to the acute stressor), and so this relatively greater increase over baseline might be responsible for the negative effect on verbal memory.<sup>31</sup>

In contrast, and in disconfirmation of Hypothesis 1, prednisone administration did not impair memory retrieval performance on any of the visual or spatial tasks. In comparison to the Control groups, the Stress groups did not display inferior performance on the recall trials in the CG Arena, nor did they show impaired recognition of the spatial layout of the landmarks in the CG Arena. This finding is consistent with the analogous results in Study 1. In addition, the finding that prednisone administration, and consequent elevated cortisol, impaired retrieval of verbal material, but not visual and spatial material, is consistent with the findings of Domes et al. (2005).

Interestingly (because it stands in direct contradiction to what was predicted), prednisone administration appeared to have a positive effect on probe trial performance in the CG Arena. On the second Day 2 recall trial in each CG Arena room, the target was, unbeknownst to the participant, absent from the room. On that trial, Stress-group participants spent longer than Control-group participants searching for the target in the quadrant of the room where it had been located. Although the omnibus analysis suggested this difference was consistent across the three rooms, closer inspection of the data revealed that the effect was largely influenced by significant between-group differences in the Cool and Hot Appetitive CG Arena rooms.

As discussed in Study A, the rationale behind the probe trial was to determine the degree of reliance on spatial (hippocampal) versus non-spatial (caudate nucleus) navigation strategies (Vorhees & Williams, 2006). If interpreted accordingly, the present findings suggest that, when searching for the hidden target, Stress-group participants relied on spatial strategies more heavily than Control-group participants did. This finding is unexpected, as previous research has reported that, under stress, humans rely more on stimulus-response

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<sup>31</sup>Increases in cortisol concentrations following prednisone administration were between 6 and 10 times higher than those induced by the FFST in Study 1. The implications of these higher cortisol concentrations are discussed further in Chapter 6.

learning strategies than they do on spatial learning strategies (Schwabe & Wolf, 2013; Schwabe et al., 2007, 2008b; Thomas et al., 2010).<sup>32</sup>

One possible explanation for this curious pattern of data is that cortisol administration had an influence on the encoding phase, but not on the retrieval phase, of memory processing. In each of the three CG Arena rooms in Study 1 and in Study 2, the probe trial followed immediately after the first recall trial. During the recall trial, participants had an opportunity to find the hidden target and, hence, to refresh their learning from the previous day or to learn, anew, the location of the target. The probe trial that followed might then have tested *recent* memory for that confirmed/relearned target location (Vorhees & Williams, 2006). If this was the case, then the effects of prednisone administration would have been on encoding rather than on retrieval. In this case, then, the results observed here would be consistent with those reported previously in suggesting that there are positive effects of cortisol administration on encoding (see, e.g., Buchanan & Lovallo, 2001; Cornelisse et al., 2011).

Hypothesis 2 stated that memory for the three CG Arena rooms would be influenced by the arousal content of the pictures used as landmarks. Specifically, I predicted that Stress-group participants would show greater retrieval impairment for the arousing stimuli than for the neutral stimuli. Conversely, I predicted that Control-group participants would show enhanced retrieval for the arousing stimuli relative to neutral content. As was the case in Study 1, this hypothesis was only partially confirmed. That is, the results were in the predicted direction for the Control groups on both the recognition tasks and on recall for the spatial layout of the Hot Defensive room. As in Study 1, the Control-group participants showed better recognition for the pictures in the arousing CG Arena rooms (irrespective of valence) than for those in the Cool room. In addition, the Control-group participants recalled the spatial layout of the landmarks in the Hot Defensive room better than that in the Cool and Hot Appetitive rooms.

However, consistent with the data obtained in Study 1, the Stress-group participants displayed the same pattern of enhanced retrieval as the Control-group participants. In other words, all participants, on average and regardless of whether they were administered prednisone or placebo, showed superior recognition for the arousing stimuli, and superior recall of the spatial layout of the Hot Defensive room. Taken together with the data from Study 1, the present findings are consistent with previous reports suggesting that emotional material is remembered better than neutral material (Heuer & Reisberg, 1990; La Bar &

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<sup>32</sup>Interestingly, low endogenous cortisol concentrations in humans are also associated with learning strategies that are biased toward stimulus-response learning (Bohbot et al., 2011).

Cabeza, 2006; McGaugh, 2003; Wolf, 2008). The present findings are, however, inconsistent with the premise that stress-induced memory impairments (whether as a result of psychosocial, physical or pharmacological exposure) are greater for emotionally arousing material (de Quervain et al., 2009; Wolf, 2008, 2009).

Hypothesis 3 predicted that women would display inferior spatial learning and memory to men. Consistent with the findings from the studies presented earlier (Chapters 2 and 4), this hypothesis was disconfirmed in the present study. In fact, rather than performing more poorly than men, women instead performed *better*, taking a shorter path length across acquisition trials in the Cool room. They also had better recognition for the pictures that had been in the Hot Appetitive room. It is possible, however, that this latter difference is related to the longer path length taken by the women in the Hot Appetitive room on acquisition Trial 6. That is to say, it is possible that the longer path length in that room might have resulted in the women becoming better acquainted with the images in the room.

## **Conclusion**

The data obtained here did not confirm most of the three hypotheses that were tested. First, despite the fact that prednisone administration impaired verbal memory retrieval, it did not impair visual or spatial memory retrieval. In disconfirmation of the first hypothesis, Stress-group participants spent longer, on average, than Control-group participants searching in the correct location for the target on the probe trials. Second, there was no exaggerated stress-induced memory impairment for the arousing visual or spatial information. In fact, participants in both the Control and Stress groups showed better recognition of the arousing stimuli, as well as better recall for the spatial layout of the Hot Defensive room. Third, there were no sex differences in favor of men in terms of memory performance. On the contrary, women outperformed men on some measures (e.g., they took, on average, a shorter path length across the acquisition trials in the Cool room, and had superior recognition for the stimuli that had been used as landmarks in the Hot Appetitive room). Further discussion of the findings from this study, as well as those from Study 1, is presented in Chapter 6. In that chapter, the findings are discussed in relation to the literature and theory surrounding the effects of stress on memory.

## CHAPTER SIX: GENERAL DISCUSSION

This dissertation examined a relatively neglected area of research in humans: the effects of stress on retrieval of visual and spatial material. Five separate studies, documented in the previous chapters, worked together to explore the topic in a programmatic and novel manner. This chapter provides an overview of the previous five chapters, and discusses the findings from the studies presented in Chapters 4 and 5 in relation to the stated hypotheses and to theory. Then, I attempt to relate the current findings on visual and spatial memory to a functional perspective of memory. Finally, I discuss the limitations of the current studies and possible directions for future research.

### Summary of Previous Chapters

Chapter 1 provided an overview of literature concerning the physiological stress response and its effects on episodic memory. As demonstrated in that chapter, a vast amount of evidence supports the notion that stress and GCs affect memory processes. Depending on the timing of the stressor exposure, GC elevations (induced via laboratory-induced stress manipulations, or via pharmacological means) can either improve or impair memory. In general, these elevations have a positive effect on memory consolidation and a negative impact on retrieval and reconsolidation. However, the effects on encoding are difficult to distinguish due, in part, to difficulty in isolating the encoding phase from the other memory phases (de Quervain et al., 2009; Joels, 2010; Roozendaal et al., 2009; Schwabe et al., 2012; Wolf, 2009).

In attempting to explain how stress and GCs influence memory processing and performance, neuroscientists have developed several theories. These theories include *state dependent learning*, the *inverted-U hypothesis*, *hot-cool theory* and the *integrated vertical and horizontal perspective theory*. Given that state-dependent learning has largely been refuted as an explanation for the effects of stress on memory (Coluccia et al., 2008; Wolf et al. 2002), this dissertation aimed to compare the predictions derived from the integrated vertical and horizontal perspective against those derived from the inverted-U hypothesis and hot-cool theory.

Both the inverted-U hypothesis (de Kloet et al., 1999) and hot-cool theory (Jacobs & Metcalf, 1998) hypothesize that the effects of glucocorticoids follow an inverted-U pattern. This hypothesis is based on the affinity of CGs to bind with Type I and Type II cortisol

receptors. According to the inverted-U hypothesis, the ratio of occupation between Type I and II receptors determines the effect on memory. When the ratio is high, memory is enhanced; however, when the ratio is low, memory is impaired. Thus, following this hypothesis, the effects of stress on memory depend on both the level of circulating endogenous GCs and the level of GC increase induced by the stressful episode (de Kloet et al., 1999).

Hot-cool theory expanded on the inverted-U hypothesis to include the effects of emotional arousal on memory. The “hot” system incorporates the adrenergic activation of the basolateral amygdala (BLA), which causes the system to become increasingly responsive under increasing stress levels. According to this theory, at low-to-moderate adrenergic and GC levels, both the ‘cool’ contextual and narrative features and the ‘hot’ fear-provoking features of the situation show enhanced encoding. At unusually high adrenergic and GC levels, however, the ‘hot’ system becomes hyper-responsive, while the ‘cool’ system breaks down and becomes dysfunctional. Thus, hot-cool systems theory predicts that at unusually high levels of stress, memory should be fragmentary rather than spatiotemporally bound, replete and coherent (Jacobs & Metcalf, 1998).

The integrated vertical and horizontal theory combines two separate models of stress and memory functioning (Schwabe et al., 2012). The vertical model explains the mechanisms that are believed to underlie the effects of stress on memory (Roosendaal, 2002; Roosendaal et al., 2006). Those mechanisms are believed to be concurrent GC and adrenergic activation of the BLA, which in turn interacts with structures in the medial temporal lobes (including, specifically, the hippocampus). The horizontal model provides an explanation as to why stress can have both a positive and a negative influence on memory (Joels et al., 2006). According to this model, the effects of stress are dependent on the timing of the stress exposure. Stress is believed to exert positive effects on memory if the stressor and memory task occur within a short space of time from each other, and/or if they share the same spatiotemporal context. Negative effects on memory retrieval are due to the stressor being experienced in a different spatiotemporal context to the memory task, or due to suppression of other cognitive processes in order to facilitate new learning.

Common to the inverted-U hypothesis, hot-cool theory, and the integrated vertical and horizontal perspective is that GCs target receptors in the hippocampus. Glucocorticoids have been reported to have both positive (non-genomic) and negative (genomic) effects on the hippocampus, thereby significantly influencing its functioning (Henckens et al., 2012; Roosendaal et al., 2009). The hippocampus is also a structure that is directly involved in

episodic memory (Scoville & Milner, 1958). Although a considerable amount of debate surrounds the hippocampus's involvement in remote memory, it is widely accepted that the hippocampus is essential for the retrieval of recent episodic memory (Squire & Bayley, 2007; Winocur et al., 2010a). Thus, the hippocampus is a common neurocorrelate involved in episodic memory and affected by stress hormones.

To explore the research question in this dissertation, I aimed to replicate, systematically, the paradigm used by de Quervain et al. (1998). They were the first to report the negative effects of stress on memory retrieval in rodents and, importantly, they demonstrated that both stress (in the form of foot-shocks) and GC treatment both impaired performance in a Morris Water Maze (MWM; Morris, 1984) environment that had been learned 24 hours prior. However, in order to replicate de Quervain et al.'s experimental design in humans, I needed to make several substitutions in terms of methodological apparatus (e.g., I could not use the MWM as the spatial environment, or foot-shocks in order to induce stress). Thus, the first two chapters of this dissertation set out to describe the validation of the various pieces of apparatus that would be used in the central studies testing the effects of stress on visual and spatial memory retrieval.

In Chapter 2, I attempted to create and verify an environment that would be a suitable human substitute for the MWM. I chose to use a virtual environment (the CG Arena) that is a human analog of the MWM. The CG Arena has been reported to have solid reliability and good construct and external validity, as data obtained from the CG Arena closely resemble those found in the MWM (Jacobs et al., 1997, 1998; Thomas et al., 2001). I created three separate environments in the CG arena. The first room featured landmarks that were neutral pictures (Cool room); these pictures were neither pleasant nor unpleasant and carried no motivational component. The second room featured landmarks that were unpleasant and arousing pictures (Hot Defensive room), and the third featured landmarks that were pleasant and emotional pictures (Hot Appetitive room). Thus, the Hot Defensive and Hot Appetitive rooms featured landmarks that contained an active motivational component, but were on the opposite extremes of emotion. These arousing pictures were selected in order to tap into the most basic of emotional/survival responses. These pictures contained content that displayed death and mutilation on the one extreme, and acts of copulation and reproduction with desirable partners on the other.

As reviewed in Chapter 1, humans process and remember emotional information more robustly than neutral material (Dolan, 2002; La Bar & Cabeza, 2006; Phelps, 2004; Reisberg & Heuer, 2004, Wolf, 2008, 2009). This preferential processing is also generally believed to

occur irrespective of the valence of the information, and is suggested to be solely dependent on the level of emotional arousal of the information (La Bar & Cabeza, 2006; Wolf, 2008). In addition, although some studies report that stress and GCs have an impairing effect on memory (e.g., see Buchanan et al., 2006; de Quervain et al., 2007; Kuhlmann et al., 2005a; Schönfeld et al., 2014; Kuhlmann et al., 2005b; Smeets et al., 2008; Tollenaar et al., 2008), this impairing effect, according to some researchers (e.g., de Quervain et al., 2009; Wolf, 2008, 2009), is greater for emotional information.

The pictures selected as landmarks in the CG Arena rooms were identified and verified in the study presented in Appendix A. In that study, 58 participants rated the three picture groups on measures of *pleasure*, *arousal*, and *dominance* using the Self-Assessment Manikin (SAM), a rating scale employed in the International Affective Picture System (IAPS; Lang et al., 1999, 2005, 2008) and in other emotional motivation studies. The ratings from this sample showed that the pictures were viewed in the intended emotion and valence direction. That is, participants judged the hot appetitive pictures as being pleasurable and arousing, and judged the hot defensive pictures as unpleasant and slightly more arousing than the appetitive pictures. They rated the cool pictures as almost neutral in pleasure, and as slightly non-arousing. Therefore, the findings from the study described in Appendix A support the notion that the three picture groups were completely different in terms of pleasure and arousal. Eight pictures that were rated as the most arousing defensive, the most arousing appetitive, and the most neutral (cool) were selected for each CG Arena room.

Study A, presented in Chapter 2, demonstrated that the Hot Defensive, Hot Appetitive, and Cool rooms created in the CG Arena were suitable tools to use in the subsequent studies investigating the effects of stress on the retrieval of spatial memory. Twenty-four participants learned the locations of the targets over seven trials in each of the three CG Arena rooms. Analysis of performance across those trials showed that the participants successfully navigated, learned, and remembered a location within the CG Arena, using landmarks that varied in valence and arousal intensity. Importantly, the data analyses detected no significant differences between the rooms in terms of navigating to, learning, and remembering the location of a hidden target. In addition, there were no between-room differences in terms of participant performance on measures of probe trial dwell time and of post-Arena spatial reconstruction of the landmarks' layout. However, recognition memory for the landmarks was influenced by the arousal content of the pictures. All the participants recognized more arousing pictures, independent of valence, than they did neutral pictures. No sex differences were evident on any of the GC Arena or Arena-related measures. Thus, Study

A served as a pilot verifying that the CG Arena rooms that were to be used in subsequent studies would not bias spatial learning and memory, and would therefore be suitable for use.

The next preliminary step was to find a suitable laboratory stressor for humans, to substitute for the foot-shock stressor used by de Quervain et al. (1998). In Chapter 3, I described the testing of a new stress paradigm that combined a commonly used physiological stressor (the Cold Pressor Test; Hines & Brown, 1932) with a commonly used psychosocial stressor (the Trier Social Stress Test; Kirschbaum et al., 1993), thereby creating a single, believable, and ethical procedure: the Fear Factor Stress Test. Ninety participants were assigned to one of three conditions: the FFST-Stress condition, the FFST-Control condition, or the TSST. I compared physiological and psychological responses induced by each condition. In comparison to participants in the TSST condition, those in the FFST-Stress condition showed sustained increased levels of cortisol responding in the absence of increased sympathetic activation and increased self-reported anxiety. In addition, there were a significantly greater number of cortisol responders in the FFST-Stress group than in the TSST group. Those participants in the FFST-Control condition did not show an increase in cortisol levels, and reported significantly lower self-reported anxiety levels than those in the FFST-Stress and TSST conditions. Hence, Study B (presented in Chapter 3) demonstrated that the FFST and its control comparison were promising research tools.

In summary, the first two studies presented in this dissertation (described in Chapters 2 and 3), in addition to the study presented in Appendix A, paved the way for the focal studies (described in Chapters 4 and 5) to explore the primary research question. Having validated the visual and spatial experimental tasks, as well as a robust stress and control manipulation, I was then able to explore the effects of stress on visual and spatial memory retrieval.

In line with de Quervain et al.'s (1998) first study, the study presented in Chapter 5 (Study 1) examined the effects of acute stress on visual and spatial memory retrieval. Sixty participants learned the location of the hidden target in the three CG Arena rooms, and learned the word pairs of the Verbal Paired Associates Test (VPA). Twenty-four hours later, the participants returned and completed either the FFST-Stress or FFST-Control conditions. They then completed memory tests for various aspects of the CG Arena, along with a delayed recall trial of the VPA. Data analyses revealed, contrary to expectations, that stress did not impair memory retrieval performance on the visual and spatial tasks, or on the verbal task. On not one of the visual, spatial, or verbal tasks did the Stress groups display impaired memory performance in comparison to the Control groups. Instead, the Stress groups showed

a similar enhanced recognition performance for the arousing stimuli (irrespective of valence) as the Control groups did.

In contrast to the failure to confirm the hypothesized retrieval impairments, the observed data suggested that the acute stressor may have had several positive effects on memory retrieval within the CG Arenas and on the VPA. Specifically, both the men and women that had been exposed to the stress manipulation displayed more accurate memory for the spatial layout of the landmarks in the Hot Appetitive room than the control participants did.<sup>33</sup> In addition, the women who had been exposed to the stress manipulation recalled more correct word pairs of the VPA than the other participants did.

The subsequent comparison of cortisol responders in the Stress group with the Control group showed an increase of effect sizes over the previously detected differences in the whole-group analysis. Of particular interest was the strengthening of the positive differences seen on memory for the word pairs of the VPA, as well as for recall of the spatial layout of the Hot Appetitive room. Thus, the increases in these differences between the cortisol responders and the control participants hinted at the possibility of cortisol being the primary modulator of performance differences on the retrieval tasks.

The study presented in Chapter 5 (Study 2) attempted to isolate cortisol as the independent variable. Continuing in the systematic replication of de Quervain et al. (1998), Study 2 was, in every respect, a replica of Study 1, except that the FFST-Stress and FFST-Control conditions were replaced by, respectively, a 25mg capsule of prednisone and a placebo. Again, 60 participants learned the same CG Arena rooms and the word pairs of the VPA. Analysis of data from the CG Arena acquisition trials revealed several notable differences. Across the acquisition trials, women took a shorter route than men did to the target in the Cool room, whereas in the Hot Appetitive room the Stress-group participants took a more direct route than Control-group participants did to the target. However, by the final acquisition trial, the above differences seen across the trials had largely disappeared. It was notable, however, that on that final trial women found the target in the Cool room more directly than they did the one in the Hot Appetitive room. Thus, the significantly shorter average path length displayed by the women in the Cool room may have remained to some degree.

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<sup>33</sup>Although improbable, the significantly better performance seen on this retrieval task might have been related to the significant differences seen between the Stress Male and the Stress Female groups across the six acquisition trials in the Hot Appetitive room. The Stress Male group showed significantly shorter path lengths across the trials in the Hot Appetitive room compared to the participants in the Stress Female group. It is, however, unlikely that the opposing performance seen across the acquisition trials would result in an analogous benefit in recalling the spatial layout of the Hot Appetitive room.

Analysis of the recall performance in Study 2 revealed a rather different pattern to that observed in Study 1. Consistent with data analyses presented in Study 1, the analyses presented in Study 2 showed that administration of prednisone did not impair retrieval of visual or spatial information; however, in contrast to the earlier analyses, the analyses presented in Study 2 showed that administration of prednisone impaired retrieval of verbal material. On average, men and women who were administered prednisone recalled significantly fewer word pairs on the delayed VPA recall trial than participants who were administered the placebo. Therefore, in contrast to Study 1 (where the acute stressor may have enhanced verbal retrieval memory in women but not in men), the Study 2 analyses suggested that administration of prednisone impaired retrieval of verbal information in both men and women.

Consistent with the data presented in Study 1, participants in Study 2, irrespective of experimental condition, showed better recognition for the arousing stimuli than for the neutral stimuli. In addition, participants in Study 2 also recalled the spatial layout of the stimuli in the Hot Defensive room more accurately than stimuli in the other two CG Arena rooms. Thus, the administration of prednisone failed to induce the hypothesized exaggerated retrieval impairment for the arousing stimuli. Instead, men and women who were administered prednisone showed enhanced retrieval for the visual and spatial information, as did control participants.

The data analyses presented in Study 2 also showed that the administration of prednisone had a positive effect on certain aspects of memory retrieval. Specifically, on the probe trial in each of the CG Arena rooms, participants who were administered prednisone spent, on average, a longer time searching for the target in the quadrant where it had been located.<sup>34</sup> In addition, in comparison to men, women displayed, on average, superior recognition for the stimuli in the Hot Appetitive room. However, this difference was not cortisol-induced, and it is uncertain whether it might have been influenced by the sex difference that was observed on the final acquisition trial in the Hot Appetitive room.

In summary, the effects of the acute stressor and administration of prednisone seemed inconsistent across memory domains. Study 1 suggested that acute stress had an enhancing effect on retrieval of verbal information in women but not in men; in contrast, Study 2 suggested that cortisol administration had an impairing effect on retrieval of verbal information in both men and women. However, both studies suggested that elevated cortisol

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<sup>34</sup>Although, subsequent statistical analyses revealed that this overall difference between the Stress and Control groups on the probe trial was driven by significant differences in the Cool and Hot Appetitive rooms.

levels do not impair visual and spatial memory retrieval. In fact, both acute stress and pharmacologically raised cortisol levels might have had selective positive effects on the retrieval of visual and spatial information. However, these positive effects were inconsistent across studies, and are in need of replication. Hence, discussion of these effects will be limited to the relevant sections at the end of Chapters 4 and 5, and will be addressed as future directions for research, which follow at the end of this chapter.

To account for the results from the studies presented in Chapters 4 and 5, I will discuss the findings in relation to the three primary hypotheses and to the theory/ies from which they were derived. Given that only the first two hypotheses concerned the effects of stress on memory, discussion relating to theoretical explanations of stress on memory will follow the discussion regarding Hypothesis 2.

### **Hypothesis 1: Stress and cortisol administration will impair memory retrieval**

Although three theoretical perspectives are compared in this dissertation (the inverted-U hypothesis, hot-cool theory and the integrated vertical and horizontal perspective), there are, in effect, only two competing predictions. Both the inverted-U hypothesis and hot-cool theory make nonspecific predictions regarding the direction of the effects of stress on memory. That is, both theories predict that small increases of GC can have either a positive effect or no effect on memory, while greater GC increases will have impairing effects on memory (de Kloet et al., 1999). Hot-cool theory expands on this inverted-U relationship between stress and memory by adding that with increasing stress levels (both adrenergic and GCs), the emotionally arousing information will be recalled, but these memories will be fragmentary and not spatially or temporally bound (Jacobs & Metcalfe, 1998). In contrast, the integrated vertical and horizontal hypothesis simply predicts that stress and GCs will have an impairing effect on memory retrieval (Schwabe et al., 2012).

The first hypothesis tested was derived from the general effects of stress and GCs reported in the literature, and is consistent with the predictions derived from integrated vertical and horizontal hypothesis. As the literature reviewed in Chapter 1 demonstrated, both stress and cortisol have been consistently demonstrated to have an impairing effect on memory retrieval (de Quervain et al., 2009; Joels, 2010; Roozendaal et al., 2009; Schwabe et al., 2012; Wolf, 2009). In humans, this impairing effect has been demonstrated, numerous times, in the verbal domain, and, to a more limited degree, in the visual and spatial domains. Across Studies 1 and 2, the effects of elevated cortisol levels had differing effects on visual

and spatial versus verbal memory. Thus, I will discuss the findings regarding verbal memory independently to the findings regarding visual and spatial memory.

In terms of verbal memory, the prediction that elevated cortisol levels would impair retrieval was only partially confirmed. That is, the prediction was confirmed only by the data analyses presented in Study 2: Cortisol administration was observed to impair retrieval of verbal material in both men and women. In contrast, the data analyses presented in Study 1 demonstrated that exposure to an acute stressor did not impair the retrieval of verbal information (and, in fact, might have enhanced retrieval in the female participants).

This latter finding, that stress can have a positive effect on memory is, however, not completely novel within the literature. As noted in earlier chapters, several studies have demonstrated that stress and GCs can enhance verbal memory retrieval (Lupien et al., 2002; Schilling et al., 2013; Schwabe et al., 2009).

A possible explanation as to why the first hypothesis was not confirmed in Study 1 but was confirmed in Study 2 might be due to differences in cortisol concentration increases across the two studies. Specifically, increases in cortisol levels following prednisone administration were roughly 6 to 10 times higher than those following the stress manipulation. Consequently, these much higher cortisol levels could be associated with the verbal memory impairment observed in Study 2. Further discussion regarding this explanation is presented below in relation to the inverted-U hypothesis.

In contrast to the findings regarding verbal memory, the findings concerning visual and spatial memory retrieval showed that neither acute stress nor prednisone administration had an impairing effect on memory performance. As was the case with the findings regarding verbal memory, the findings regarding visual and spatial memory are not completely consistent with the general direction of effects reported in the literature. As discussed earlier, previous studies have demonstrated that stress has an impairing effect on visual and spatial cognition in both humans and animals (e.g., Buchanan & Tranel, 2008; de Quervain et al., 1998; Schwabe & Wolf, 2009; Quesada et al., 2012). However, the administration of GCs has only been demonstrated to have an impairing effect on spatial memory retrieval in animals (e.g., Atsak et al., 2012; de Quervain et al., 1998; Rashidy-Pouret et al., 2004; Roozendaal et al., 2003, 2004; Sajadi et al., 2007). Human studies have yet to confirm the same impairing effects on visual and spatial memory retrieval that have been widely reported for verbal memory retrieval (de Quervain et al., 2009; Domes et al., 2005; Het et al., 2005). Therefore, the findings from the present studies serve, along with those from a few previous studies

(Domes et al., 2005; Schilling et al., 2013), to contest the impairing effects of stress on visual and spatial memory retrieval.

To account for the discrepancy between the current findings and those of previous studies that report the impairing effects of stress on visual and spatial information, I will explore possible explanations for why the first hypothesis was not confirmed. These explanations include ceiling/floor effects, encoding differences, and contextual or relaxed testing conditions.

**Ceiling/floor effects.** A logical explanation for not confirming the first hypothesis regarding the visual and spatial tasks is that these tasks may have been subject to ceiling or floor effects. That is, the measures used to examine the participants' memory of the CG Arena were not sensitive enough to detect underlying impairing effects of the acute stressor or administration of prednisone.

Although this explanation might not be applicable across all of the visual and spatial tasks, it may possibly account for the absence of differences in wayfinding performance seen on the recall trials in the CG arena. Participants in both Study 1 and 2 had to learn the location of a hidden target in three separate environments. The participants had one session of six acquisition trials in each environment to learn the target location. This learning paradigm was selected because it resembled the paradigm used by de Quervain et al. (1998). Those researchers allowed rats one session of eight acquisition trials to learn a single location in the MWM. However, in the presented studies, the number of allocated acquisition trials (in order to learn a small number of locations) may have resulted in the spatial tasks in the CG Arena being too easy for humans. Animal studies have suggested that the effects of stress or GCs are more prominent when the difficulty of the task is increased (Diamond, 1999). Therefore, the masking of possible wayfinding differences in Studies 1 and 2 might have been due to the task not being difficult enough, which may have resulted in ceiling effects on performance.

In addition to wayfinding, both acute stress and prednisone administration had little effect on participants' recognition of the stimuli used in the CG arena rooms. Despite recognition performance being influenced by the arousal content of the stimuli in the rooms, neither stress nor cortisol administration were shown to influence recognition performance (i.e., there were between-room differences, but not between-group differences). This finding stands in contrast to that of Buchanan and Tranel (2008), who reported recognition impairments for the emotional stimuli in participants who were cortisol responders (see Chapter 4). This contrasting result is surprising as the recognition task used in Studies 1 and 2 was relatively similar to that used by Buchanan and Tranel (2008). For instance, Buchanan

and Tranel (2008) showed their participants 20 pictures (10 featuring negative arousal content), and tested recognition performance for those pictures against 20 distracter pictures. The participants in Studies 1 and 2 were exposed to 24 images (8 in each CG Arena room), which were paired with 24 distracter images.

However, a key methodological difference between Buchanan and Tranel's (2008) study and Studies 1 and 2 was the length of time that the participants were exposed to the picture stimuli. Buchanan and Tranel (2008) showed their participants each of their 20 pictures for a period of 8 seconds. In contrast, participants in the Studies 1 and 2 were exposed to the stimuli for the duration of each acquisition trial in the CG Arena, which could last up to 2 minutes per trial, and the participants completed six acquisition trials in each room.<sup>35</sup> Although there were notable task differences in encoding the pictures between the studies, the current participants were exposed to the picture stimuli for a substantially longer period than the participants were in Buchanan and Tranel's (2008) study. Hence, this extended exposure may have increased the participants' familiarity with the stimuli, thereby again resulting in a ceiling effect on recognition performance.

Arguing against the possibility of floor or ceiling effects on the other retrieval tasks (i.e., spatial reconstruction and dwell time) are the findings of positive effects on memory retrieval performance. These positive effects demonstrate that these two tasks were sensitive enough to detect differences that might have been induced by stress and cortisol administration. Thus, although ceiling or floor effects could possibly explain the null effects of stress and cortisol administration on wayfinding and recognition, they are unlikely to account for either (a) the positive effect of the acute stressor, as seen on the spatial reconstruction task for the Hot Appetitive room, or (b) the effects of prednisone administration on dwell time.

**Encoding differences.** As noted previously, the findings regarding verbal memory differed from those on visual and spatial memory. It is possible that these differences were due to the encoding instructions provided for the relevant tasks. The verbal task (VPA) used in the present studies was an intentional encoding task, while the visual and spatial task (the CG Arena) was an incidental encoding task. Intentional encoding differs from incidental encoding in that in the former, the participant is aware that s/he is encoding information that will need to be recalled at a later stage. In incidental learning, on the other hand, the

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<sup>35</sup>It is also unlikely that participants would have looked at each picture for an equal amount of time. That is, they might have spent more time looking at the pictures that were closer to the target than at those further from the target.

participant is not aware that s/he will be required to recall the presented information at a later stage. Intentional encoding leads to better recall performance, as the information is encoded in a deeper manner (as the participant uses conscious semantic strategies) than is the case with incidental encoding (Lupien et al., 2002; Trammell, Beck, Bottalico, & Molloy, 1990).

However, human studies have shown that stress and GCs usually have a negative impact on information that has been encoded incidentally (Buchanan & Tranel, 2008; Eich & Metcalfe, 2009; Lupien & McEwen, 1997). Thus, the finding that the acute stressor and administration of prednisone did not impair the incidentally encoded visual and spatial tasks, whereas the administration of prednisone may have impaired the intentionally encoded verbal task, makes it improbable that the encoding instructions might be responsible for the null effects observed for the visual and spatial results.

**Congruent learning/testing context or relaxed testing conditions.** A third possible explanation for failing to confirm the hypothesized retrieval impairments on the visual and spatial memory domain might be the testing conditions used in the present studies. That is, either the use of congruent learning and testing environments, or overly informal or relaxed testing conditions, may have masked the impairing effects of stress and GCs. As noted in Chapter 4, Schwabe and Wolf (2009) demonstrated that stress-induced retrieval impairments for spatial memory were only apparent when incongruent learning and testing environments were used (i.e., participants who were tested in the same environment in which they learned the material did not show a retrieval impairment).

Similarly, Kuhlmann and Wolf (2006b) demonstrated that the use of informal or relaxed testing conditions alleviated the impairing effects of GCs. The authors reported that under less formal testing conditions, a single 30mg dose of cortisol did not reduce memory performance for words that had been learned 5 hours earlier. In contrast, the same authors demonstrated that under more formal testing conditions, a similar dose of cortisol had a significant impairing effect for the negative words from the same word list that had also been learned five hours earlier (Kuhlmann et al., 2005a). The authors attributed the differences in retrieval performance to the varying arousal levels elicited under the different testing conditions. As discussed in Chapter 1, emotional arousal and the consequential activation of the BLA appear to be concomitant triggers of the cortisol-induced retrieval memory impairment (de Quervain et al., 2009; Roozendaal et al., 2009; Schwabe et al., 2012; Wolf, 2009). Despite the fact that Kuhlmann and Wolf (2006b) did not report measures of autonomic activity during testing, they speculate that the adrenergic response during the formal testing situation may have been greater than in the less formal condition. Thus,

increased arousal combined with increased cortisol resulted in an impaired memory retrieval performance under formal testing conditions.

Two findings argue against the possibility that the testing conditions and environment that were used in the current studies were not suitable to elicit the impairing effects of stress and GCs. First, as noted previously, several positive and negative effects were observed. These effects indicate that the testing environment and conditions were sufficient to elicit a limited number of possible stress-induced differences (albeit not always in the hypothesized direction). Second, the testing conditions in Study 1 were a great deal more arousing than the conditions in Study 2. In Study 1, participants in the FFST-Stress condition showed marked increases in both autonomic activation (measured through heart rate and skin conductance) and subjective anxiety. Regardless of these increases in arousal levels, those participants did not show impaired retrieval of verbal, visual, or spatial information. In contrast, the administration of prednisone in Study 2 resulted in a testing situation that was far less formal. Following prednisone/placebo ingestion, the participants watched a documentary for an hour until the retrieval testing took place. The participants subsequently reported no significant changes in self-reported anxiety across the testing session. Despite this more relaxed testing session, prednisone administration had an impairing effect on verbal memory, but not on visual and spatial memory. Thus, even though the testing conditions were more relaxed in the latter study, prednisone administration had an impairing effect on verbal but not visual and spatial memory, while the arousing testing conditions in the former study seemed to have no negative stress-related effects. These results suggest that neither congruent learning/testing environments, nor relaxed testing conditions, are likely responsible for the failure to confirm the first hypothesis regarding visual and spatial memory retrieval in the studies presented here.

In summary, the findings from Study 1 and Study 2 show that the acute stressor and administration of prednisone had differing effects on retrieval of verbal versus visual and spatial information. The findings showed that the first hypothesis was confirmed in Study 2 for retrieval of verbal information but not in Study 1. In contrast, the first hypothesis was not confirmed for the retrieval of visual and spatial information in either study. Despite possible explanations for not confirming the first hypothesis being ceiling/floor effects, encoding differences and congruent learning/testing context and/or relaxed testing conditions, these explanations are unable to account fully for all of the observed data on all the tasks (although ceiling effects may have masked the effects of acute stress and prednisone administration on the wayfinding and recognition tasks).

Further explanations from a theoretical perspective are presented below, after the discussion regarding Hypothesis 2.

**Hypothesis 2: Memory for the different CG Arena rooms will be influenced by the arousal content of the pictures used as landmarks in the rooms**

The second hypothesis focused on the effects of stress or cortisol administration on retrieval of emotionally arousing material. This hypothesis was effectively a within-group prediction, and comprised two separate hypotheses. First, the participants who were exposed to the FFST-Control condition in Study 1, or who received the placebo dose in Study 2, were predicted to show superior memory retrieval for the arousing environments in comparison to the neutral environment. This first part of the hypothesis concerning the control groups' performance is derived from previously published studies showing, consistently, that emotional material is recalled better than neutral material (Dolan, 2002; Heuer & Reisberg, 1990; La Bar & Cabeza, 2006; Packard & Goodman, 2012; Payne et al., 2006; Phelps, 2004; Reisberg & Heuer, 2004). Thus, under non-stressful conditions, material contained within the emotional environments should be retrieved better than that contained within the neutral environment.

Second, participants who were exposed to the FFST-Stress condition, and those who were administered the cortisol dose, were predicted to show an even greater retrieval impairment (over and above the general stress-induced impairment predicted in Hypothesis 1) for the arousing pictures versus the neutral pictures. As introduced in Chapter 1, the effects of stress on memory are, in part, due to adrenergic activation of the BLA, and to its modulation of the memory in the hippocampus. Some researchers (e.g., de Quervain et al., 2009; Wolf, 2008, 2009) have speculated that the impairing effects of stress and GCs are directly proportional to the level of emotional arousal of the material. That is, under stressful conditions, there should be a greater retrieval impairment, related to higher levels of emotional arousal. Thus, the second hypothesis predicted that the Stress and Control groups would show contrasting patterns of retrieval for the arousing versus the neutral stimuli.

The observed data from the two major studies presented here confirmed the first part of the hypothesis (that regarding the performance of the Control groups). In both these studies, the Control groups, irrespective of gender, displayed superior recognition memory for the arousing stimuli in comparison to the neutral stimuli. The Control groups in Study 2 also recalled the spatial layout of the CG Arena room that contained negative arousing (Hot Defensive) pictures better than the other two rooms, including the other arousing CG Arena

room that contained erotic (Hot Appetitive) pictures. However, apart from these differences, emotional arousal had no effect on wayfinding and dwell time performance in the Control groups. These results indicate that arousal conditions that lead to improvements in recognition and recall performance do not necessarily benefit navigational performance, suggesting that the mechanisms underlying the arousal effects on the various tasks might be different.

The second part of the hypothesis, that concerning the performance of the Stress groups, was not confirmed by the data from either Study 1 or 2. Exposure to the acute stressor and ingestion of prednisone, did not, as noted above, have an impairing effect on visual and spatial memory, and did not have an exaggerated impairing effect for the emotionally arousing stimuli.<sup>36</sup> In contrast, participants who had been administered the FFST-Stress manipulation, or who had received the prednisone dose, displayed the same pattern of enhanced recognition for the emotionally arousing information as the control participants did. Additionally, similar to the control participants, those who were administered prednisone also displayed better recall of the spatial layout of the Hot Defensive CG Arena room. Thus, results from both studies showed no evidence that stress had a greater impairing effect on memory retrieval for the emotionally arousing spatial environments in comparison to the neutral environment.

In direct contrast to the hypothesized exaggerated memory impairing effects, stress was shown in Study 1 to possibly enhance memory for the spatial layout of the arousing Hot Appetitive room. This positive effect was not evident in the participants who were administered prednisone in Study 2. Therefore, it is likely that the combination of the highly arousing testing conditions, along with moderate increases in cortisol concentrations, might be behind this positive retrieval performance. This finding is therefore consistent with the notion that the recall of material under stressful conditions is influenced by the nature of the material (i.e., whether it is emotionally arousing or neutral); however, the direction of the influence was opposite to what was initially hypothesized.

The possible explanations for not seeing the exaggerated retrieval impairment under stress or cortisol administration are possibly the same as those listed above for the first hypothesis. That is, these possible explanations include ceiling/floor effects, incidental versus intentional encoding, congruent learning/testing context, and relaxed testing conditions.

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<sup>36</sup>A limitation of this dissertation, discussed below, was that the effect of stress on verbal emotionally arousing stimuli was not explored. Thus, discussion on the effects of emotional arousal on memory retrieval is limited to visual and spatial memory.

However, the same counter arguments for these explanations, discussed above, are also applicable to the second hypothesis.

Alternatively, it is possible that the length of time between learning and retrieval was not sufficient to elicit the predicted arousal differences. Here, some researchers have reported that emotional and neutral material is retrieved equally well in immediate recall tests, while performance differences due to the differentially arousing nature of the material only becomes obvious with longer delays of days to weeks (Christianson, 1984; Quevedo et al., 2003). However, arguing against this possibility is the fact that memory (specifically recognition of stimulus material and recall for of the spatial layout of the CG Arena rooms) was influenced by emotional arousal in both the Stress and Control conditions. Thus, the length of time between learning and retrieval is unlikely to account for the failure to confirm the second hypothesis, although the possibility still remains that the effects might have been larger if memory was tested after a longer delay.

Thus, the current series of studies demonstrated that exposure to the acute stressor and administration of prednisone had very little effect on the recall of emotionally arousing information. The little effect that stress did have seemed beneficial to memory retrieval. The following section aims to relate the findings from Studies 1 and 2 to theories concerning the effects of stress on memory.

### **Findings in Relation to Theoretical Explanations**

As discussed previously, the integrated vertical and horizontal hypothesis predicts that stress will have an impairing effect on memory retrieval (Schwabe et al., 2012). In contrast, both the inverted-U hypothesis and hot-cool theory predict that small increases of GC can have either a positive effect or no effect on memory, while greater GC increases will have impairing effects on memory (de Kloet et al., 1999). Hot-cool theory expands on this inverted-U relationship and predicts that under conditions of stress, memory for emotional material should be stronger but fragmentary, without spatial or temporal contextual reference (Jacobs & Metcalf, 1998). Thus, in terms of likely hot-cool theory predictions for the present studies, high-levels of stress should enhance recognition of the arousing material ('hot' system) but impair retrieval of the spatial and temporal aspects (the 'cool' system). As was the case previously, I will here discuss verbal memory independently from visual and spatial memory.

**Verbal memory.** The theoretical position of the integrated vertical and horizontal perspective was the basis for the prediction of my first hypothesis. As discussed above, the

prediction that the acute stressor and administration of prednisone will have an impairing effect on verbal memory was confirmed in Study 2 but not in Study 1. Thus, a prediction derived from the integrated vertical and horizontal perspective cannot account for the findings presented here: That prediction stands in direct contrast to the finding that stress might have a positive effect on retrieval of verbal material in the female participants in Study 1.

Alternatively, the prediction derived from the inverted-U hypothesis is confirmed more completely by the observed data.<sup>37</sup> Underlying the inverted-U hypothesis is the notion that the ratio of occupation between Type I and II receptors determines the effect of stress on memory. When the occupation ratio is high (i.e., when most of the Type I and only part of the Type II receptors are occupied) then the effects on memory are positive (enhancing); however, when ratio is low (i.e., when both Type I and II receptors are either saturated, or are only partly occupied) then the effects on memory are negative or impairing (de Kloet et al., 1999).

The Type I: Type II receptor occupation ratio can be influenced by both the time of day and by dose-dependent effects of cortisol. Time of day influences the occupation ratio because the release of cortisol follows a circadian rhythm. Peak cortisol levels are experienced in the morning; these levels then slowly decline through the day until the circadian trough, which is experienced around the late afternoon, evening, and nocturnal period. Cortisol levels then start to show an abrupt elevation following the first few hours of sleep (Lupien et al., 2007; Rosmond, Dallman, & Björntorp, 1998). As discussed in Chapter 1, GC receptors differ in terms of their affinity for circulating GCs. Type I receptors bind GCs with a greater affinity than Type II receptors (van der Laan & Meijer, 2008). Type I receptors are, therefore, more likely to become occupied, and thereby saturated with GCs, than Type II receptors. Thus, endogenous levels of GCs and the resulting activation of Type I and Type II receptors will fluctuate across the day in accordance with cortisol's circadian rhythm (Lupien et al., 2007). The higher levels of endogenous GCs in the morning hours will result in an already low occupation ratio between Type I and Type II receptors. A further increase in CGs (as experienced after, for instance, the experience of an acute stressor or prednisone administration) would only lower the ratio, and would therefore have a negative effect on memory performance (de Kloet et al., 1999; Lupien et al., 2002). Lower levels of endogenous GCs in the afternoon hours would produce a high occupation ratio between the

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<sup>37</sup>Hot-cool theory is not discussed in relation to the findings on verbal memory as the VPA was a non-emotional memory task.

Type I and Type II receptors. Depending on the size of the cortisol increase, an increase in GCs might only serve to increase the ratio due to the Type I receptors' greater affinity for GCs. Thus, in the afternoon, smaller increases in cortisol might have either a positive effect or no effect on memory, whereas larger increases might have a negative effect. Lupien et al. (2002) initially demonstrated that the effects of stress on memory might be influenced by time of day; they showed that CG administration had impairing effects in the morning and enhancing effects in the afternoon. These findings were later corroborated in a meta-analysis that confirmed the time-dependent effects of increased GCs, and noted that such increases are more likely to impair memory performance in the morning, while enhancing it in the afternoon (Het et al., 2005).<sup>38</sup>

Support for the association between cortisol levels and memory functioning can also be found in rodent studies. That being, previous studies have documented significant decreases in long term potentiation (LTP) are observed after adrenalectomy (Dubrovsky, Liquornik, Noble, & Gijsbers, 1987; Filipini, Gijsbers, Birmingham, & Dubrovsky, 1991). In contrast, other studies have noted that after exogenous administration of synthetic glucocorticoids (Bennett, Diamond, Fleshner, & Rose, 1991; Pavlides, Watanabe, & McEwen, 1993), which result in a high occupation ratio between the Type I and Type II receptors, also decreases LTP.

In terms of the present findings, the positive effect of stress on verbal retrieval memory in Study 1 might, therefore, be due to the time of day and the associated basal cortisol concentrations. All testing sessions in both Studies 1 and 2 took place in the afternoon hours. Hence, the participants are likely to have started the testing sessions with lower levels of endogenous GCs and, consequently, with a likely high occupation ratio between the Type I and II receptors. The nominal increase in cortisol concentrations induced by exposure to the FFST-Stress condition might have caused a favorable increase in the occupation ratio, particularly with the female participants. As a result, the acute stressor might have had a positive effect on female participants' retrieval of verbal material.

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<sup>38</sup>Although some studies have reported stress-induced memory retrieval impairments after participants were tested in the morning (e.g., Kuhlmann et al., 2005b), others have reported retrieval impairments during midday (e.g., Tollenaar et al., 2008) and afternoon testing sessions (e.g., Buchanan et al., 2006; Domes et al., 2004; Merz et al., 2010; Smeets et al., 2008). In addition, Smeets (2011) demonstrated that stress exposure resulted in impaired retrieval for both neutral and negative words, independent of whether the participants were tested in the morning or during the afternoon. However, the cortisol concentrations induced by the FFST in Study 1 were substantially lower than in many of these studies (e.g., Buchanan et al., 2006; Domes et al., 2004; Kuhlmann et al., 2005b; Smeets 2011). The enhancing effect of stress on verbal memory retrieval in the women might instead, therefore, have been due to low (or optimal) cortisol concentration increases following exposure to the FFST-Stress condition, which led to positive effects on memory retrieval.

In contrast, the impairing effects of prednisone administration on verbal memory seen in both men and women in Study 2 might be related to the obtained cortisol concentrations. As mentioned previously, the cortisol concentrations induced through prednisone administration were between 6 and 10 times higher than those induced by the FFST. In other words, the pharmacologically induced increase, but not exposure to the acute stressor, resulted in cortisol concentrations in the upper physiological range. Such high concentrations might saturate both the Type I and the Type II receptors, resulting in a low occupancy ratio and subsequent verbal memory impairment (de Kloet et al., 1999; Lupien et al., 2002).

Thus, the inconsistent effects of stress and prednisone administration on verbal memory retrieval seen in Studies 1 and 2 can be accounted for by the inverted-U hypothesis. Specifically, the findings across the two studies might be attributable to a combination of the time of day and dose-dependent effects of cortisol.

**Visual and spatial memory.** As was the case with verbal memory, the present findings regarding visual and spatial memory do not confirm the predictions derived from the integrated vertical and horizontal theory. In fact, the lack of a retrieval impairment, and the selective positive effects in both Studies 1 and 2, stand in direct contrast to the impairing effects that are predicted by the theory.

In contrast, the predictions derived from the inverted-U hypothesis and hot-cool theory might, to a small degree, be confirmed by the observed data. That is, the predictions might account for the null and the positive effects seen in Study 1, but both theories fail to account for the consistent findings across both Studies 1 and 2. Consistent with the explanation for the findings on verbal memory, the time of day and the dose-dependent effects of cortisol might partly explain the null and positive effects on the visual and spatial findings in Study 1. As discussed previously, the afternoon testing session might have enabled a favourable Type I and II receptor occupation ratio. The modest increases in cortisol following the stressor may have had little effect on memory except for selective positive influences on memory retrieval. However, both the inverted-U hypothesis and hot-cool theory are unable to account for why, in Study 2, the large increases in cortisol concentrations (following prednisone administration) only resulted in separate selective positive effects and not in negative effects on visual and spatial memory retrieval. If the effects of elevated cortisol are to follow an inverted-U pattern, then one would expect to see contrasting effects on memory retrieval performance with higher levels of cortisol, similar to those seen for verbal memory. Instead, neither the stressor nor administration of prednisone appeared to

impair retrieval of visual and spatial material, suggesting that the effects seen in the present studies are more linear than inverted-U in nature.

In addition, hot-cool theory predicts that high-levels of stress should enhance recognition of the arousing material but impair retrieval of the spatial and temporal aspects. However, the findings from Studies 1 and 2 showed that the stressor and administration of prednisone did not have an effect on recognition of the emotional stimuli. Instead, they may have had positive effects on the recall of the *spatial* layout of the Hot Appetitive room in Study 1 and on dwell time (indicating the possible use of *spatial* strategies in wayfinding) in Study 2. Thus, the positive effects seen in Studies 1 and 2 are inconsistent with predictions derived from hot-cool theory. However, it may be possible that the non-arousing testing conditions in Study 2 did not induce sufficient adrenergic arousal levels, and that, therefore, the ‘hot’ system was not activated.<sup>39</sup> If this was indeed the case, then the administration of cortisol would only have affected the ‘cool’ system, and one would expect to see an inverted-U relationship in performance on the retrieval tasks. Nonetheless, one would still question why prednisone administration did not impair visual and spatial memory as it did verbal memory?

Both the inverted-U hypothesis and hot-cool theory, however, do not make specific predictions about memory performance, but instead propose a description of the relationship between stress and memory (Landers, 2007). The findings from Studies 1 and 2 therefore demonstrate that the relationship between stress and verbal memory might differ from the relationship between stress and visual and spatial memory.

In summary, it appears that predictions derived from the inverted-U hypothesis might account for the current findings regarding verbal memory. In contrast, neither the inverted-U hypothesis, nor hot-cool theory, nor the integrated vertical and horizontal theory can account fully for the findings pertaining to visual and spatial memory. The current results indicate that the effects of elevated cortisol levels might have differing effects on verbal memory relative to visual and spatial memory: The latter might be more resilient to the impairing effects of cortisol than the former. The findings that the effects of the stressor and administration of prednisone might vary across memory domains are consistent with those of Domes et al. (2005). As discussed in Chapter 5, Domes et al. (2005) demonstrated that cortisol administration impaired memory retrieval for verbal information, but not for visual and spatial information.

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<sup>39</sup>One argument against this explanation is that the emotional stimuli were selected on the grounds of their arousing content; therefore, the images themselves were meant to activate the ‘hot’ system.

The possible theory that predicts that the effects of stress are domain-specific is rooted in an evolutionary basis, and is addressed in the following section.

### **Findings in Relation to the Functional Perspective of Memory**

As noted in Chapters 1 and 4, the hypothesis that stress has an impairing effect on all episodic memory retrieval seems counterintuitive from an evolutionary point of view. From a functional perspective, both memory and stress systems have functions, and these functions have been shaped by our evolutionary past. That is, both memory and stress systems evolved to serve as psychological and physiological mechanisms to help solve adaptive problems that occurred in our ancestral past (Nairne, 2005).

The stress response system (introduced in Chapter 1) is the body's adaptive response to a threatening situation. When triggered, this system prepares the body for a change in homeostasis by activating a series of physiological mechanisms that help the organism deal with the threatening situation. Specifically, the rapid release of catecholamines increases heart rate, blood pressure and respiration, while the slower release of GCs, via the HPA axis, serves to influence the peripheral organs and brain functioning (Joels, 2010). In conjunction, the stress systems serve to generate more energy for the body so that the organism might overcome the threatening situation (Smeets et al., 2012).

If memory serves a similar functional purpose to the stress system (i.e., to increase chances of survival and, consequently, to increase chances of successful sexual selection; Nairne, 2005), then it is likely that similar adaptive processes shaped both the memory and stress systems. It would not make logical sense that one system should operate in isolation from another; for instance, it seems logical that stress systems would generate more energy for the body to overcome threatening situations, and that memory systems would subsequently help the organism avoid similar situations.

Although evidence demonstrating that memory systems have evolved in an adaptive manner is limited, recent studies (introduced in Chapter 4) have reported that processing information from a survival perspective enhances subsequent recall (e.g., see Burns et al., 2011; Howe & Derbish, 2010; Kang et al., 2008; Nairne & Pandeirada, 2008a; Nairne et al., 2012; Otgaar & Smeets, 2010; Otgaar et al., 2010; Smeets et al., 2012; Weinstein et al., 2008). Recently, Smeets et al. (2012) demonstrated that processing words in terms of survival relevance boosted memory independently from the enhancing effects of stress on memory encoding. In Smeets et al.'s (2012) study, participants were exposed to either the TSST or a control manipulation, and were then required to rate words in terms of relevance in either a

survival or neutral scenario. Memory for the words was tested following a brief (2-3 min) distracter task. The authors reported that both stress and the processing of words in terms of survival relevance increased subsequent recall, but that a combination of survival processing while being stressed did not result in an even larger mnemonic benefit. The authors concluded that stress does not serve as a proximate mechanism for the positive effects of processing information from a survival perspective. Thus, limited evidence suggests that memory systems, similar to stress response systems, may have evolved in order to help ensure survival.

In support of a functional perspective of memory under stress, recent evidence from both human and animal studies suggests that learning under stress promotes a shift from a flexible cognitive (hippocampal-dependent) memory system to a rigid habit (dorsal striatum-dependent) memory system (Schwabe & Wolf, 2013). This shift has been documented in stress and cortisol studies examining visual and spatial learning tasks, including virtual environment tasks (Bohbot et al., 2011; Schwabe et al., 2007, 2008b, 2009b). These studies suggest that the shift in learning from a higher-order cognitive system to a lower-order habit system is an adaptive mechanism. That is, stress hormones shift cognitive systems towards encoding the event so that the organism can avoid or prepare for similar situations in the future (Schwabe & Wolf, 2013).

If memory and stress systems have evolved simultaneously, through processes of natural or sexual selection, then the structural properties of memory under stressful conditions should reflect their functions (Tooby & Cosmides, 1992). In turn, if memory systems have evolved to serve us in the present, or to help predict the future, then it is also likely that the evolution of the systems would be domain-specific (Nairne & Pandeirada, 2008b). After all, it would be beneficially adaptive in a threatening situation to recall germane information that would help to overcome the threat as opposed to less relevant information.

In terms of the current incongruent findings regarding verbal versus visual and spatial memory retrieval, one might speculate, from a survival perspective, that the recall of relevant visual and spatial information might be more beneficial than the recall of verbal information. Given that language is species- and culture-specific, the recall of verbal information might only be useful in escaping situations involving a human threat. In contrast, if stress triggers a fight-or-flight response, the retrieval of visual and spatial information would be essential to the flight response. In short, being able to physically escape by retrieving information that enables successful navigation away from the threatening situation will increase chances of

survival, and consequently increase reproductive fitness (Nairne et al., 2012). Thus, one might speculate that the retrieval of visual and spatial information that would aid in escaping a threatening situation would be an adaptive response.

Despite the findings from the present studies being consistent with the notion that the effects of stress might be domain-specific, there is little evidence of this specificity in the literature. In contradiction to a functional perspective of memory, rodent studies have consistently demonstrated that both stress and cortisol administration impair performance in the MWM (de Quervain et al., 1998; Diamond et al., 2006). In addition, human studies that have employed psychosocial stressors have also demonstrated impairing effects on visual and spatial memory (Buchanan & Tranel, 2008; Quesada et al., 2012; Schwabe & Wolf, 2009).<sup>40</sup> However, as discussed in Chapter 4, there are potential problems with the nature of the memory tasks and the measures of spatial memory used in previous animal and human studies. First, rodent studies are restricted by their measure of spatial memory, which is wayfinding performance. Wayfinding involves the interpretation of spatial memory through other cognitive functions (attention, orientation, and navigation), which may be influenced by stress (de Kloet et al., 1999; Diamond et al., 2004; Roozendaal, 2002). Furthermore, in threatening situations, many animals use freezing or evasive fleeing tactics (such as weaving in an erratic manner) to escape potential predators (Blanchard, Blanchard, Takahashi, & Kelley, 1977). Therefore, examining a rodent's spatial performance in a water maze might not be a true reflection of spatial memory.

Second, human studies have tested memory using tasks such as viewing pictures on a computer screen, or 2-dimensional object location tasks. Such tasks have little evolutionary relevance (that is, they do not resemble critical adaptive problems that could have shaped our evolutionary past), and it would therefore be unlikely that memory systems have adapted to solve these kinds of tasks under stress.

Further research is needed to elaborate upon the findings of the studies presented here. Future studies should explore and compare the effects of stress on different memory domains. In addition, future studies might utilize tasks that are more evolutionarily relevant, as this may allow for a better understanding of which memory domains are affected (and which are preserved) by stress. Further directions for future research are outlined at the end of this chapter.

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<sup>40</sup> Although, as noted above, human studies are yet to demonstrate that cortisol administration impairs visual and spatial memory retrieval. In addition, consistent with the findings from the present studies, Domes et al. (2005) demonstrated that cortisol administration impaired verbal but not visual and spatial information.

**Hypothesis 3: Women will display inferior spatial memory in comparison to men**

Despite not being a primary focus of this dissertation, previous research findings (reviewed in Chapter 2) indicate that men and women perform differently on certain tests of spatial memory. Specifically, men seem to perform better than women on virtual navigation tasks (Andreano & Cahill, 2009; Astur et al., 1998; Iaria et al., 2003; Moffat et al., 1998; Mueller et al., 2008; Ross et al., 2006; Sandstrom et al., 1998). Thus, in the two major studies presented here, a secondary prediction was that, regardless of experimental condition, men would outperform the women on the CG Arena tasks.

However, the observed data produced few sex differences in spatial memory. Although there were several sex differences (as noted previously) on the acquisition trials (most in favour of women outperforming men), there were no such differences in terms of wayfinding on the recall trial, or in terms of dwell time on the probe trial. There were also no significant sex differences in terms of recall of the spatial layout of the CG Arena rooms. In fact, the only sex difference in memory performance detected in the series of studies was in Study 2. There, as discussed previously, women showed superior recognition for the erotic images in the Hot Appetitive room. However, it is possible that this sex difference might be related to sex differences on the acquisition trials in the Hot Appetitive CG Arena room; therefore, the finding is in need of replication. Nevertheless, the finding that women performed better than men on visual recognition tests is not an isolated one in the literature. Some previous studies have reported that, in comparison to men, women recognize more landmarks from previously viewed scenes, especially when, on the recognition trial, the landmarks are isolated from their backgrounds (Barkley & Gabriel, 2007).

The lack of sex difference findings in the studies presented here are, therefore, inconsistent with previous reports that men perform better than women on navigational memory tasks in a virtual environment. Possible explanations for this disjunction between current and previous findings might again be that the visual and spatial tasks used in this dissertation were not sensitive enough to detect the subtle memory differences between the sexes. In addition to the possible ceiling effects discussed previously, the CG Arena tasks used in the presented studies might have allowed for the use of both allocentric and egocentric navigational strategies.

In line with the explanation introduced in Chapter 2 (pg. 74), men and women differ in their use of spatial navigation strategies. Whereas men have been reported to prefer allocentric strategies, women prefer to use more egocentric/landmark strategies when

navigating (Choi & Silverman, 1996; Dabbs et al., 1998; Down & Stea, 1977; Rahman et al., 2005). In finding the target in the CG Arena, participants had to use the distal cues, which acted as landmarks, on the walls of the Arena. Thus, it is possible that, in the presented studies, participants were able to utilize a landmark-based (in addition to, or in preference to, an allocentric) spatial navigation strategy when locating the target in the current CG Arena experimental rooms.<sup>41</sup> The possible use of a landmark-based strategy might have enabled women to perform equivalently to the men on the spatial navigation tasks. Furthermore, if participants were able to use landmark-based navigational strategies in the CG Arena, this explanation could account for the sex differences seen in the acquisition trials (as these were overwhelmingly in favor of female participants).

In support of the navigational strategy explanation, previous studies that have used virtual water mazes have reported that sex differences in navigational performance depend on the relevance of the information provided by the landmarks. When landmarks in a maze are not visible, or not in stable positions, then men perform significantly better than women. However, when landmarks are stable and provide relevant information regarding the position of the target, then men and women perform equivalently (Sandstrom et al. 1998; Rizk-Jackson et al., 2006). In the CG Arena rooms used in Study 1 and 2, all landmarks were visible, regardless of one's position in the room. Also, the hidden target remained in a fixed position relative to the landmarks. Thus, in the current studies, otherwise present sex differences may have been attenuated by the stability and relevance of the landmarks in the CG Arena.

If the use of a landmark-based navigational strategy does indeed account for the lack of sex differences in the present studies, then it is also possible that this same explanation might account for the non-significant wayfinding differences observed between the Stress and Control groups. Brain imaging studies have revealed significantly different patterns of activation when different cognitive navigational strategies are used (Gramann, Müller, Schönebeck, & Debus, 2006; Iaria et al. 2003; Jordan, Schadow, Wuestenberg, Heinze, & Jäncke, 2004). In comparison to allocentric strategies, egocentric strategies are associated with decreased activity in medial temporal areas, including the hippocampus and parahippocampal region (Jordan et al. 2004). In addition, Gramann et al. (2006) reported in their EEG study that individuals using egocentric strategies primarily recruited posterior-

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<sup>41</sup>However, previous CG Arena studies have demonstrated that men and women use allocentric spatial strategies in order to find the hidden target (Goodrich-Hunsaker, Livingstone, Skelton, & Hopkins, 2010; Jacobs et al., 1997, 1998; Skelton et al., 2000; Thomas et al., 2001). Therefore this explanation is tentative and might only be applicable to the current CG Arena rooms.

premotor networks, whereas individuals using allocentric strategies recruited more temporal lobe structures.<sup>42</sup>

As discussed previously, cortisol targets receptors in the frontal and medial temporal lobes. The influence of cortisol on the hippocampus is of specific interest in the present studies. If, in the present studies, participants were able to use landmark or egocentric navigation strategies in the CG Arena rooms (and these strategies do not rely on medial temporal structures such as the hippocampus), then the effects of cortisol on navigation would have been minimized. Thus, there remains a possibility that the use of landmark-based navigational strategies in the CG Arena might have eliminated both the stress and sex differences observed in the present studies.

A second, less probable explanation for the lack of observed sex differences, and one that is only applicable to the Stress groups, might be due to the complex interaction between GCs and sex hormones. Previous studies suggest that the effects of stress on memory might be different in men and women (Andreano & Cahill, 2006; Cahill, 2005; Gabriel, Hong, Chandra, Lonborg, & Barkley, 2011; Wolf et al., 2001b). For instance, Wolf et al. (2001b) reported that retrieval memory was affected by cortisol administration in men but not in women. Therefore, it is possible that men's memory is especially susceptible to the influences of stressors (Schwabe et al., 2009). Consequently, it might be possible that stress impaired retrieval more in men than it did in women, thereby reducing the male advantage on the spatial tasks. This hypothesis would only apply to the Stress groups in the present studies, however, given that men and women in the control conditions (in both Study 1 and Study 2) performed equivalently on the spatial memory tasks.

In contrast, it is possible that the complex interaction between GCs and sex hormones might account for the verbal memory advantage that was observed in the women who were exposed to the FFST-Stress condition in Study 1. In this study, the female participants in the Stress group recalled more word pairs from the VPA than all the other groups did. Although women are generally reported to outperform men on verbal memory tests (Andreano & Cahill, 2009), it is interesting that the highly arousing testing conditions, and the relatively low cortisol increase induced by the FFST-Stress condition, would enhance verbal memory in women. There is a possibility that the combined influence of stress, along with factors such

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<sup>42</sup>Interestingly, women have also been reported to engage their hippocampal structures significantly less than men do during navigation (Grön, Wunderlich, Spitzer, Tomczak, & Riepe, 2000), a finding believed to be linked to women using predominantly egocentric strategies (Andreano & Cahill, 2009). However, Ohnishi et al. (2006) found no evidence of an interaction between navigation strategies and sex, even in anticipated regions of interest (and using a lenient statistical threshold) shown to be sexually dimorphic in previous studies (Ohnishi, Matsuda, Hirakata, & Ugawa, 2006).

as sex hormones and stage of the menstrual cycle, could account for this superior performance (Kudielka et al., 2009).

In summary, the hypothesis that men would perform better than women on the spatial navigation (and related) tasks was not confirmed. Amongst other reasons, it might be possible that, in the presented studies, men and women displayed similar performances on the CG Arena navigational tasks due to the availability of a landmark spatial navigation strategy.

In conclusion, none of the three hypotheses tested in Studies 1 and 2 were fully confirmed. Despite potentially reasonable explanations for not confirming those hypotheses, the failure to confirm them indicates that there may have been several limitations to the series of studies presented here. These limitations are addressed in the following section, which also presents some suggestions for improving the research design.

### **Limitations**

Several limitations of Studies 1 and 2 need to be addressed, as this may assist future researchers who wish to either investigate the effects of stress on visual and spatial memory, or who wish to compare the effects of stress across different memory domains. The limitations discussed below pertain to: the sample used; the time of day that the studies were run; change in apparatus and loss of data in Study 2; the spatial environments; inter-individual variation on the wayfinding tasks; the use of a non-emotional verbal task; and not comparing cortisol responders to non-responders.

**Sample used in the current studies.** The participants recruited for the studies in this dissertation were all from a university population, with the vast majority being undergraduate students aged between 18 and 22 years old. This exclusive use of young participants limits the generalizability of the present findings, as cortisol response has been reported to vary with age (Gunnar, Talge, & Herrera, 2009; Kudielka et al., 2000, 2004; Rohleder et al., 2002).<sup>43</sup> In addition to influencing cortisol response, age has also been reported to influence spatial navigation strategies (e.g., Bohbot et al., 2012; Harris et al., 2012). Future studies might therefore improve on the generalizability of the present studies by recruiting a more diverse sample of participants in terms of age.

In addition to age, other factors have also been shown to influence cortisol response and memory. These factors include sex hormones, the stage of the menstrual cycle, use of oral contraceptives in women, race, genetics, previous exposure to pre- and post-natal stress,

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<sup>43</sup>Although see Nicolson, Storms, Ponds, and Sulon (1997), and Kudielka, Schmidt-Reinwald, Hellhammer, and Kirschbaum (1999) for exceptions.

medication use, psychiatric disorders, personality and mood (Chong, Uhart, McCaul, Johnson, & Wand, 2008; Eich, Kihlstrom, Bower, Forgas & Nieden-Thal, 2000; Kudielka et al., 2009). Although the design of the current studies attempted to control for many of these factors (e.g., oral contraceptives, use of medication, psychiatric disorders, and mood), other factors (e.g., menstrual cycle, race, and personality) were not controlled for, as the purpose of this research was to explore the effects of stress on a relatively broad population group. However, future studies that investigate the effects of stress on memory might control for these additional factors, as well as include more diverse samples in order to untangle the relationship between stress and memory.

**Time of day.** Test sessions were run in the afternoon hours (between 14h00 and 18h00) in an attempt to control for circadian fluctuations in cortisol levels. As discussed previously, the consequence of testing in the afternoon is that it is associated with low endogenous cortisol levels. According to the inverted U-hypothesis, lower levels of endogenous cortisol are linked to a high occupation ratio between Type I and II receptors and, therefore, with an increased possibility of seeing positive effects on memory.

Further research is needed to explore the role that the time of day has on the effects of stress on visual and spatial memory.<sup>44</sup> Studies that incorporate testing sessions at various times of the day (such as Maheu et al., 2005, and Smeets, 2011) may finally determine for certain whether natural variations in cortisol levels are capable of swaying the direction of the effects of stress on memory.

**Change in apparatus and loss of data in Study 2.** A further limitation in the present study was the decision to use an alternative saliva collection apparatus (the eyespear instead of the salivette) in Study 2 (see pg. 153). Although the eyespear was only used temporally, it not only resulted in the loss of a number of cortisol samples but the change in methodology also compromised the validity of comparisons within Study 2 and between Studies 1 and 2. In addition, I lost a large amount of cortisol, anxiety and depression data due to experimenter error in Study 2 (see pg. 156). This loss led to a significantly smaller dataset for these measures, thereby resulting in the power of the relevant analyses being greatly reduced (Howell, 2012). Both the change in the methodology, and the loss of the data, were significant limitations to Study 2 and such occurrences should be avoided in future studies.

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<sup>44</sup>As discussed earlier in this chapter, Smeets (2011) recently tested the effects of stress on verbal memory retrieval in the morning and in the afternoon and reported that stress impaired retrieval, irrespective of time. However, the current findings (especially those in Study 1) and those of Lupien et al. (2002), Schilling et al. (2013) and Schwabe et al. (2009) contradict Smeets's finding. Hence, further research is needed in order to tease out the factors that are responsible for these conflicting results.

**Spatial environments.** A major concern in the present studies was that the analyses detected no significant differences in wayfinding performance. These results are unexpected, as numerous rodent studies have demonstrated that stress impairs retrieval performance in the MWM (Atsak et al., 2012; de Quervain et al., 1998; Rashidy-Pouret et al., 2004; Roozendaal et al., 2003, 2004; Sajadi et al., 2007). Failure to confirm this result in the human sample, as noted previously, might be due to the presence of ceiling effects. The participants had only three target locations to learn, and six acquisition trials in each room in order to ensure that each location was successfully learned. It is possible that either too many acquisition trials, or the presence of too few target locations to remember, might have resulted in ceiling effects in the participants' performances. Future studies might be able to avoid these effects by increasing the number of target locations that participants need to remember. Increasing the difficulty of the task might also result in memory being more susceptible to the effects of stress (Diamond, 1999; Lupien et al., 2002).

In addition, as discussed previously, it might be possible that, in the present studies, spatial navigation in the CG Arena rooms allowed for the use of landmark or egocentric strategies. Egocentric strategies are believed to be independent of the hippocampus and might be prone to a sex bias. Despite the fact that the CG Arena has been validated and used extensively as a human analogue of the MWM (Jacobs et al., 1997, 1998; Kallai et al., 2005; Skelton, Ross, Nerad, & Livingstone, 2006; Thomas et al., 2001; Thomas, 2003), it might be possible that the CG Arena rooms used in the current studies were not best suited for research exploring the effects of stress on memory and/or sex differences. Future research might include another spatial maze task, such as a virtual radial arm maze (e.g., see Astur et al., 2005; Bohbot et al., 2011; Guenzel et al., 2013; Goodrich-Hunsaker & Hopkins, 2010), in addition to the CG Arena tasks.

**Inter-individual variation on wayfinding task.** Another potential problem with the measure of wayfinding performance in the present studies was that there were large variations in performance between the participants. It is possible that this variation masked underlying differences between the groups. Although the purpose of the set of training trials was to reduce this variation, training might not have been sufficient to ensure equal competency across participants on the more difficult invisible target acquisition and recall trials.

Future studies could therefore improve on the current design by attempting to reduce between-participant variation in CG Arena performance. For instance, the training phase could be extended and could include training trials with an invisible target. More training in

the CG Arena might further ensure that all participants enter the acquisition trials on a more equal footing. However, the logistics involved in standardizing training so as to be certain that all participants are performing at an equivalent level might prove time-consuming and impractical, as some participants will take longer than others to familiarize themselves with the CG Arena. Alternatively, studies could employ a within-subject experimental design. By utilizing a counterbalanced design, participants could complete both the stress/GC administration and the control conditions.

**Non-emotional verbal task.** Despite the aim of this dissertation being to examine the effects of stress on visual and spatial memory, it also included a verbal component in order to relate current findings to previous research. In addition, a verbal component allowed for comparison between the effects of stress on verbal versus visual and spatial memory. However, the VPA used in Studies 1 and 2 was an oral memory test that contained only neutral or non-emotional words.

Future studies comparing the effects of stress on different memory domains could improve on the present studies by matching the verbal task as closely as possible with the visual and spatial task. For instance, to contrast the CG Arena tasks, the verbal task should be an incidental learning computer-based task, and should contain the same amount of acquisition trials and a similar number of items that need to be remembered. The task should also contain emotionally arousing words (varying in valence) in addition to neutral words. Such a task would therefore introduce fewer confounding variables, and would allow for more valid comparisons between the effects of stress on visual and spatial memory versus its effects on verbal memory.

**Cortisol responders versus non-responders.** In Study 1, the participants in the Stress groups were exposed to the FFST-Stress condition. Although this method induced a cortisol response in most participants exposed to it, 9 participants showed only an active autonomic response and little or no cortisol response. Those 9 participants could be termed ‘cortisol non-responders’. As noted in the preceding chapters, some previous studies (e.g., Buchanan & Tranel, 2008; Elzinga & Roelofs, 2005) have compared the memory performance of cortisol responders to that of non-responders separately, and have reported differences between these groups. Similar analyses were not performed in Study 1 because the control groups showed comparable autonomic increases to the stress groups. Those control groups were then, in a sense, a cortisol non-responder group, or at least not distinguishable from the stress group non-responders in terms of adrenergic and HPA axis response.

Although not explored in this dissertation, further research is needed to identify the individual effects of the fast (adrenergic) system and the slow (HPA axis) system on memory. However, the validity of post-hoc analyses between responders versus non-responders is questionable due to the temporal gradient of the stress response. In stress studies, testing usually occurs when cortisol levels are at their peak. Unfortunately, this is about 15 to 20 minutes after the termination of the stress manipulation, by which time the fast autonomic response has subsided to near baseline levels (see, e.g., Smeets et al., 2012). Thus, the only difference between cortisol responders and non-responders at the time of testing is in cortisol levels, while autonomic activation in both stress and control groups is neither present nor different between them. Attributing effects to the autonomic nervous system when it is, in fact, absent at the time of testing may lead to inaccurate conclusions.

Future studies might compare the effects of the autonomic response versus the HPA-axis response on memory more accurately by making this the primary research question (see Schönfeld et al., 2014), rather than doing it via post-hoc analysis. Isolating both adrenergic and HPA-axis activation in the study design, as well as interactions between the two, may help to tease out the individual workings of the stress systems on memory. Determining whether these effects are consistent across different memory domains is another research question that is in need of exploration.

### **Conclusions and Future Research Directions**

The aim of this dissertation was to gain a better understanding of the effects of stress on visual and spatial memory. Interestingly, none of the hypotheses regarding the effects of stress on memory were completely confirmed in Studies 1 and 2. Instead, the findings in those studies indicated that being exposed to an acute stressor or being administered prednisone might have had varying effects across memory domains. Neither means of elevating cortisol levels impaired retrieval of visual and spatial information. In contrast, exposure to the acute stressor appeared to have an enhancing effect on verbal memory in women, and prednisone administration appeared to impair verbal memory in both men and women.

Relating the current findings to theory revealed that only the inverted-U hypothesis was capable of accounting for the observed pattern of data with regard to verbal memory. Specifically, congruent with predictions from the inverted-U hypothesis, a combination of low levels of endogenous cortisol due to the time of day, along with the dose-dependent

effects of cortisol, might account for the verbal memory performance described in Studies 1 and 2.

However, none of the three theories were capable of explaining the effects of the acute stressor and administration of prednisone on visual and spatial memory. That is, the finding that visual and spatial memory was not impaired, even at high cortisol levels, is not accounted for by any of the theories discussed here. Alternatively, from a functional perspective, the findings that visual and spatial, and not verbal, information is recalled equally well, if not better under stress, is consistent with notion of domain-specific effects of stress (Nairne & Pandeirada, 2008b).

Under perceived threat, the body's stress systems activate hormones in preparation for a change in homeostasis. If stress systems serve to generate more energy for the body to overcome the threatening situation through a possible fight-or-flight response, then it would make sense that there is also a shift in the accompanying cognitive resources. After all, what good is the flight response if we are unable to retrieve spatial information in order to guide our escape?

As the literature pertaining to this topic has advanced, it has become increasingly apparent that the effects of stress and cortisol on memory are not uniform. First, stress has been demonstrated to have varying effects on different memory types (i.e., on working memory versus episodic memory versus conditioning). Next, research that narrowed the focus on episodic memory has demonstrated that the effects of stress differ depending on the stage of memory (i.e., on encoding versus consolidation versus retrieval). More recently, a growing trend in research indicates that the effects of stress on isolated memory stages (for instance, retrieval) can be influenced by factors such as emotional arousal, the context, and the testing environment. Research is therefore gradually revealing that the effects of stress on memory might be more intricate than they were first thought to be.

The results from this dissertation indicate that further investigation into a possible functional perspective regarding the effects of stress on memory might be a rewarding area of inquiry. Adopting a functional perspective regarding stress and memory systems, instead of a structural one, might lead to researchers asking "why" instead of "how". Asking "why" might help to introduce novel ideas, while opening up new avenues of research that may, in due course, provide the empirical and theoretical structure that is required to untangle "how" stress effects memory (Nairne & Pandeirada, 2008b, 2010).

Specifically, three findings in Studies 1 and 2 indicate the need for further research. First, the finding that stress had varying effects across memory domains warrants further

inquiry. Demonstrating that stress hormones influence brain function selectively would provide evidence that human memory operates in functionally relevant situations. As mentioned previously, however, care should be taken to ensure that the verbal and visual-spatial tasks are methodologically similar and allow for accurate comparison between tasks.

Second, as discussed previously, two unanticipated findings from Studies 1 and 2 require replication. In Study 1, the participants who were assigned to the FFST-Stress condition recalled the spatial layout of the Hot Appetitive room better than the control participants. In Study 2, the participants who were administered cortisol spent significantly longer searching for the target in the correct location of all three CG Arena rooms on the probe trial than the control participants did. Replication of these results would not only provide further evidence for the domain-specific effects of stress, but also indicate that the effects within the memory domain are dependent on cortisol concentrations. In addition, replication of the findings in Study 2 would indicate that cortisol can also influence spatial strategies during memory retrieval.

Finally, the findings from Studies 1 and 2 that neither the acute stressor nor administration of prednisone had an impairing effect on memory for the images in the CG Arena is inconsistent with previous reports (e.g., Buchanan & Tranel, 2008; Schönfeld et al., 2014). A possibility that needs to be explored is whether encoding the images in a spatial setting (i.e., incidental encoding while actively using the images as a spatial reference) results in memory for the images being more resistant to stress than merely viewing and encoding images in a passive manner on a computer screen. If this is indeed the case, then it could demonstrate that the nature of the memory tasks that are used in stress research may influence the direction of the effects of stress; this would provide further evidence that memory under stress has a function. However, future studies will need to carefully design the encoding task so that participants are exposed to the images for equal amounts of time.

In conclusion, although this dissertation failed to confirm the majority of the hypotheses tested, it has opened up a relatively unexplored frontier of research. The present findings show that the effects of stress might not be homogeneous across memory domains; this is a topic that is, surprisingly, absent from the current literature and theory. It is possible, however, that the current literature and theory has focused predominately on a structural perspective of memory. Adopting a new perspective on the study of the relationship between stress and memory might lead to innovative questions that will ultimately improve our understanding of this topic.

## REFERENCES

- Abercrombie, H. C., Kalin, N. H., Thurow, M. E., Rosenkranz, M. A., & Davidson, R. J. (2003). Cortisol variation in humans affects memory for emotionally laden and neutral information. *Behavioral neuroscience*, *117*(3), 505–516.
- Adolphs, R., Tranel, D., & Buchanan, T. W. (2005). Amygdala damage impairs emotional memory for gist but not details of complex stimuli. *Nature neuroscience*, *8*(4), 512–518.
- Alexander, M. G., & Wood, W. (2000). Women, men, and positive emotions: A social role interpretation. In A. H. Fischer (Ed.), *Gender and emotion: Social psychology perspectives* (pp. 189–210). New York: Cambridge University Press.
- Allen, G. L. (2003). *Human Spatial Memory: Remembering Where*. Mahwah, N.J.: Psychology Press.
- Andreano, J. M., & Cahill, L. (2006). Glucocorticoid release and memory consolidation in men and women. *Psychological science*, *17*(6), 466–470.
- Andreano, J. M., & Cahill, L. (2009). Sex influences on the neurobiology of learning and memory. *Learning & Memory*, *16*(4), 248–266.
- Andersen, N. E., Dahmani, L., Konishi, K., & Bohbot, V. D. (2012). Eye tracking, strategies, and sex differences in virtual navigation. *Neurobiology of Learning and Memory*, *97*(1), 81–89.
- Arbel, I., Kadar, T., Silbermann, M., & Levy, A. (1994). The effects of long-term corticosterone administration on hippocampal morphology and cognitive performance of middle-aged rats. *Brain research*, *657*(1-2), 227–235.
- Arnsten, A. F. T. (2009). Stress signalling pathways that impair prefrontal cortex structure and function. *Nature reviews. Neuroscience*, *10*(6), 410–422.
- Astur, R. S., Ortiz, M. L., & Sutherland, R. J. (1998). A characterization of performance by men and women in a virtual Morris water task: a large and reliable sex difference. *Behavioural brain research*, *93*(1-2), 185–190.
- Astur, R. S., St Germain, S. A., Baker, E. K., Calhoun, V., Pearlson, G. D., & Constable, R. T. (2005). fMRI hippocampal activity during a virtual radial arm maze. *Applied Psychophysiology and Biofeedback*, *30*(3), 307–317.
- Astur, R. S., Tropp, J., Sava, S., Constable, R. T., & Markus, E. J. (2004). Sex differences and correlations in a virtual Morris water task, a virtual radial arm maze, and mental rotation. *Behavioural Brain Research*, *151*(1-2), 103–115.
- Atsak, P., Hauer, D., Campolongo, P., Schelling, G., McGaugh, J. L., & Roozendaal, B. (2012). Glucocorticoids interact with the hippocampal endocannabinoid system in impairing retrieval of contextual fear memory. *Proceedings of the National Academy of Sciences*, 201200742.

- Austin, M.-P., Mitchell, P., & Goodwin, G. M. (2001). Cognitive deficits in depression: Possible implications for functional neuropathology. *The British Journal of Psychiatry*, *178*(3), 200–206.
- Baddeley, A. (1992). Working memory. *Science*, *255*(5044), 556–559.
- Barkley, C. L., & Gabriel, K. I. (2007). Sex differences in cue perception in a visual scene: investigation of cue type. *Behavioral neuroscience*, *121*(2), 291–300.
- Barsegyan, A., Mackenzie, S. M., Kurose, B. D., McGaugh, J. L., & Roozendaal, B. (2010). Glucocorticoids in the prefrontal cortex enhance memory consolidation and impair working memory by a common neural mechanism. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(38), 16655–16660.
- Beatty, W. W., Bierley, R. A., & Boyd, J. G. (1985). Preservation of accurate spatial memory in aged rats. *Neurobiology of aging*, *6*(3), 219–225.
- Beck, A. T., Steer, R. A., & Brown, G. K. (1996). *Beck Depression Inventory manual (2nd ed.)*. San Antonio, TX: Psychological Corporation
- Beckner, V. E., Tucker, D. M., Delville, Y., & Mohr, D. C. (2006). Stress facilitates consolidation of verbal memory for a film but does not affect retrieval. *Behavioral neuroscience*, *120*(3), 518–527.
- Beckwith, B. E., Petros, T. V., Scaglione, C., & Nelson, J. (1986). Dose-dependent effects of hydrocortisone on memory in human males. *Physiology & behavior*, *36*(2), 283–286.
- Bennett, M. C., Diamond, D. M., Fleshner, M., & Rose, G. M. (2013). Serum corticosterone level predicts the magnitude of hippocampal primed burst potentiation and depression in urethane-anesthetized rats. *Psychobiology*, *19*(4), 301–307.
- Biondi, M., & Picardi, A. (1999). Psychological stress and neuroendocrine function in humans: The last two decades of research. *Psychotherapy and Psychosomatics*, *68*(3), 114–150.
- Blanchard, R. J., Blanchard, D. C., Takahashi, T., & Kelley, M. J. (1977). Attack and defensive behaviour in the albino rat. *Animal Behaviour*, *25*, Part 3, 622–634.
- Bohbot, V. D., Gupta, M., Banner, H., & Dahmani, L. (2011). Caudate nucleus-dependent response strategies in a virtual navigation task are associated with lower basal cortisol and impaired episodic memory. *Neurobiology of learning and memory*, *96*(2), 173–180.
- Bohbot, V. D., McKenzie, S., Konishi, K., Fouquet, C., Kurdi, V., Schachar, R., ... Robaey, P. (2012). Virtual navigation strategies from childhood to senescence: evidence for changes across the life span. *Frontiers in Aging Neuroscience*, *4*.
- Bohus, B., & Lissák, K. (1968). Adrenocortical hormones and avoidance behaviour of rats. *International journal of neuropharmacology*, *7*(4), 301–306.
- Bradley, M. M. (2009). Natural selective attention: orienting and emotion. *Psychophysiology*, *46*(1), 1–11.

- Bradley, M. M., Keil, A., & Lang, P. J. (2012). Orienting and emotional perception: facilitation, attenuation, and interference. *Frontiers in Psychology*, *3*, 493.
- Bradley, M. M., & Lang, P. J. (1994). Measuring emotion: the Self-Assessment Manikin and the Semantic Differential. *Journal of Behavior Therapy and Experimental Psychiatry*, *25*(1), 49–59.
- Bradley, M. M., & Lang, P. J. (1999a). *Affective norms for English words (ANEW): Instruction manual and affective ratings* (Tech. Rep. No. C-1). Gainesville, FL: University of Florida, The Center for Research in Psychophysiology.
- Bradley, M. M., & Lang, P. J. (1999b). *International affective digitized sounds (IAD): Instruction manual and affective ratings* (Tech. Rep. No. B-1). Gainesville, FL: University of Florida, The Center for Research in Psychophysiology.
- Bradley, M. M., Codispoti, M., Cuthbert, B. N., & Lang, P. J. (2001). Emotion and motivation I: defensive and appetitive reactions in picture processing. *Emotion (Washington, D.C.)*, *1*(3), 276–298.
- Bradley, M. M., Codispoti, M., Sabatinelli, D., & Lang, P. J. (2001). Emotion and motivation II: sex differences in picture processing. *Emotion (Washington, D.C.)*, *1*(3), 300–319.
- Broadbent, D. E. (1965). A Reformulation of the Yerkes-Dodson Law. *British Journal of Mathematical and Statistical Psychology*, *18*(2), 145–157.
- Broadbent, N. J., Squire, L. R., & Clark, R. E. (2006). Reversible hippocampal lesions disrupt water maze performance during both recent and remote memory tests. *Learning & memory (Cold Spring Harbor, N.Y.)*, *13*(2), 187–191.
- Brooks, B. M., McNeil, J. E., Rose, F. D., Greenwood, R. J., Attree, E. A., & Leadbetter, A. G. (1999). Route learning in a case of amnesia: A preliminary investigation into the efficacy of training in a virtual environment. *Neuropsychological Rehabilitation*, *9*, 63-76.
- Brunyé, T. T., Gardony, A., Mahoney, C. R., & Taylor, H. A. (2012). Going to Town: Visualized Perspectives and Navigation Through Virtual Environments. *Computers in Human Behavior*, *28*(1), 257–266.
- Buchanan, T. W., & Lovallo, W. R. (2001). Enhanced memory for emotional material following stress-level cortisol treatment in humans., *26*(3), 307–317.
- Buchanan, T. W., & Tranel, D. (2008). Stress and emotional memory retrieval: Effects of sex and cortisol response. *Neurobiology of learning and memory*, *89*(2), 134–141.
- Buchanan, T. W., Tranel, D., & Adolphs, R. (2006). Impaired memory retrieval correlates with individual differences in cortisol response but not autonomic response. *Learning & Memory*, *13*(3), 382–387.
- Burkitt, J., Widman, D., & Saucier, D. M. (2007). Evidence for the influence of testosterone in the performance of spatial navigation in a virtual water maze in women but not in men. *Hormones and Behavior*, *51*(5), 649–654.

- Burnham, W. H. (1904). Retroactive Amnesia: Illustrative Cases and a Tentative Explanation. *The American Journal of Psychology*, *14*(3/4), 118–132.
- Burns, D. J., Burns, S. A., & Hwang, A. J. (2011). Adaptive memory: determining the proximate mechanisms responsible for the memorial advantages of survival processing. *Journal of experimental psychology. Learning, memory, and cognition*, *37*(1), 206–218.
- Buss, D. M. (1994). *The evolution of desire: Strategies of human mating*. New York: Basic Books.
- Buss, C., Wolf, O. T., Witt, J., & Hellhammer, D. H. (2004). Autobiographic memory impairment following acute cortisol administration. *Psychoneuroendocrinology*, *29*(8), 1093–1096.
- Cacioppo, J. T., & Berntson, G. G. (1994). Relationship between attitudes and evaluative space: A critical review, with emphasis on the separability of positive and negative substrates. *Psychological Bulletin*, *115*(3), 401–423.
- Cahill, L., Babinsky, R., Markowitsch, H. J., & McGaugh, J. L. (1995). The amygdala and emotional memory. *Nature*, *377*(6547), 295–296.
- Cahill, L., Gorski, L., Belcher, A., & Huynh, Q. (2004). The influence of sex versus sex-related traits on long-term memory for gist and detail from an emotional story. *Conscious and Cognition*, *13*, 391–400.
- Cahill, L., Gorski, L., & Le, K. (2003). Enhanced human memory consolidation with post-learning stress: interaction with the degree of arousal at encoding. *Learning & memory (Cold Spring Harbor, N.Y.)*, *10*(4), 270–274.
- Cahill, L., Haier, R. J., Fallon, J., Alkire, M. T., Tang, C., Keator, D., ... McGaugh, J. L. (1996). Amygdala activity at encoding correlated with long-term, free recall of emotional information. *Proceedings of the National Academy of Sciences of the United States of America*, *93*(15), 8016–8021.
- Cahill, L., Prins, B., Weber, M., & McGaugh, J. L. (1994). Beta-adrenergic activation and memory for emotional events. *Nature*, *371*(6499), 702–704.
- Cai, W.-H., Blundell, J., Han, J., Greene, R. W., & Powell, C. M. (2006). Postreactivation glucocorticoids impair recall of established fear memory. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *26*(37), 9560–9566.
- Canli, T., Zhao, Z., Brewer, J., Gabrieli, J. D., & Cahill, L. (2000). Event-related activation in the human amygdala associates with later memory for individual emotional experience. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *20*(19), RC99.
- Chai, X. J., & Jacobs, L. F. (2009). Sex differences in directional cue use in a virtual landscape. *Behavioral Neuroscience*, *123*(2), 276–283.
- Champaneri, S., Xu, X., Carnethon, M. R., Bertoni, A. G., Seeman, T., DeSantis, A. S., ... Golden, S. H. (2013). Diurnal Salivary Cortisol is Associated With Body Mass Index

- and Waist Circumference: The Multi-Ethnic Study of Atherosclerosis. *Obesity (Silver Spring, Md.)*, 21(1), E56–E63.
- Chan, E., Baumann, O., Bellgrove, M. A., & Mattingley, J. B. (2012). From objects to landmarks: the function of visual location information in spatial navigation. *Frontiers in Psychology*, 3, 304.
- Chong, R. Y., Uhart, M., McCaul, M. E., Johnson, E., & Wand, G. S. (2008). Whites have a more robust hypothalamic-pituitary-adrenal axis response to a psychological stressor than blacks. *Psychoneuroendocrinology*, 33(2), 246–254.
- Choi, J., & Silverman, I. (1996). Sexual dimorphism in spatial behaviors: Applications to route learning. *Evolution and Cognition*, 2, 165–171.
- Christianson, S. A. (1984). The relationship between induced emotional arousal and amnesia. *Scandinavian Journal of Psychology*, 25(2), 147–160.
- Clark, R. E., Broadbent, N. J., & Squire, L. R. (2005a). Hippocampus and remote spatial memory in rats. *Hippocampus*, 15(2), 260–272.
- Clark, R. E., Broadbent, N. J., & Squire, L. R. (2005b). Impaired Remote Spatial Memory After Hippocampal Lesions Despite Extensive Training Beginning Early in Life. *Hippocampus*, 15(3), 340–346.
- Clark, M. S., Milberg, S., & Ross, J. (1983). Arousal cues arousal-related material in memory: implications for understanding effects of mood on memory. *Journal of Verbal Learning and Verbal Behavior*, 22(6), 633–649.
- Clark, K. B., Naritoku, D. K., Smith, D. C., Browning, R. A., & Jensen, R. A. (1999). Enhanced recognition memory following vagus nerve stimulation in human subjects. *Nature neuroscience*, 2(1), 94–98.
- Clint, E. K., Sober, E., Garland, T., Jr, & Rhodes, J. S. (2012). Male superiority in spatial navigation: adaptation or side effect? *The Quarterly Review of Biology*, 87(4), 289–313.
- Coluccia, D., Wolf, O. T., Kollias, S., Roozendaal, B., Forster, A., & Quervain, D. J.-F. de. (2008). Glucocorticoid Therapy-Induced Memory Deficits: Acute versus Chronic Effects. *The Journal of Neuroscience*, 28(13), 3474–3478.
- Cornelisse, S., Joëls, M., & Smeets, T. (2011). A randomized trial on mineralocorticoid receptor blockade in men: effects on stress responses, selective attention, and memory. *Neuropsychopharmacology: official publication of the American College of Neuropsychopharmacology*, 36(13), 2720–2728.
- Cornelisse, S., Van Stegeren, A. H., & Joëls, M. (2011). Implications of psychosocial stress on memory formation in a typical male versus female student sample. *Psychoneuroendocrinology*, 36(4), 569–578.
- Couclelis, H., Golledge, R. G., Gale, N., & Tobler, W. (1987). Exploring the anchor-point hypothesis of spatial cognition. *Journal of Environmental Psychology*, 5, 99–122.

- Cuthbert, B. N., Schupp, H. T., Bradley, M., McManis, M., & Lang, P. J. (1998). Probing affective pictures: attended startle and tone probes. *Psychophysiology*, *35*(3), 344–347.
- Davis, M. (2000). The role of the amygdala in conditioned and unconditioned fear and anxiety. In J. P. Aggleton (Ed.), *The amygdala, Vol. 2* (pp. 213–287). Oxford, England: Oxford University Press.
- de Geus, E. J. C., & van Doornen, L. J. P. (1996). Ambulatory assessment of parasympathetic/sympathetic balance by impedance cardiography. In: Fahrenberg, J., Myrtek, M. (eds) *Ambulatory assessment. Computer assisted psychological and psychophysiological methods in monitoring and field studies*. Hogrefe & Huber, Berlin, pp 141-164.
- de Kloet, E. R., Joëls, M., & Holsboer, F. (2005). Stress and the brain: from adaptation to disease. *Nature reviews. Neuroscience*, *6*(6), 463–475.
- de Kloet, E. R., Oitzl, M. S., & Joëls, M. (1999). Stress and cognition: are corticosteroids good or bad guys? *Trends in neurosciences*, *22*(10), 422–426.
- de Quervain, D. J.-F., Aerni, A., & Roozendaal, B. (2007). Preventive effect of beta-adrenoceptor blockade on glucocorticoid-induced memory retrieval deficits. *The American journal of psychiatry*, *164*(6), 967–969.
- de Quervain, D. J.-F., Aerni, A., Schelling, G., & Roozendaal, B. (2009). Glucocorticoids and the regulation of memory in health and disease. *Frontiers in Neuroendocrinology*, *30*(3), 358–370.
- de Quervain, D. J.-F., Henke, K., Aerni, A., Treyer, V., McGaugh, J. L., Berthold, T., ... Hock, C. (2003). Glucocorticoid-induced impairment of declarative memory retrieval is associated with reduced blood flow in the medial temporal lobe. *The European journal of neuroscience*, *17*(6), 1296–1302.
- de Quervain, D. J., Roozendaal, B., & McGaugh, J. L. (1998). Stress and glucocorticoids impair retrieval of long-term spatial memory. *Nature*, *394*(6695), 787–790.
- de Quervain, D. J., Roozendaal, B., Nitsch, R. M., McGaugh, J. L., & Hock, C. (2000). Acute cortisone administration impairs retrieval of long-term declarative memory in humans. *Nature neuroscience*, *3*(4), 313–314.
- Dickerson, S. S., & Kemeny, M. E. (2002). Acute stressors and cortisol reactivity: A meta-analytic review. *Psychosomatic Medicine*, *54*, 105–123.
- Dickerson, S. S., & Kemeny, M. E. (2004). Acute stressors and cortisol responses: a theoretical integration and synthesis of laboratory research. *Psychological Bulletin*, *130*(3), 355–391.
- Dickerson, S. S., Mycek, P. J., & Zaldivar, F. (2008). Negative social evaluation, but not mere social presence, elicits cortisol responses to a laboratory stressor task. *Health Psychology: Official Journal of the Division of Health Psychology, American Psychological Association*, *27*(1), 116–121.

- Dickinson, A., & Dearing, M. F. (1979). Appetitive-aversive interactions and inhibitory processes. In A. Dickinson & R. A. Boakes (Eds.), *Mechanisms of learning and motivation* (pp. 203-231). Hillsdale, NJ: Lawrence Erlbaum Associates.
- Diamond, D. M., Bennett, M. C., Fleshner, M., & Rose, G. M. (1992). Inverted-U relationship between the level of peripheral corticosterone and the magnitude of hippocampal primed burst potentiation. *Hippocampus*, *2*(4), 421–430.
- Diamond, D. M., Campbell, A. M., Park, C. R., Woodson, J. C., Conrad, C. D., Bachstetter, A. D., et al. (2006). Influence of predator stress on the consolidation versus retrieval of long-term spatial memory and hippocampal spinogenesis. *Hippocampus*, *16*, 571-576.
- Diamond, D. M., Campbell, A. M., Park, C. R., Halonen, J., & Zoladz, P. R. (2007). The Temporal Dynamics Model of Emotional Memory Processing: A Synthesis on the Neurobiological Basis of Stress-Induced Amnesia, Flashbulb and Traumatic Memories, and the Yerkes-Dodson Law. *Neural Plasticity*, *2007*, 1–33.
- Diamond, D. M., Park, C. R., Heman, K. L., & Rose, G. M. (1999). Exposing rats to a predator impairs spatial working memory in the radial arm maze. *Hippocampus*, *9*, 542-552.
- Diamond, D. M., Park, C. R., & Woodson, J. C. (2004). Stress generates emotional memories and retrograde amnesia by inducing an endogenous form of hippocampal LTP. *Hippocampus*, *14*(3), 281–291.
- Dolan, R. J. (2002). Emotion, cognition, and behavior. *Science (New York, N.Y.)*, *298*(5596), 1191–1194.
- Domes, G., Heinrichs, M., Reichwald, U., & Hautzinger, M. (2002). Hypothalamic-pituitary-adrenal axis reactivity to psychological stress and memory in middle-aged women: high responders exhibit enhanced declarative memory performance. *Psychoneuroendocrinology*, *27*(7), 843–853.
- Domes, G., Heinrichs, M., Rimmele, U., Reichwald, U., & Hautzinger, M. (2004). Acute stress impairs recognition for positive words--association with stress-induced cortisol secretion. *Stress (Amsterdam, Netherlands)*, *7*(3), 173–181.
- Domes, G., Rothfischer, J., Reichwald, U., & Hautzinger, M. (2005). Inverted-U function between salivary cortisol and retrieval of verbal memory after hydrocortisone treatment. *Behavioral Neuroscience*, *119*(2), 512–517.
- Dozois, D. J. A., Dobson, K. S., & Ahnberg, J. L. (1998). A psychometric evaluation of the Beck Depression Inventory–II. *Psychological Assessment*, *10*(2), 83–89.
- Dabbs, J. M., Chang, E. L., Strong, R. A., & Milun, R. (1998). Spatial ability, navigation strategy, and geographic knowledge among men and women. *Evolution and Human Behavior*, *19*, 89–98.
- Downs, R. M., & Stea, D. (Eds.) (1973). *Image and environment*. London: Edward Arnold.

- Downs, R. M., & Stea, D. (1977). *Maps in minds: Reflections on cognitive mapping*. Harper and Row: New York.
- Driscoll, I., Hamilton, D. A., Yeo, R. A., Brooks, W. M., & Sutherland, R. J. (2005). Virtual navigation in humans: the impact of age, sex, and hormones on place learning. *Hormones and Behavior*, *47*(3), 326–335.
- Dubrovsky, B. O. (n.d.). P. Noble, and K. Gijbers (1987) Effects of 5 alpha-dihydrocorticosterone on evoked responses and long-term potentiation. *Brain. Res. Bull*, *19*, 635–638.
- Dudai, Y. (2004). The neurobiology of consolidations, or, how stable is the engram? *Annual review of psychology*, *55*, 51–86.
- Dudai, Y. (2006). Reconsolidation: the advantage of being refocused. *Current opinion in neurobiology*, *16*(2), 174–178.
- Duncko, R., Cornwell, B., Cui, L., Merikangas, K. R., & Grillon, C. (2007). Acute exposure to stress improves performance in trace eyeblink conditioning and spatial learning tasks in healthy men. *Learning & Memory*, *14*(5), 329–335.
- Eich, E., Kihlstrom, J. F., Bower, G. H., Forgas, J. P., & Nieden-Thal, P. M. (2000).. *Cognition and emotion*. Oxford; New York: Oxford University Press.
- Eich, T. S., & Metcalfe, J. (2009). Effects of the stress of marathon running on implicit and explicit memory. *Psychonomic Bulletin & Review*, *16*(3), 475–479.
- Elzinga, B. M., Bakker, A., & Bremner, J. D. (2005). Stress-induced cortisol elevations are associated with impaired delayed, but not immediate recall. *Psychiatry research*, *134*(3), 211–223.
- Epp, J., Keith, J. R., Spanswick, S. C., Stone, J. C., Prusky, G. T., & Sutherland, R. J. (2008). Retrograde amnesia for visual memories after hippocampal damage in rats. *Learning & memory (Cold Spring Harbor, N.Y.)*, *15*(4), 214–221.
- Erickson, K., Drevets, W., & Schulkin, J. (2003). Glucocorticoid regulation of diverse cognitive functions in normal and pathological emotional states. *Neuroscience and Biobehavioral Reviews*, *27*(3), 233–246.
- Fanselow, M. S. (1994). Neural organization of the defensive behavior system responsible for fear. *Psychonomic Bulletin & Review*, *1*(4), 429–438. doi:10.3758/BF03210947
- Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G\*Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, *39*, 175-191.
- Faul, F., Erdfelder, E., Buchner, A., & Lang, A.-G. (2009). Statistical power analyses using G\*Power 3.1: Tests for correlation and regression analyses. *Behavior Research Methods*, *41*, 1149-1160.
- Ferrari, V., Bradley, M. M., Codispoti, M., & Lang, P. J. (2011). Repetitive exposure: brain and reflex measures of emotion and attention. *Psychophysiology*, *48*(4), 515–522.

- Filioini, D., Gijsbers, K., Birmingham, M. K., & Dubrovsky, B. (1991). Effects of adrenal steroids and their reduced metabolites on hippocampal long-term potentiation. *The Journal of Steroid Biochemistry and Molecular Biology*, 40(1–3), 87–92.
- Finn, B., & Roediger, H. L., 3rd. (2011). Enhancing retention through reconsolidation: negative emotional arousal following retrieval enhances later recall. *Psychological science*, 22(6), 781–786.
- Finn, B., Roediger, H. L., 3rd, & Rosenzweig, E. (2012). Reconsolidation from negative emotional pictures: Is successful retrieval required? *Memory & cognition*, 40(7), 1031–1045.
- Fischer, A. H., & Manstead, A. S. R. (2000). The relation between gender and emotions in different cultures. In A. H. Fischer (Ed.), *Gender and emotion: Social psychology perspectives* (pp. 71–94). New York: Cambridge University Press.
- Flood, J. F., Vidal, D., Bennett, E. L., Orme, A. E., Vasquez, S., & Jarvik, M. E. (1978). Memory facilitating and anti-amnesic effects of corticosteroids. *Pharmacology, biochemistry, and behavior*, 8(1), 81–87.
- Foerde, K., Knowlton, B. J., & Poldrack, R. A. (2006). Modulation of competing memory systems by distraction. *Proceedings of the National Academy of Sciences of the United States of America*, 103(31), 11778–11783.
- Foo, P., Warren, W. H., Duchon, A., & Tarr, M. J. (2005). Do humans integrate routes into a cognitive map? Map- versus- landmark-based navigation. *Journal of Experimental Psychology*, 31, 195–215.
- Foley, P., & Kirschbaum, C. (2010). Human hypothalamus-pituitary-adrenal axis responses to acute psychosocial stress in laboratory settings. *Neuroscience and Biobehavioral Reviews*, 35(1), 91–96.
- Frankland, P. W., & Bontempi, B. (2005). The organization of recent and remote memories. *Nature Reviews Neuroscience*, 6(2), 119–130.
- Freud, S. (1915). Repression. In J. Strachey, A. Freud, A. Strachey, A. Tyson (Eds.), *The Standard Edition of the Complete Works of Sigmund Freud*, Vol. 14 (pp. 143–158). London: The Hogarth Press and the Institute of Psychoanalysis.
- Frey, A., Hartig, J., Ketzler, A., Zinkernagel, A., & Moosbrugger, H. (2007). The use of virtual environments based on a modification of the computer game Quake III Arena® in psychological experimenting. *Computers in Human Behavior*, 23(4), 2026–2039.
- Fugate, J. M. B., Gouzoules, H., & Barrett, L. F. (2009). Separating production from perception: Perceiver-based explanations for sex differences in emotion. *Behavioral and Brain Sciences*, 32(05), 394–395.
- Gabriel, K. I., Hong, S. M., Chandra, M., Lonborg, S. D., & Barkley, C. L. (2011). Gender Differences in the Effects of Acute Stress on Spatial Ability. *Sex Roles*, 64(1–2), 81–89.

- Galea, L. A. M., & Kimura, D. (1993). Sex differences in route-learning. *Personality and Individual Differences, 14*(1), 53–65.
- Garde, A. H., & Hansen, A. M. (2005). Long-term stability of salivary cortisol. *Scandinavian journal of clinical and laboratory investigation, 65*(5), 433–436.
- Gelinas, J. N., & Nguyen, P. V. (2005).  $\beta$ -Adrenergic Receptor Activation Facilitates Induction of a Protein Synthesis-Dependent Late Phase of Long-Term Potentiation. *The Journal of Neuroscience, 25*(13), 3294–3303.
- Ghacibeh, G. A., Shenker, J. I., Shenal, B., Uthman, B. M., & Heilman, K. M. (2006). The influence of vagus nerve stimulation on memory. *Cognitive and behavioral neurology: official journal of the Society for Behavioral and Cognitive Neurology, 19*(3), 119–122.
- Gibbon, C. J. (Ed.) (2000). *SA medicines formulary (5<sup>th</sup> ed)*. Pinelands, South Africa: South African Medical Association: Health and Medical Publishing group.
- Gluck, M. (1990). Making sense of human wayfinding: A review of cognitive and linguistic knowledge for personal navigation with a new research direction. Myke Gluck School of Information Studies, Syracuse University, Syracuse, NY.
- Golledge, R. G., & Stimson, R. J. (1997). *Spatial behavior: A geographic perspective*. New York: Guilford.
- Golledge, R. G. (1999). *Wayfinding behaviour*. Baltimore: The John Hopkins University Press.
- Goodrich-Hunsaker, N. J., & Hopkins, R. O. (2010). Spatial memory deficits in a virtual radial arm maze in amnesic participants with hippocampal damage. *Behavioral Neuroscience, 124*(3), 405–413.
- Goodrich-Hunsaker, N. J., Livingstone, S. A., Skelton, R. W., & Hopkins, R. O. (2010). Spatial deficits in a virtual water maze in amnesic participants with hippocampal damage. *Hippocampus, 20*(4), 481–491.
- Gordon, M. T., & Riger, S. (1991). *The female fear: The social costs of rape*. Chicago: University of Illinois Press.
- Graham, F. K. (1979). Distinguishing among orienting, defense, and startle reflexes. In H. D. Kimmel, E. H. van Olst, & J. F. Orlebeke (Eds.), *The orienting reflex in humans. An international conference sponsored by the Scientific Affairs Division of the North Atlantic Treaty Organization* (pp. 137–167). Hillsdale, NJ: Erlbaum.
- Gramann, K., Müller, H. J., Schönebeck, B., & Debus, G. (2006). The neural basis of ego- and allocentric reference frames in spatial navigation: evidence from spatio-temporal coupled current density reconstruction. *Brain Research, 1118*(1), 116–129.
- Groeneweg, F. L., Karst, H., De Kloet, E. R., & Joëls, M. (2011). Rapid non-genomic effects of corticosteroids and their role in the central stress response. *The Journal of endocrinology, 209*(2), 153–167.

- Grön, G., Wunderlich, A. P., Spitzer, M., Tomczak, R., & Riepe, M. W. (2000). Brain activation during human navigation: gender-different neural networks as substrate of performance. *Nature Neuroscience*, *3*(4), 404–408. doi:10.1038/73980
- Guenzel, F. M., Wolf, O. T., & Schwabe, L. (2013). Stress disrupts response memory retrieval. *Psychoneuroendocrinology*, *38*(8), 1460–1465.
- Gunnar, M. R., Talge, N. M., & Herrera, A. (2009). Stressor paradigms in developmental studies: what does and does not work to produce mean increases in salivary cortisol. *Psychoneuroendocrinology*, *34*(7), 953–967.
- Hamm, A. O., Cuthbert, B. N., Globisch, J., & Vaitl, D. (1997). Fear and the startle reflex: blink modulation and autonomic response patterns in animal and mutilation fearful subjects. *Psychophysiology*, *34*(1), 97–107.
- Hampson, E., Finestone, J. M., & Levy, N. (2005). Menstrual cycle effects on perceptual closure mediate changes in performance on a fragmented objects test of implicit memory. *Brain and Cognition*, *57*, 107–110.
- Harley, C. (1991). Noradrenergic and locus coeruleus modulation of the perforant path-evoked potential in rat dentate gyrus supports a role for the locus coeruleus in attentional and memorial processes. *Progress in Brain Research*, *88*, 307–321.
- Harris, M. A., Wiener, J. M., & Wolbers, T. (2012). Aging specifically impairs switching to an allocentric navigational strategy. *Frontiers in aging neuroscience*, *4*, 29.
- Hebb, D. O. (1949). *The organization of behaviour*. New York: Wiley-Interscience.
- Hellhammer, J., & Schubert, M. (2012). The physiological response to Trier Social Stress Test relates to subjective measures of stress during but not before or after the test. *Psychoneuroendocrinology*, *37*(1), 119–124.
- Henckens, M. J. A. G., Pu, Z., Hermans, E. J., van Wingen, G. A., Joëls, M., & Fernández, G. (2012). Dynamically changing effects of corticosteroids on human hippocampal and prefrontal processing. *Human Brain Mapping*, *33*(12), 2885–2897.
- Henckens, M. J. A. G., Wingen, G. A. van, Joëls, M., & Fernández, G. (2010). Time-Dependent Effects of Corticosteroids on Human Amygdala Processing. *The Journal of Neuroscience*, *30*(38), 12725–12732.
- Herbart, J. F. (1824). *Psychologie als Wissenschaft neu gegründet auf Erfahrung, Metaphysik und Mathematik: Erster, synthetischer Theil* [Psychology as science newly based on experience, metaphysics, and mathematics: First, synthetic part]. Königsberg: Unzer.
- Herbert, J., Goodyer, I. M., Grossman, A. B., Hastings, M. H., De Kloet, E. R., Lightman, S. L., ... Seckl, J. R. (2006). Do corticosteroids damage the brain? *Journal of neuroendocrinology*, *18*(6), 393–411.
- Henry, J. P., & Grim, C. E. (1990). Psychosocial mechanisms of primary hypertension. *Journal of hypertension*, *8*(9), 783–793.

- Het, S., Rohleder, N., Schoofs, D., Kirschbaum, C., & Wolf, O. T. (2009). Neuroendocrine and psychometric evaluation of a placebo version of the “Trier Social Stress Test.” *Psychoneuroendocrinology*, *34*(7), 1075–1086.
- Het, S., Ramlow, G., & Wolf, O. T. (2005). A meta-analytic review of the effects of acute cortisol administration on human memory. *Psychoneuroendocrinology*, *30*, 771-784.
- Het, S., & Wolf, O. T. (2007). Mood changes in response to psychosocial stress in healthy young women: effects of pretreatment with cortisol. *Behavioral Neuroscience*, *121*, 11-20.
- Heuer, F., & Reisberg, D. (1990). Vivid memories of emotional events: The accuracy of remembered minutiae. *Memory & Cognition*, *18*, 496-506.
- Hines, E. A., & Brown, G. E. (1932). A standard stimulus for measuring vasomotor reactions: its application in the study of hypertension. In *Mayo Clin Proc* (Vol. 7, p. 332)
- Hirshhorn, M., Grady, C., Rosenbaum, R. S., Winocur, G., & Moscovitch, M. (2012). The hippocampus is involved in mental navigation for a recently learned, but not a highly familiar environment: a longitudinal fMRI study. *Hippocampus*, *22*(4), 842–852.
- Holding, C. S., & Holding, D. H. (1989). Acquisition of route network knowledge by males and females. *Journal of General Psychology*, *116*, 29–41.
- Hopkins, W. F., & Johnston, D. (1984). Frequency-dependent noradrenergic modulation of long-term potentiation in the hippocampus. *Science (New York, N.Y.)*, *226*(4672), 350–352.
- Howe, M. L., & Derbish, M. H. (2010). On the susceptibility of adaptive memory to false memory illusions. *Cognition*, *115*(2), 252–267.
- Howell, D. (2012). *Statistical methods for psychology*. Cengage Learning.
- Huang, Y. Y., & Kandel, E. R. (1996). Modulation of both the early and the late phase of mossy fiber LTP by the activation of beta-adrenergic receptors. *Neuron*, *16*(3), 611–617.
- Human, R., Thomas, K. G., Dreyer, A., Amod, A. R., Wolf, P. S., & Jacobs, W. J. (2013). Acute psychosocial stress enhances visuospatial memory in healthy males. *South African Journal of Psychology*, *43*(3), 300–313.
- Hyde, J. S., Mezulis, A. H., & Abramson, L. Y. (2008). The ABCs of depression: Integrating affective, biological, and cognitive models to explain the emergence of the gender difference in depression. *Psychological Review*, *115*(2), 291–313.
- Iaria, G., Petrides, M., Dagher, A., Pike, B., & Bohbot, V. D. (2003). Cognitive strategies dependent on the hippocampus and caudate nucleus in human navigation: variability and change with practice. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, *23*(13), 5945–5952.
- Jacobs, W. J., & Metcalfe, J. (1998). Emotional memory: The effects of stress on ‘cool’ and ‘hot’ memory systems. *The Psychology of Learning and Motivation*, *38*, 187-222.

- Jacobs, W. J., Laurance, H. E., & Thomas, K. G. F. (1997). Place learning in virtual space I: Acquisition, overshadowing, and transfer. *Learning & Motivation, 28*, 521-541.
- Jacobs, W. J., Thomas, K. G. F., Laurance, H. E., & Nadel, L. (1998). Place learning in virtual space II: Topographical relations as one dimension of stimulus control. *Learning & Motivation, 29*, 288-308.
- Jansen-Osmann, P., & Wiedenbauer, G. (2004). The representation of landmarks and routes in children and adults: A study in a virtual environment. *Journal of Experimental Psychology, 24*, 247-257.
- Joëls, M. (2006). Corticosteroid effects in the brain: U-shape it. *Trends in pharmacological sciences, 27*(5), 244–250.
- Joëls, M. (2010). Impact of glucocorticoids on brain function: relevance for mood disorders. *Psychoneuroendocrinology, 36*(3), 406–414.
- Joëls, M., Fernandez, G., & Roozendaal, B. (2011). Stress and emotional memory: a matter of timing. *Trends in Cognitive Sciences, 15*(6), 280–288.
- Joëls, M., Pu, Z., Wiegert, O., Oitzl, M. S., & Krugers, H. J. (2006). Learning under stress: how does it work? *Trends in cognitive sciences, 10*(4), 152–158.
- Johnson, W., & Bouchard, T. J. (2005). Constructive replication of the visual-perceptual-image rotation (VPR) model in Thurstone's (1941) battery of 60 tests of mental ability. *Intelligence, 33*, 417-430.
- Johnson, W., & Bouchard, T. J. (2007). Sex differences in mental abilities: g masks the dimension on which they lie. *Intelligence, 35*, 23-39.
- Jordan, K., Schadow, J., Wuestenberg, T., Heinze, H.-J., & Jäncke, L. (2004). Different cortical activations for subjects using allocentric or egocentric strategies in a virtual navigation task. *Neuroreport, 15*(1), 135–140.
- Joshi, M. S., Mac Lean, M., & Carter, W. (1999). Children's journey to school: spatial skills, knowledge and perceptions of the environment. *British Journal of Developmental Psychology, 17*, 125–139.
- Kahneman, D., & Tversky, A. (1984). Choices, values, and frames. *American Psychologist, 39*, 341-350.
- Kallai, J., Makany, T., Karadi, K., & Jacobs, W. J. (2005). Spatial orientation strategies in Morris-type virtual water task for humans. *Behavioural Brain Research, 159*(2), 187–196.
- Kang, S. H. K., McDermott, K. B., & Cohen, S. M. (2008). The mnemonic advantage of processing fitness-relevant information. *Memory & cognition, 36*(6), 1151–1156.
- Kapp, B. S., Frysinger, R. C., Gallagher, M., & Haselton, J. R. (1979). Amygdala central nucleus lesions: Effect on heart rate conditioning in the rabbit. *Physiology & Behavior, 23*(6), 1109–1117.

- Karst, H., Berger, S., Erdmann, G., Schütz, G., & Joëls, M. (2010). Metaplasticity of amygdala responses to the stress hormone corticosterone. *Proceedings of the National Academy of Sciences of the United States of America*, *107*(32), 14449–14454.
- Karst, H., Berger, S., Turiault, M., Tronche, F., Schütz, G., & Joëls, M. (2005). Mineralocorticoid receptors are indispensable for nongenomic modulation of hippocampal glutamate transmission by corticosterone. *Proceedings of the National Academy of Sciences of the United States of America*, *102*(52), 19204–19207.
- Katsuki, H., Izumi, Y., & Zorumski, C. F. (1997). Noradrenergic regulation of synaptic plasticity in the hippocampal CA1 region. *Journal of neurophysiology*, *77*(6), 3013–3020.
- Kavushansky, A., & Richter-Levin, G. (2006). Effects of stress and corticosterone on activity and plasticity in the amygdala. *Journal of neuroscience research*, *84*(7), 1580–1587.
- Kim, J. J., & Diamond, D. M. (2002). The stressed hippocampus, synaptic plasticity and lost memories. *Nature reviews. Neuroscience*, *3*(6), 453–462.
- Kim, J. J., Lee, H. J., Han, J.-S., & Packard, M. G. (2001). Amygdala Is Critical for Stress-Induced Modulation of Hippocampal Long-Term Potentiation and Learning. *The Journal of Neuroscience*, *21*(14), 5222–5228.
- Kimura, D. (1999). *Sex and cognition*. Cambridge, MA: MIT Press.
- Kimura, D. (2004). Human sex differences. *Sexuality, Evolution & Gender*, *6*, 45-53.
- Kimura, D., & Hampson, E. (1994). Cognitive pattern in men and women is influenced by fluctuations in sex hormones. *Current directions in Psychological science*, *3*, 57-61.
- Kirschbaum, C., Kudielka, B. M., Gaab, J., Schommer, N. C., & Hellhammer, D. H. (1999). Impact of gender, menstrual cycle phase, and oral contraceptives on the activity of the hypothalamus-pituitary-adrenal axis. *Psychosomatic Medicine*, *61*(2), 154–162.
- Kirschbaum, C., Pirke, K. M., & Hellhammer, D. H. (1993). The “Trier Social Stress Test”--a tool for investigating psychobiological stress responses in a laboratory setting. *Neuropsychobiology*, *28*(1-2), 76–81.
- Kirschbaum, C., Wolf, O. T., May, M., Wippich, W., & Hellhammer, D. H. (1996). Stress- and treatment-induced elevations of cortisol levels associated with impaired declarative memory in healthy adults. *Life sciences*, *58*(17), 1475–1483.
- Kirschbaum, C., Wüst, S., & Hellhammer, D. (1992). Consistent sex differences in cortisol responses to psychological stress. *Psychosomatic Medicine*, *54*(6), 648–657.
- Kensinger, E. A. (2004). Remembering emotional experiences: the contribution of valence and arousal. *Reviews in the neurosciences*, *15*(4), 241–251.
- Kleen, J. K., Sitomer, M. T., Killeen, P. R., & Conrad, C. D. (2006). Chronic stress impairs spatial memory and motivation for reward without disrupting motor ability and motivation to explore. *Behavioral Neuroscience*, *120*, 842-851.

- Knowlton, B. J., & Fanselow, M. S. (1998). The hippocampus, consolidation and on-line memory. *Current opinion in neurobiology*, 8(2), 293–296.
- Knowlton, B. J., Mangels, J. A., & Squire, L. R. (1996). A neostriatal habit learning system in humans. *Science (New York, N.Y.)*, 273(5280), 1399–1402.
- Krauth, J. (2000). *Experimental design: a handbook and dictionary for medical and behavioral research* (Vol. 14). Elsevier.
- Kret, M. E., & De Gelder, B. (2012). A review on sex differences in processing emotional signals. *Neuropsychologia*, 50(7), 1211–1221.
- Kring, A. M., & Gordon, A. H. (1998). Sex differences in emotion: expression, experience, and physiology. *Journal of Personality and Social Psychology*, 74(3), 686–703.
- Kudielka, B. M., Buske-Kirschbaum, A., Hellhammer, D. H., & Kirschbaum, C. (2004). HPA axis responses to laboratory psychosocial stress in healthy elderly adults, younger adults, and children: impact of age and gender. *Psychoneuroendocrinology*, 29(1), 83–98.
- Kudielka, B. M., Buske-Kirschbaum, A., Hellhammer, D. H., & Kirschbaum, C. (2004). Differential heart rate reactivity and recovery after psychosocial stress (TSST) in healthy children, younger adults, and elderly adults: The impact of age and gender. *International Journal of Behavioral Medicine*, 2, 116–121.
- Kudielka, B. M., Hellhammer, D. H., & Wüst, S. (2009). Why do we respond so differently? Reviewing determinants of human salivary cortisol responses to challenge. *Psychoneuroendocrinology*, 34(1), 2–18.
- Kudielka, B. M., & Kirschbaum, C. (2005). Sex differences in HPA axis responses to stress: a review. *Biological psychology*, 69(1), 113–132.
- Kudielka, B. M., Schmidt-Reinwald, A. K., Hellhammer, D. H., & Kirschbaum, C. (1999). Psychological and endocrine responses to psychosocial stress and dexamethasone/corticotropin-releasing hormone in healthy postmenopausal women and young controls: the impact of age and a two-week estradiol treatment. *Neuroendocrinology*, 70(6), 422–430.
- Kudielka, B. M., Schmidt-Reinwald, A. K., Hellhammer, D. H., Schürmeyer, T., & Kirschbaum, C. (2000). Psychosocial stress and HPA functioning: no evidence for a reduced resilience in healthy elderly men. *Stress (Amsterdam, Netherlands)*, 3(3), 229–240.
- Kudielka, B. M., & Wüst, S. (2010). Human models in acute and chronic stress: assessing determinants of individual hypothalamus-pituitary-adrenal axis activity and reactivity. *Stress (Amsterdam, Netherlands)*, 13(1), 1–14.
- Kuhlmann, S., Kirschbaum, C., & Wolf, O. T. (2005a). Effects of oral cortisol treatment in healthy young women on memory retrieval of negative and neutral words. *Neurobiology of learning and memory*, 83(2), 158–162.

- Kuhlmann, S., Piel, M., & Wolf, O. T. (2005b). Impaired Memory Retrieval after Psychosocial Stress in Healthy Young Men. *The Journal of Neuroscience*, 25(11), 2977–2982.
- Kuhlmann, S., & Wolf, O. T. (2005). Cortisol and memory retrieval in women: influence of menstrual cycle and oral contraceptives. *Psychopharmacology*, 183(1), 65–71.
- Kuhlmann, S., & Wolf, O. T. (2006a). Arousal and cortisol interact in modulating memory consolidation in healthy young men. *Behavioral neuroscience*, 120(1), 217–223.
- Kuhlmann, S., & Wolf, O. T. (2006b). A non-arousing test situation abolishes the impairing effects of cortisol on delayed memory retrieval in healthy women. *Neuroscience letters*, 399(3), 268–272.
- LaBar, K. S., & Cabeza, R. (2006). Cognitive neuroscience of emotional memory. *Nature Reviews Neuroscience*, 7(1), 54–64.
- LaFrance, M., & Banaji, M. (1992). Towards a reconsideration of the gender emotion relationship. In M. S. Clard (Ed.), *Emotions and social behavior: Review of personality and social psychology* (Vol. 14, pp. 178–201). Beverly Hills, CA: Sage.
- Landers, D. M. (2007). The arousal-performance relationship revisited. In D. Smith & M. Bar-Eli (Eds.), *Essential Readings in Sport and Exercise Psychology*. (pp. 211–218). Champaign, IL US: Human Kinetics.
- Lang, P. J. (1980). Behavioral treatment and bio-behavioral assessment: Computer applications. In J. B. Sidowski, J. H. Johnson, & T. A. Williams (Eds.), *Technology in mental health care delivery systems* (pp. 119–137). Norwood, NJ: Ablex Publishing.
- Lang, P. J., & Bradley, M. M. (2010). Emotion and the motivational brain. *Biological Psychology*, 84(3), 437–450.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1990). Emotion, attention, and the startle reflex. *Psychological Review*, 97(3), 377–395.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). Motivated attention: Affect, activation, and action. In P. J. Lang, R. F. Simons, & M. T. Balaban (Eds.), *Attention and orienting: Sensory and motivational processes* (pp. 97–135). Hillsdale, NJ: Erlbaum.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1997). Motivated attention: Affect, activation, and action. In P. J. Lang, R. F. Simons, & M. T. Balaban (Eds.), *Attention and orienting: Sensory and motivational processes* (pp. 97–135). Hillsdale, NJ: Erlbaum.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1999). *International affective picture system (IAPS): Technical manual and affective ratings*. The Center for Research in Psychophysiology, University of Florida, Gainesville.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2005). *International affective picture system (IAPS): Instruction manual and affective picture ratings*. Technical Report A-6, The Center for Research in Psychophysiology, University of Florida.

- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (2008). *International affective picture system (IAPS): Instruction manual and affective picture ratings*. Technical Report A-8, The Center for Research in Psychophysiology, University of Florida.
- Lawton, C. A. (1994). Gender differences in way-finding strategies: Relationship to spatial ability and spatial anxiety. *Sex Roles, 30*(11-12), 765–779.
- Lawton, C. A., Charleston, S. I., & Zieles, A. S. (1996). Individual- and Gender-Related Differences in Indoor Wayfinding. *Environment and Behavior, 28*(2), 204–219.
- Lazarus, R. S. (1993). Coping theory and research: past, present, and future. *Psychosomatic medicine, 55*(3), 234–247.
- LeDoux, J. E. (1990). Information flow from sensation to emotion plasticity in the neural computation of stimulus values. In M. Gabriel & J. Moore (Eds.), *Learning and computational neuroscience: Foundations of adaptive networks* (pp. 3–52). Cambridge, MA: Bradford Books/ MIT Press.
- Lepow, B., Lehnung, M., Pohl, J., Herzog, A., Ferstl, R., & Mehdorn, M. (2003). Navigational place learning in children and young adults as assessed with a standardized locomotor search task. *British Journal of Psychology (London, England: 1953), 94*(Pt 3), 299–317.
- Levelt, W. J. M. (1982). Cognitive styles in the use of spatial direction terms. In R. Jarvella, & W. Klein (Eds.), *Speech, place, and action: Studies in deixis and related topics* (pp. 251-268). Chichester: Wiley.
- Levine, S. (2005). Developmental determinants of sensitivity and resistance to stress. *Psychoneuroendocrinology, 30*(10), 939–946.
- Linde, C., & Labov, W. (1975). Spatial Networks as a Site for the Study of Language and Thought. *Language, 51*(4), 924–939.
- Linn, M. C., & Petersen, A. C. (1985). Emergence and characterization of sex differences in spatial ability: a meta-analysis. *Child Development, 56*(6), 1479–1498.
- Lopez, J., Herbeaux, K., Cosquer, B., Engeln, M., Muller, C., Lazarus, C., ... De Vasconcelos, A. P. (2012). Context-dependent modulation of hippocampal and cortical recruitment during remote spatial memory retrieval. *Hippocampus, 22*(4), 827–841.
- Lovallo, W. R., Robinson, J. L., Glahn, D. C., & Fox, P. T. (2010). Acute effects of hydrocortisone on the human brain: an fMRI study. *Psychoneuroendocrinology, 35*(1), 15–20.
- Lovallo, W. R., & Thomas, T. L. (2000). Stress hormones in psychophysiological research: Emotional, behavioral and cognitive implications. In J. T. Cacioppo, L. G. Tassinary, & G. G. Berntson (Eds.), *Handbook of psychophysiology (2nd ed.)*. Cambridge: Cambridge University Press.

- Luethi, M., Meier, B., & Sandi, C. (2009). Stress Effects on Working Memory, Explicit Memory, and Implicit Memory for Neutral and Emotional Stimuli in Healthy Men. *Frontiers in Behavioral Neuroscience*, 2.
- Luine, V. N., Spencer, R. L., & McEwen, B. S. (1993). Effects of chronic corticosterone ingestion on spatial memory performance and hippocampal serotonergic function. *Brain research*, 616(1-2), 65–70.
- Lupien, S. J., Gillin, C. J., & Hauger, R. L. (1999). Working memory is more sensitive than declarative memory to the acute effects of corticosteroids: a dose-response study in humans. *Behavioral neuroscience*, 113(3), 420–430.
- Lupien, S. J., Gaudreau, S., Tchiteya, B. M., Maheu, F., Sharma, S., Nair, N. P., ... Meaney, M. J. (1997). Stress-induced declarative memory impairment in healthy elderly subjects: relationship to cortisol reactivity. *The Journal of clinical endocrinology and metabolism*, 82(7), 2070–2075.
- Lupien, S. J., Maheu, F., Tu, M., Fiocco, A., & Schramek, T. E. (2007). The effects of stress and stress hormones on human cognition: Implications for the field of brain and cognition. *Brain and cognition*, 65(3), 209–237.
- Lupien, S. J., & McEwen, B. S. (1997). The acute effects of corticosteroids on cognition: integration of animal and human model studies. *Brain Research. Brain Research Reviews*, 24(1), 1–27.
- Lupien, S. J., Ouellet-Morin, I., Hupbach, A., Tu, M. T., Buss, C., Walker, D., ... McEwen, B. S. (2006). Beyond the stress concept: Allostatic load--a developmental biological and cognitive perspective. In D. Cicchetti D. J. Cohen (Ed.), *Developmental psychopathology, Vol 2: Developmental neuroscience (2nd ed.)* (pp. 578–628). Hoboken, NJ, US: John Wiley & Sons Inc.
- Lupien, S. J., Wilkinson, C. W., Brière, S., Ménard, C., Ng Ying Kin, N. M. K., & Nair, N. P. V. (2002). The modulatory effects of corticosteroids on cognition: studies in young human populations. *Psychoneuroendocrinology*, 27(3), 401–416.
- Lynch, K. (1960). *The image of the city*. Cambridge: M. I. T. Press.
- Maguire, E. A., Nannery, R., & Spiers, H. J. (2006). Navigation around London by a taxi driver with bilateral hippocampal lesions. *Brain: a journal of neurology*, 129(Pt 11), 2894–2907.
- Maguire, E. A., Woollett, K., & Spiers, H. J. (2006). London taxi drivers and bus drivers: a structural MRI and neuropsychological analysis. *Hippocampus*, 16(12), 1091–1101. doi:10.1002/hipo.20233
- Maheu, F. S., Jooper, R., Beaulieu, S., & Lupien, S. J. (2004). Differential effects of adrenergic and corticosteroid hormonal systems on human short- and long-term declarative memory for emotionally arousing material. *Behavioral Neuroscience*, 118(2), 420–428.

- Malinowski, J. C., & Gillespie, W. T. (2001). Individual differences in performance on a large-scale, real-world wayfinding task. *Journal of Environmental Psychology, 21*(1), 73–82.
- Maroun, M., & Akirav, I. (2008). Arousal and stress effects on consolidation and reconsolidation of recognition memory. *Neuropsychopharmacology: official publication of the American College of Neuropsychopharmacology, 33*(2), 394–405.
- Martin, S. J., De Hoz, L., & Morris, R. G. M. (2005). Retrograde amnesia: neither partial nor complete hippocampal lesions in rats result in preferential sparing of remote spatial memory, even after reminding. *Neuropsychologia, 43*(4), 609–624.
- Mason, J. W. (1968). A review of psychoendocrine research on the pituitary-adrenal cortical system. *Psychosomatic medicine, 30*(5), Suppl:576–607.
- McDonald, R. J., & White, N. M. (1993). A triple dissociation of memory systems: hippocampus, amygdala, and dorsal striatum. *Behavioral Neuroscience, 107*(1), 3–22.
- McEwen, B. S. (1998). Protective and damaging effects of stress mediators. *The New England journal of medicine, 338*(3), 171–179.
- McEwen, B. S. (2001). Commentary on PTSD discussion. *Hippocampus, 11*(2), 82–84.
- McEwen, B. S., Weiss, J. M., & Schwartz, L. S. (1968). Selective Retention of Corticosterone by Limbic Structures in Rat Brain. *Nature, 220*(5170), 911–912.
- McGaugh, J. L. (2003). *Memory and Emotion: The Making of Lasting Memories*. Columbia University Press.
- McGregor, A., Hayward, A.J., Pearce, J.M., & Good, M.A. (2004). Hippocampal lesions disrupt navigation based on the shape of the environment. *Behavioral Neuroscience, 118*, 1011-1021.
- McNamara, T.P., & Shelton, A.L. (2003). Cognitive maps and the hippocampus. *Trends in Cognitive Science, 7*, 333-335.
- McRae, A. L., Saladin, M. E., Brady, K. T., Upadhyaya, H., Back, S. E., & Timmerman, M. A. (2006). Stress reactivity: biological and subjective responses to the cold pressor and Trier Social stressors. *Human Psychopharmacology, 21*(6), 377–385.
- Mehrabian, A., & Russell, J. A. (1974). *An approach to environmental psychology*. Cambridge, MA: MIT Press.
- Mendl, M. (1999). Performing under pressure: stress and cognitive function. *Applied Animal Behaviour Science, 65*(3), 221–244.
- Merz, C. J., Wolf, O. T., & Hennig, J. (2010). Stress impairs retrieval of socially relevant information. *Behavioral neuroscience, 124*(2), 288–293.
- Miller, N. E. (1959). Liberalization of the basic S-R concepts: Extensions to conflict behavior, motivation, and social learning. In S. Kock (Ed.), *Psychology: A study or a science* (pp. 198-292). New York: McGraw-Hill

- Mill, J. S. (1843). *A system of logic, ratiocinative and inductive, being a connected view of the principles of evidence and the methods of scientific investigation*. John W. Parker, London.
- Milner, B., Corkin, S., & Teuber, H.-L. (1968). Further analysis of the hippocampal amnesic syndrome: 14-year follow-up study of H.M. *Neuropsychologia*, *6*(3), 215–234.
- Milner, B., Squire, L. R., & Kandel, E. R. (1998). Cognitive neuroscience and the study of memory. *Neuron*, *20*(3), 445–468.
- Moffat, S. D., Hampson, E., & Hatzipantelis, M. (1998). Navigation in a “Virtual” Maze: Sex Differences and Correlation With Psychometric Measures of Spatial Ability in Humans. *Evolution and Human Behavior*, *19*(2), 73–87.
- Morales, A. (2002). *Modeling wayfinding and spatial abilities*. Unpublished doctoral thesis, University of Arizona, United States of America.
- Morris, R. G. M. (1981). Spatial localization does not require the presence of local cues. *Learning and Motivation*, *12*, 239–260.
- Morris, R. (1984). Developments of a water-maze procedure for studying spatial learning in the rat. *Journal of Neuroscience Methods*, *11*(1), 47–60.
- Mueller, S. C., Jackson, C. P. T., & Skelton, R. W. (2008). Sex differences in a virtual water maze: an eye tracking and pupillometry study. *Behavioural Brain Research*, *193*(2), 209–215.
- Muller, G. E., & Pilzecker, A. (1900). Experimentelle beitrage zur lehre vom gedachtnis. *Zeitschrift fur Psychologie und Physiologie der Sinnesorgane*, *51*, 1–288.
- Nadel, L., & Moscovitch, M. (1997). Memory consolidation, retrograde amnesia and the hippocampal complex. *Current opinion in neurobiology*, *7*(2), 217–227.
- Nadel, L., & Moscovitch, M. (1998). Hippocampal contributions to cortical plasticity. *Neuropharmacology*, *37*(4-5), 431–439.
- Nairne, J. S. (2005). The functionalist agenda in memory research. In A. F. Healy (Ed.), *Experimental cognitive psychology and its applications* (pp. 115–126). Washington, DC: American Psychological Association.
- Nairne, J. S., & Pandeirada, J. N. S. (2008a). Adaptive Memory: Is Survival Processing Special? *Journal of Memory and Language*, *59*(3), 377–385.
- Nairne, J. S., & Pandeirada, J. N. S. (2008b). Adaptive Memory: Remembering With a Stone-Age Brain. *Current Directions in Psychological Science*, *17*(4), 239–243.
- Nairne, J. S., & Pandeirada, J. N. S. (2010). Adaptive memory: ancestral priorities and the mnemonic value of survival processing. *Cognitive Psychology*, *61*(1), 1–22.
- Nairne, J. S., Vanarsdall, J. E., Pandeirada, J. N. S., & Blunt, J. R. (2012). Adaptive memory: enhanced location memory after survival processing. *Journal of experimental psychology. Learning, memory, and cognition*, *38*(2), 495–501.

- Nater, U. M., Moor, C., Okere, U., Stallkamp, R., Martin, M., Ehlert, U., & Kliegel, M. (2007). Performance on a declarative memory task is better in high than low cortisol responders to psychosocial stress. *Psychoneuroendocrinology*, *32*(6), 758–763.
- Neisser, R. V. (1976). *Cognition and reality*. San Francisco: Freeman.
- New, J., Krasnow, M. M., Truxaw, D., & Gaulin, S. J. C. (2007). Spatial adaptations for plant foraging: Women excel and calories count. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 2679–2684.
- Newcomer, J. W., Selke, G., Melson, A. K., Hershey, T., Craft, S., Richards, K., et al. (1999). Decreased memory performance in healthy humans induced by stress-level cortisol treatment. *Archives of General Psychiatry*, *56*, 527–533.
- Nicolson, N., Storms, C., Ponds, R., & Sulon, J. (1997). Salivary cortisol levels and stress reactivity in human aging. *The Journals of Gerontology. Series A, Biological Sciences and Medical Sciences*, *52*(2), M68–75.
- Nolen-Hoeksema, S. (2001). Gender Differences in Depression. *Current Directions in Psychological Science*, *10*(5), 173–176.
- Oei, N. Y. L., Elzinga, B. M., Wolf, O. T., De Ruiter, M. B., Damoiseaux, J. S., Kuijter, J. P. A., ... Rombouts, S. A. R. B. (2007). Glucocorticoids Decrease Hippocampal and Prefrontal Activation during Declarative Memory Retrieval in Young Men. *Brain Imaging and Behavior*, *1*(1-2), 31–41.
- Ohnishi, T., Matsuda, H., Hirakata, M., & Ugawa, Y. (2006). Navigation ability dependent neural activation in the human brain: an fMRI study. *Neuroscience Research*, *55*(4), 361–369.
- Oitzl, M. S., Reichardt, H. M., Joëls, M., & De Kloet, E. R. (2001). Point mutation in the mouse glucocorticoid receptor preventing DNA binding impairs spatial memory. *Proceedings of the National Academy of Sciences of the United States of America*, *98*(22), 12790–12795.
- O'Keefe, J., & Nadel, L. (1978). *The hippocampus as a cognitive map*. Oxford: Oxford University Press.
- Otgaar, H., & Smeets, T. (2010). Adaptive memory: Survival processing increases both true and false memory in adults and children. *Journal of experimental psychology. Learning, memory, and cognition*, *36*(4), 1010–1016.
- Otgaar, H., Smeets, T., & van Bergen, S. (2010). Picturing survival memories: enhanced memory after fitness-relevant processing occurs for verbal and visual stimuli. *Memory & cognition*, *38*(1), 23–28.
- Packard, M. G., & Goodman, J. (2012). Emotional arousal and multiple memory systems in the mammalian brain. *Frontiers in Behavioral Neuroscience*, *6*.
- Packard, M. G., Hirsh, R., & White, N. M. (1989). Differential effects of fornix and caudate nucleus lesions on two radial maze tasks: evidence for multiple memory systems. *The*

*Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, 9(5), 1465–1472.

- Packard, M. G., & McGaugh, J. L. (1996). Inactivation of hippocampus or caudate nucleus with lidocaine differentially affects expression of place and response learning. *Neurobiology of learning and memory*, 65(1), 65–72.
- Payne, J. D., Jackson, E. D., Hoscheidt, S., Ryan, L., Jacobs, W. J., & Nadel, L. (2007). Stress administered prior to encoding impairs neutral but enhances emotional long-term episodic memories. *Learning & Memory*, 14(12), 861–868.
- Payne, J. D., Jackson, E. D., Ryan, L., Hoscheidt, S., Jacobs, J. W., & Nadel, L. (2006). The impact of stress on neutral and emotional aspects of episodic memory. *Memory (Hove, England)*, 14(1), 1–16.
- Paz-Villagran, V., Save, E., & Poucet, B. (2004). Independent coding of connected environments by place cells. *European Journal of Neuroscience*, 20, 1379–1390.
- Pavlidis, C., Watanabe, Y., & McEwen, B. S. (1993). Effects of glucocorticoids on hippocampal long-term potentiation. *Hippocampus*, 3(2), 183–192.
- Penfield, W., & Milner, B. (1958). Memory deficit produced by bilateral lesions in the hippocampal zone. *A.M.A. archives of neurology and psychiatry*, 79(5), 475–497.
- Peponis, J., Zimring, C., & Choi, Y. K. (1990). Finding the building in wayfinding. *Environment and Behavior*, 22, 555–590.
- Peruch, P., Gaunet, F., Thinus-Blanc, C., Loomis, J. (2000). Understanding and learning virtual spaces. In Kitchin, R., & Freundschuh, S. (Eds.). *Cognitive mapping: past, present and future*. London: Routledge.
- Péruch, P., Vercher, J. L., & Gauthier, G. M. (1995). Acquisition of spatial knowledge through visual exploration of simulated environments. *Ecological Psychology*, 7, 1–20.
- Pham, T. V. (2003). Gender differences in cardiac development: are hormones at the heart of the matter? *Cardiovascular Research*, 57(3), 591–593.
- Phelps, E. A. (2004). Human emotion and memory: interactions of the amygdala and hippocampal complex. *Current opinion in neurobiology*, 14(2), 198–202.
- Pillay, T. S., Haumann, C., Bonito Attwood, C., Omar, F., & Thomas, K. G. F. (2008). Salivary free cortisol reference range on the Roche E170 platform after collection with Salimetrics Sorbette® (“Eyespear”). *Annals of Clinical Biochemistry*, 45, 111.
- Poldrack, R. A., Clark, J., Paré-Blagoev, E. J., Shohamy, D., Creso Moyano, J., Myers, C., & Gluck, M. A. (2001). Interactive memory systems in the human brain. *Nature*, 414(6863), 546–550.
- Postma, A., Jager, G., Kessels, R. P. C., Koppeschaar, H. P. F., & van Honk, J. (2004). Sex differences for selective forms of spatial memory. *Brain and Cognition*, 54(1), 24–34.

- Quesada, A. A., Wiemers, U. S., Schoofs, D., & Wolf, O. T. (2012). Psychosocial stress exposure impairs memory retrieval in children. *Psychoneuroendocrinology*, *37*(1), 125–136.
- Quevedo, J., Sant'Anna, M. K., Madruga, M., Lovato, I., de-Paris, F., Kapczinski, F., ... Cahill, L. (2003). Differential effects of emotional arousal in short- and long-term memory in healthy adults. *Neurobiology of learning and memory*, *79*(2), 132–135.
- Rahman, Q., Andersson, D., & Govier, E. (2005). A specific sex orientation-related difference in navigation strategy. *Behavioral neuroscience*, *119*, 311–316.
- Ramos, J. M. (1998). Retrograde amnesia for spatial information: a dissociation between intra and extramaze cues following hippocampus lesions in rats. *The European journal of neuroscience*, *10*(10), 3295–3301.
- Rashidy-Pour, A., Sadeghi, H., Taherain, A. A., Vafaei, A. A., & Fathollahi, Y. (2004). The effects of acute restraint stress and dexamethasone on retrieval of long-term memory in rats: an interaction with opiate system. *Behavioural brain research*, *154*(1), 193–198.
- Reisberg, D., & Heuer, F. (2004). Memory for emotional events. In D. Reisberg & P. Hertel (Eds.), *Memory and emotion* (pp. 3–41). London: Oxford University Press.
- Richardson, A. E., & VanderKaay Tomasulo, M. M. (2011). Influence of acute stress on spatial tasks in humans. *Physiology & Behavior*, *103*(5), 459–466.
- Ribot, R. (1882). *Diseases of memory*. New York: Appleton.
- Rizk-Jackson, A. M., Acevedo, S. F., Inman, D., Howieson, D., Benice, T. S., & Raber, J. (2006). Effects of sex on object recognition and spatial navigation in humans. *Behavioural brain research*, *173*(2), 181–190.
- Roche, R. A. P., Mangaoang, M. A., Commins, S., & O'Mara, S. M. (2005). Hippocampal contributions to neurocognitive mapping in humans: A new model. *Hippocampus*, *15*, 622–641.
- Rohleder, N., Kudielka, B. M., Hellhammer, D. H., Wolf, J. M., & Kirschbaum, C. (2002). Age and sex steroid-related changes in glucocorticoid sensitivity of pro-inflammatory cytokine production after psychosocial stress. *Journal of Neuroimmunology*, *126*(1–2), 69–77.
- Rolls, E. T. (2000). Précis of The brain and emotion. *The Behavioral and Brain Sciences*, *23*(2), 177–191; discussion 192–233.
- Roosendaal, B. (2000). 1999 Curt P. Richter award. Glucocorticoids and the regulation of memory consolidation. *Psychoneuroendocrinology*, *25*(3), 213–238.
- Roosendaal, B. (2002). Stress and memory: opposing effects of glucocorticoids on memory consolidation and memory retrieval. *Neurobiology of learning and memory*, *78*(3), 578–595.

- Roozendaal, B. (2003). Systems mediating acute glucocorticoid effects on memory consolidation and retrieval. *Progress in Neuro-Psychopharmacology & Biological Psychiatry*, 27(8), 1213–1223.
- Roozendaal, B., Barsegyan, A., & Lee, S. (2008). Adrenal stress hormones, amygdala activation, and memory for emotionally arousing experiences. *Progress in brain research*, 167, 79–97.
- Roozendaal, B., De Quervain, D. J.-F., Schelling, G., & McGaugh, J. L. (2004). A systemically administered beta-adrenoceptor antagonist blocks corticosterone-induced impairment of contextual memory retrieval in rats. *Neurobiology of learning and memory*, 81(2), 150–154.
- Roozendaal, B., Griffith, Q. K., Buranday, J., De Quervain, D. J.-F., & McGaugh, J. L. (2003). The hippocampus mediates glucocorticoid-induced impairment of spatial memory retrieval: dependence on the basolateral amygdala. *Proceedings of the National Academy of Sciences of the United States of America*, 100(3), 1328–1333.
- Roozendaal, B., Hahn, E. L., Nathan, S. V., Quervain, D. J.-F. de, & McGaugh, J. L. (2004). Glucocorticoid Effects on Memory Retrieval Require Concurrent Noradrenergic Activity in the Hippocampus and Basolateral Amygdala. *The Journal of Neuroscience*, 24(37), 8161–8169.
- Roozendaal, B., Hernandez, A., Cabrera, S. M., Hagewoud, R., Malvaez, M., Stefanko, D. P., ... Wood, M. A. (2010). Membrane-associated glucocorticoid activity is necessary for modulation of long-term memory via chromatin modification. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, 30(14), 5037–5046.
- Roozendaal, B., McEwen, B. S., & Chattarji, S. (2009). Stress, memory and the amygdala. *Nature reviews. Neuroscience*, 10(6), 423–433.
- Roozendaal, B., McReynolds, J. R., & McGaugh, J. L. (2004). The basolateral amygdala interacts with the medial prefrontal cortex in regulating glucocorticoid effects on working memory impairment. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, 24(6), 1385–1392.
- Roozendaal, B., Okuda, S., De Quervain, D. J.-F., & McGaugh, J. L. (2006). Glucocorticoids interact with emotion-induced noradrenergic activation in influencing different memory functions. *Neuroscience*, 138(3), 901–910.
- Rose, R. M. (1980). Endocrine responses to stressful psychological events. *Psychiatric Clinics of North America*, 3, 251–276.
- Rosenbaum, R. S., Gao, F., Richards, B., Black, S. E., & Moscovitch, M. (2005). “Where to?” remote memory for spatial relations and landmark identity in former taxi drivers with Alzheimer’s disease and encephalitis. *Journal of cognitive neuroscience*, 17(3), 446–462.
- Rosenbaum, R. S., Moscovitch, M., Foster, J. K., Schnyer, D. M., Gao, F., Kovacevic, N., ... Levine, B. (2008). Patterns of autobiographical memory loss in medial-temporal lobe amnesic patients. *Journal of cognitive neuroscience*, 20(8), 1490–1506.

- Rosenbaum, R. S., Winocur, G., Grady, C. L., Ziegler, M., & Moscovitch, M. (2007). Memory for familiar environments learned in the remote past: fMRI studies of healthy people and an amnesic person with extensive bilateral hippocampal lesions. *Hippocampus*, *17*(12), 1241–1251.
- Rosenbaum, R. S., Priselac, S., Köhler, S., Black, S. E., Gao, F., Nadel, L., & Moscovitch, M. (2000). Remote spatial memory in an amnesic person with extensive bilateral hippocampal lesions. *Nature Neuroscience*, *3*(10), 1044–1048.
- Rosenthal, R., Rosnow, R. L., Rubin, D. B. (2000). *Contrasts and effect sizes in behavioral research: A correctional approach*. Cambridge: Cambridge University Press.
- Rosmond, R., Dallman, M. F., & Björntorp, P. (1998). Stress-related cortisol secretion in men: relationships with abdominal obesity and endocrine, metabolic and hemodynamic abnormalities. *The Journal of clinical endocrinology and metabolism*, *83*(6), 1853–1859.
- Ross, S. P., Skelton, R. W., & Mueller, S. C. (2006). Gender differences in spatial navigation in virtual space: implications when using virtual environments in instruction and assessment. *Virtual Reality*, *10*(3), 175–184.
- Rossiter, J. R., & Percy, L. (1997). *Advertising communications and promotion management*. New York: Irwin McGraw-Hill.
- Sachs-Ericsson, N., & Ciarlo, J. A. (2000). Gender, Social Roles, and Mental Health: An Epidemiological Perspective. *Sex Roles*, *43*(9-10), 605–628.
- Sajadi, A. A., Samaei, S. A., & Rashidy-Pour, A. (2007). Blocking effects of intra-hippocampal naltrexone microinjections on glucocorticoid-induced impairment of spatial memory retrieval in rats. *Neuropharmacology*, *52*(2), 347–354.
- Salehi, B., Cordero, M. I., & Sandi, C. (2010). Learning under stress: the inverted-U-shape function revisited. *Learning & memory (Cold Spring Harbor, N.Y.)*, *17*(10), 522–530.
- Sandi, C. (1998). The Role and Mechanisms of Action of Glucocorticoid Involvement in Memory Storage. *Neural Plasticity*, *6*(3), 41–52.
- Sandi, C., Loscertales, M., & Guaza, C. (1997). Experience-dependent Facilitating Effect of Corticosterone on Spatial Memory Formation in the Water Maze. *European Journal of Neuroscience*, *9*(4), 637–642.
- Sandstrom, N. J., Kaufman, J., & Huettel, S. A. (1998). Males and females use different distal cues in a virtual environment navigation task. *Brain research. Cognitive brain research*, *6*(4), 351–360.
- Sapolsky, R. M. (1993). Endocrinology alfresco: psychoendocrine studies of wild baboons. *Recent progress in hormone research*, *48*, 437–468.
- Sapolsky, R. M. (2000). Glucocorticoids and hippocampal atrophy in neuropsychiatric disorders. *Archives of general psychiatry*, *57*(10), 925–935.

- Saucier, D. M., Green, S. M., Leason, J., MacFadden, A., & Elias, L. J. (2002). Are sex differences in navigation caused by sexually dimorphic strategies or by differences in the ability to use the strategies? *Behavioral Neuroscience*, *116*, 403–410.
- Schilling, T. M., Kölsch, M., Larra, M. F., Zech, C. M., Blumenthal, T. D., Frings, C., & Schächinger, H. (2013). For whom the bell (curve) tolls: cortisol rapidly affects memory retrieval by an inverted U-shaped dose-response relationship. *Psychoneuroendocrinology*, *38*(9), 1565–1572.
- Schmidt, K., Patnaik, P., & Kensinger, E. A. (2011). Emotion's influence on memory for spatial and temporal context. *Cognition & emotion*, *25*(2), 229–243.
- Schönfeld, P., Ackermann, K., & Schwabe, L. (2014). Remembering under stress: different roles of autonomic arousal and glucocorticoids in memory retrieval. *Psychoneuroendocrinology*, *39*, 249–256.
- Schoofs, D., Preuss, D., & Wolf, O. T. (2008). Psychosocial stress induces working memory impairments in an n-back paradigm. *Psychoneuroendocrinology*, *33*(5), 643–653.
- Schoofs, D., & Wolf, O. T. (2009). Stress and memory retrieval in women: no strong impairing effect during the luteal phase. *Behavioral neuroscience*, *123*(3), 547–554.
- Schramke, C. J., & Bauer, R. M. (1997). State-dependent learning in older and younger adults. *Psychology and aging*, *12*(2), 255–262.
- Schwabe, L., Bohringer, A., Chatterjee, M., & Schächinger, H. (2008a). Effects of pre-learning stress on memory for neutral, positive and negative words: Different roles of cortisol and autonomic arousal. *Neurobiology of learning and memory*, *90*(1), 44–53.
- Schwabe, L., Dalm, S., Schächinger, H., & Oitzl, M. S. (2008b). Chronic stress modulates the use of spatial and stimulus-response learning strategies in mice and man. *Neurobiology of Learning and Memory*, *90*(3), 495–503.
- Schwabe, L., Joëls, M., Roozendaal, B., Wolf, O. T., & Oitzl, M. S. (2012). Stress effects on memory: an update and integration. *Neuroscience and biobehavioral reviews*, *36*(7), 1740–1749.
- Schwabe, L., Haddad, L., & Schächinger, H. (2008c). HPA axis activation by a socially evaluated cold-pressor test. *Psychoneuroendocrinology*, *33*(6), 890–895.
- Schwabe, L., Oitzl, M. S., Philippson, C., Richter, S., Bohringer, A., Wippich, W., & Schächinger, H. (2007). Stress modulates the use of spatial versus stimulus-response learning strategies in humans. *Learning & Memory*, *14*(1-2), 109–116.
- Schwabe, L., Oitzl, M. S., Richter, S., & Schächinger, H. (2009b). Modulation of spatial and stimulus-response learning strategies by exogenous cortisol in healthy young women. *Psychoneuroendocrinology*, *34*(3), 358–366.
- Schwabe, L., Römer, S., Richter, S., Dockendorf, S., Bilak, B., & Schächinger, H. (2009). Stress effects on declarative memory retrieval are blocked by a beta-adrenoceptor antagonist in humans. *Psychoneuroendocrinology*, *34*(3), 446–454.

- Schwabe, L., Schächinger, H., de Kloet, E. R., & Oitzl, M. S. (2010). Corticosteroids operate as a switch between memory systems. *Journal of Cognitive Neuroscience*, *22*(7), 1362–1372.
- Schwabe, L., Tegenthoff, M., Höffken, O., & Wolf, O. T. (2010). Concurrent glucocorticoid and noradrenergic activity shifts instrumental behavior from goal-directed to habitual control. *The Journal of Neuroscience: The Official Journal of the Society for Neuroscience*, *30*(24), 8190–8196.
- Schwabe, L., & Wolf, O. T. (2009). The context counts: congruent learning and testing environments prevent memory retrieval impairment following stress. *Cognitive, Affective & Behavioral Neuroscience*, *9*(3), 229–236.
- Schwabe, L., & Wolf, O. T. (2009). Stress Prompts Habit Behavior in Humans. *The Journal of Neuroscience*, *29*(22), 7191–7198.
- Schwabe, L., & Wolf, O. T. (2010a). Learning under stress impairs memory formation. *Neurobiology of learning and memory*, *93*(2), 183–188.
- Schwabe, L., & Wolf, O. T. (2010b). Stress impairs the reconsolidation of autobiographical memories. *Neurobiology of learning and memory*, *94*(2), 153–157.
- Schwabe, L., & Wolf, O. T. (2011). Stress increases behavioral resistance to extinction. *Psychoneuroendocrinology*, *36*(9), 1287–1293.
- Schwabe, L., & Wolf, O. T. (2013). Stress and multiple memory systems: from “thinking” to “doing.” *Trends in Cognitive Sciences*, *17*(2), 60–68.
- Schwabe, L., Wolf, O. T., & Oitzl, M. S. (2010). Memory formation under stress: quantity and quality. *Neuroscience and biobehavioral reviews*, *34*(4), 584–591.
- Schwegler, K., Ettlin, D., Buser, I., Klaghofer, R., Goetzmann, L., Buddeberg, C., ... De Quervain, D. J.-F. (2010). Cortisol reduces recall of explicit contextual pain memory in healthy young men. *Psychoneuroendocrinology*, *35*(8), 1270–1273.
- Scoville, W. B., & Milner, B. (1957). Loss of recent memory after bilateral hippocampal lesions. *Journal of Neurology, Neurosurgery, and Psychiatry*, *20*(1), 11–21.
- Selye, H. (1936). A syndrome produced by diverse noxious agents. *Nature*, *138*, 32.
- Shapiro, A. K., & Morris, L. A. (1978). The placebo effect in medical and psychological therapies. *Handbook of psychotherapy and behavior change*, *2*, 369-409.
- Siegel, A. W., & White, S. H. (1975). The development of spatial representation of large-scale environments. In H.W. Reese (Ed.), *Advances in Child Development and Behavior*. New York: Academic Press.
- Silverman, I., Choi, J., Mackewn, A., Fisher, M., Moro, J., & Olshansky, E. (2000). Evolved mechanisms underlying wayfinding: Further studies on the hunter-gatherer theory of spatial sex differences. *Evolution and Human Behavior*, *21*, 201–213.

- Skelton, R. W., Bukach, C., Laurance, H. E., Thomas, K. G. F., & Jacobs, W. J. (2000). Humans with traumatic brain injuries show place-learning deficits in computer-generated virtual space. *Journal of Clinical & Experimental Neuropsychology*, *22*, 157-175.
- Skelton, R. W., Ross, S. P., Nerad, L., & Livingstone, S. A. (2006). Human spatial navigation deficits after traumatic brain injury shown in the arena maze, a virtual Morris water maze. *Brain Injury: [BI]*, *20*(2), 189–203.
- Smeets, T. (2011). Acute stress impairs memory retrieval independent of time of day. *Psychoneuroendocrinology*, *36*(4), 495–501.
- Smeets, T., Cornelisse, S., Quaedflieg, C. W. E. M., Meyer, T., Jelicic, M., & Merckelbach, H. (2012). Introducing the Maastricht Acute Stress Test (MAST): a quick and non-invasive approach to elicit robust autonomic and glucocorticoid stress responses. *Psychoneuroendocrinology*, *37*(12), 1998–2008.
- Smeets, T., Giesbrecht, T., Jelicic, M., & Merckelbach, H. (2007). Context-dependent enhancement of declarative memory performance following acute psychosocial stress. *Biological psychology*, *76*(1-2), 116–123.
- Smeets, T., Jelicic, M., & Merckelbach, H. (2006). The effect of acute stress on memory depends on word valence. *International journal of psychophysiology: official journal of the International Organization of Psychophysiology*, *62*(1), 30–37.
- Smeets, T., Otgaar, H., Candel, I., & Wolf, O. T. (2008). True or false? Memory is differentially affected by stress-induced cortisol elevations and sympathetic activity at consolidation and retrieval. *Psychoneuroendocrinology*, *33*(10), 1378–1386.
- Smeets, T., Otgaar, H., Raymaekers, L., Peters, M. J. V., & Merckelbach, H. (2012). Survival processing in times of stress. *Psychonomic bulletin & review*, *19*(1), 113–118.
- Smeets, T., Wolf, O. T., Giesbrecht, T., Sijstermans, K., Telgen, S., & Joëls, M. (2009). Stress selectively and lastingly promotes learning of context-related high arousing information. *Psychoneuroendocrinology*, *34*(8), 1152–1161.
- Smith, C. A., & Ellsworth, P. C. (1985). Patterns of cognitive appraisal in emotion. *Journal of Personality and Social Psychology*, *48*(4), 813–838.
- Song, L., Che, W., Min-wei, W., Murakami, Y., & Matsumoto, K. (2006). Impairment of the spatial learning and memory induced by learned helplessness and chronic mild stress. *Pharmacology, Biochemistry and Behavior*, *83*, 186-193.
- Southwick, S. M., Davis, M., Horner, B., Cahill, L., Morgan, C. A., 3rd, Gold, P. E., ... Charney, D. C. (2002). Relationship of enhanced norepinephrine activity during memory consolidation to enhanced long-term memory in humans. *The American journal of psychiatry*, *159*(8), 1420–1422.
- Spielberger, C. D., Gorsuch, R. L., Lushene, R., Vagg, P. R., & Jacobs, G. A. (1983). *Manual for the State-Trait Anxiety Inventory*. Palo Alto, CA: Consulting Psychologists Press.

- Speilberger, C. D., & Vagg, P. R. (1984). Psychometric Properties of the STAI: A Reply to Ramanaiah, Franzen, and Schill. *Journal of Personality Assessment*, 48(1), 95–97.
- Squire, L. R., & Bayley, P. J. (2007). The neuroscience of remote memory. *Current opinion in neurobiology*, 17(2), 185–196.
- Strange, B. A., & Dolan, R. J. (2004). Beta-adrenergic modulation of emotional memory-evoked human amygdala and hippocampal responses. *Proceedings of the National Academy of Sciences of the United States of America*, 101(31), 11454–11458.
- Strazdins, L., Meyerkort, S., Brent, V., D'Souza, R. M., Broom, D. H., & Kyd, J. M. (2005). Impact of saliva collection methods on sIgA and cortisol assays and acceptability to participants. *Journal of Immunological Methods*, 307(1-2), 167–171.
- Sternberg, R. J. (2006). *Cognitive psychology (4<sup>th</sup> ed.)*. Belmont, USA: Thomson Wadsworth.
- Sutherland, R. J., & Lehmann, H. (2011). Alternative conceptions of memory consolidation and the role of the hippocampus at the systems level in rodents. *Current opinion in neurobiology*, 21(3), 446–451.
- Sutherland, R. J., Weisend, M. P., Mumby, D., Astur, R. S., Hanlon, F. M., Koerner, A., ... Hoising, J. M. (2001). Retrograde amnesia after hippocampal damage: recent vs. remote memories in two tasks. *Hippocampus*, 11(1), 27–42.
- Taverniers, J., Smeets, T., Lo Bue, S., Syroit, J., Van Ruysseveldt, J., Pattyn, N., & Von Grumbkow, J. (2011a). Visuo-spatial path learning, stress, and cortisol secretion following military cadets' first parachute jump: the effect of increasing task complexity. *Cognitive, affective & behavioral neuroscience*, 11(3), 332–343.
- Taverniers, J., Smeets, T., Van Ruysseveldt, J., Syroit, J., & Von Grumbkow, J. (2011b). The risk of being shot at: Stress, cortisol secretion, and their impact on memory and perceived learning during reality-based practice for armed officers. *International Journal of Stress Management*, 18(2), 113–132.
- Teng, E., & Squire, L. R. (1999). Memory for places learned long ago is intact after hippocampal damage. *Nature*, 400(6745), 675–677.
- Thomas, K. G. F. (2003). *Cognitive mapping and spatial navigation in patients with anterior temporal lobectomy*. Unpublished doctoral thesis, University of Arizona, United States of America.
- Thomas, K. G. F., Hsu, M., Laurance, H. E., Nadel, L., & Jacobs, W. J. (2001). Place learning in virtual space III: Investigation of spatial navigation training procedures and their application to fMRI and clinical neuropsychology. *Behavior Research Methods, Instruments, & Computers*, 33, 21-37.
- Thomas, K. G. F., Laurance, H. E., Nadel, L., & Jacobs, W. J. (2010). Stress-Induced Impairment of Spatial Navigation in Females. *South African Journal of Psychology*, 40(1), 32–43.

- Tollenaar, M. S., Elzinga, B. M., Spinhoven, P., & Everaerd, W. A. M. (2008). The effects of cortisol increase on long-term memory retrieval during and after acute psychosocial stress. *Acta psychologica*, *127*(3), 542–552.
- Tollenaar, M. S., Elzinga, B. M., Spinhoven, P., & Everaerd, W. (2009). Immediate and prolonged effects of cortisol, but not propranolol, on memory retrieval in healthy young men. *Neurobiology of learning and memory*, *91*(1), 23–31.
- Tolman, E. C. (1948). Cognitive maps in rats and men. *Psychological review*, *55*, 189–208.
- Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J.H. Barkow, L. Cosmides, & J. Tooby (Eds.), *The adapted mind: Evolutionary psychology and the generation of culture* (pp. 19–136). New York, NY: Oxford University Press.
- Tops, M., Van der Pompe, G., Baas, D., Mulder, L. J. M., Den Boer, J. A., Meijman, T. F., & Korf, J. (2003). Acute cortisol effects on immediate free recall and recognition of nouns depend on stimulus valence. *Psychophysiology*, *40*(2), 167–173.
- Trammell, W., Beck, J. L., Bottalico, K. S., & Molloy, R. D. (1990). Effects of intentional versus incidental learning on explicit and implicit tests of memory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *16*(3), 457–463
- Tse, D., Langston, R. F., Kakeyama, M., Bethus, I., Spooner, P. A., Wood, E. R., ... Morris, R. G. M. (2007). Schemas and Memory Consolidation. *Science*, *316*(5821), 76–82.
- Tulving, E. (1985). *Elements of episodic memory*. Oxford: Clarendon.
- Ulrich-Lai, Y. M., & Herman, J. P. (2009). Neural regulation of endocrine and autonomic stress responses. *Nature Reviews Neuroscience*, *10*(6), 397–409.
- Ursin, H., & Eriksen, H. R. (2004). The cognitive activation theory of stress. *Psychoneuroendocrinology*, *29*(5), 567–592.
- Uttl, B., Graf, P., & Richter, L. K. (2002). Verbal Paired Associates tests limits on validity and reliability. *Archives of clinical neuropsychology: the official journal of the National Academy of Neuropsychologists*, *17*(6), 567–581.
- Van der Laan, S., & Meijer, O. C. (2008). Pharmacology of glucocorticoids: beyond receptors. *European journal of pharmacology*, *585*(2-3), 483–491.
- Van Stegeren, A. H., Goekoop, R., Everaerd, W., Scheltens, P., Barkhof, F., Kuijjer, J. P. A., & Rombouts, S. A. R. B. (2005). Noradrenaline mediates amygdala activation in men and women during encoding of emotional material. *NeuroImage*, *24*(3), 898–909.
- Van Stegeren, A. H., Wolf, O. T., Everaerd, W., Scheltens, P., Barkhof, F., & Rombouts, S. A. R. B. (2007). Endogenous cortisol level interacts with noradrenergic activation in the human amygdala. *Neurobiology of learning and memory*, *87*(1), 57–66.
- Van Stegeren, A. H., Wolf, O. T., Everaerd, W., & Rombouts, S. A. R. B. (2008). Interaction of endogenous cortisol and noradrenaline in the human amygdala. *Progress in brain research*, *167*, 263–268.

- Vasey, M. W., & Thayer, J. F. (1987). The continuing problem of false positives in repeated measures ANOVA in psychophysiology: a multivariate solution. *Psychophysiology*, *24*(4), 479–486.
- Vorhees, C. V., & Williams, M. T. (2006). Morris water maze: procedures for assessing spatial and related forms of learning and memory. *Nature Protocols*, *1*(2), 848–858.
- Voyer, D., Voyer, S., & Bryden, M. P. (1995). Magnitude of sex differences in spatial abilities: a meta-analysis and consideration of critical variables. *Psychological Bulletin*, *117*(2), 250–270.
- Vrana, S. R., Spence, E. L., & Lang, P. J. (1988). The startle probe response: a new measure of emotion? *Journal of Abnormal Psychology*, *97*(4), 487–491.
- Wang, S.-H., Teixeira, C. M., Wheeler, A. L., & Frankland, P. W. (2009). The precision of remote context memories does not require the hippocampus. *Nature Neuroscience*, *12*(3), 253–255.
- Wang, X.-Y., Zhao, M., Ghitza, U. E., Li, Y.-Q., & Lu, L. (2008). Stress Impairs Reconsolidation of Drug Memory via Glucocorticoid Receptors in the Basolateral Amygdala. *The Journal of Neuroscience*, *28*(21), 5602–5610.
- Weeks, J. W., & Heimberg, R. G. (2005). Evaluation of the psychometric properties of the Beck Depression Inventory in a non-elderly adult sample of patients with generalized anxiety disorder. *Depression and Anxiety*, *22*(1), 41–44.
- Weinstein, Y., Bugg, J. M., & Roediger, H. L., 3rd. (2008). Can the survival recall advantage be explained by basic memory processes? *Memory & cognition*, *36*(5), 913–919.
- Weymar, M., Schwabe, L., Löw, A., & Hamm, A. O. (2012). Stress sensitizes the brain: increased processing of unpleasant pictures after exposure to acute stress. *Journal of cognitive neuroscience*, *24*(7), 1511–1518.
- Wiener, S. I., Berthoz, A., & Zugaro, M. B. (2002). Multisensory processing in the elaboration of place and head direction responses by limbic system neurons. *Cognitive Brain Research*, *14*, 75–90.
- Wilson, S., Darling, S., & Sykes, J. (2011). Adaptive memory: fitness relevant stimuli show a memory advantage in a game of pelmanism. *Psychonomic bulletin & review*, *18*(4), 781–786.
- Wilson, P., Foreman, N., & Tlauka, M. (1997). Transfer of spatial information from a virtual to a real environment. *Human Factors*, *39*, 526–531.
- Wingenfeld, K., Driessen, M., Terfehr, K., Schlosser, N., Fernando, S. C., Otte, C., ... Wolf, O. T. (2012). Cortisol has enhancing, rather than impairing effects on memory retrieval in PTSD. *Psychoneuroendocrinology*, *37*(7), 1048–1056.
- Winocur, G., Moscovitch, M., & Bontempi, B. (2010a). Memory formation and long-term retention in humans and animals: convergence towards a transformation account of hippocampal-neocortical interactions. *Neuropsychologia*, *48*(8), 2339–2356.

- Winocur, G., Moscovitch, M., Caruana, D. A., & Binns, M. A. (2005a). Retrograde amnesia in rats with lesions to the hippocampus on a test of spatial memory. *Neuropsychologia*, *43*(11), 1580–1590. doi:10.1016/j.neuropsychologia.2005.01.013
- Winocur, G., Moscovitch, M., Fogel, S., Rosenbaum, R. S., & Sekeres, M. (2005b). Preserved spatial memory after hippocampal lesions: effects of extensive experience in a complex environment. *Nature Neuroscience*, *8*(3), 273–275.
- Winocur, G., Moscovitch, M., Rosenbaum, R. S., & Sekeres, M. (2010b). An investigation of the effects of hippocampal lesions in rats on pre- and postoperatively acquired spatial memory in a complex environment. *Hippocampus*, *20*(12), 1350–1365.
- Wirtz, P. H., Ehlert, U., Emini, L., & Suter, T. (2008). Higher body mass index (BMI) is associated with reduced glucocorticoid inhibition of inflammatory cytokine production following acute psychosocial stress in men. *Psychoneuroendocrinology*, *33*(8), 1102–1110.
- Witmer, B. G., Bailey, J. H., Knerr, B. W., & Parsons, K. C. (1996). Virtual spaces and real world places transfer of route knowledge. *International Journal of Human–Computer Studies*, *45*, 413–428.
- Wolf, O. T. (2008). The influence of stress hormones on emotional memory: relevance for psychopathology. *Acta psychologica*, *127*(3), 513–531.
- Wolf, O. T. (2009). Stress and memory in humans: twelve years of progress? *Brain research*, *1293*, 142–154.
- Wolf, O. T., Convit, A., McHugh, P. F., Kandil, E., Thorn, E. L., De Santi, S., ... De Leon, M. J. (2001). Cortisol differentially affects memory in young and elderly men. *Behavioral neuroscience*, *115*(5), 1002–1011.
- Wolf, O. T., Schommer, N. C., Hellhammer, D. H., McEwen, B. S., & Kirschbaum, C. (2001). The relationship between stress induced cortisol levels and memory differs between men and women. *Psychoneuroendocrinology*, *26*(7), 711–720.
- Wolf, O. T., Schommer, N. C., Hellhammer, D. H., Reischies, F. M., & Kirschbaum, C. (2002). Moderate psychosocial stress appears not to impair recall of words learned 4 weeks prior to stress exposure. *Stress (Amsterdam, Netherlands)*, *5*(1), 59–64.
- Young, A. H., Sahakian, B. J., Robbins, T. W., & Cowen, P. J. (1999). The effects of chronic administration of hydrocortisone on cognitive function in normal male volunteers. *Psychopharmacology*, *145*(3), 260–266.
- Yerkes, R. M., & Dodson, J. D. (1908). The relation of strength of stimulus to rapidity of habit-formation. *Journal of Comparative Neurology and Psychology*, *18*(5), 459–482.
- Zhao, L.-Y., Zhang, X.-L., Shi, J., Epstein, D. H., & Lu, L. (2009). Psychosocial stress after reactivation of drug-related memory impairs later recall in abstinent heroin addicts. *Psychopharmacology*, *203*(3), 599–608.

Zimring, C., & Gross, M. (1991). Searching for the environment in environmental cognition research. In Garling, T., & Evans, G. W. (Eds.), *Environment, cognition, and action*. Oxford: Oxford University Press.

Zola-Morgan, S., Squire, L. R., & Amaral, D. G. (1986). Human amnesia and the medial temporal region: enduring memory impairment following a bilateral lesion limited to field CA1 of the hippocampus. *The Journal of neuroscience: the official journal of the Society for Neuroscience*, 6(10), 2950–2967.

## **APPENDIX A:**

### **Validation of Visual Stimuli**

Emotional arousal has a significant influence on memory, in general, and is suggested to be a facilitating factor in the stress-induced effects on memory (e.g., see de Quervain et al., 2009, Roozendaal et al., 2009, Schwabe et al., 2012; Wolf, 2008, 2009). In the present study, I attempt to firstly introduce the theories behind emotion and secondly, to use those theories to identify and obtain psychometric properties for the stimuli to be used in Chapters 2, 4 and 5.

Lang, Bradley, and Cuthbert (1997) view emotion arousal as comprising two fundamental systems, one appetitive and one defensive. These systems have evolved through situational interactions with the environment that either threaten or promote survival. The appetitive system is primarily activated in contexts that promote survival, such as procreation, sustenance and nurturance. These contexts promote a basic survival behaviour repertoire based on copulation, ingestion, care giving and exploration. The defensive system, in contrast, is activated in situations of threat that trigger such basic behaviours as escape, avoidance, attack or defence (Bradley, Codispoti, Cuthbert, & Lang, 2001).

In trying to obtain a better understanding of emotion, a motivational model involving two simple factors has been proposed by a number of theorists (Dickinson & Dearing, 1979; Hebb, 1949; Mehrabian & Russell, 1974; Lang, Bradley, & Cuthbert, 1990; Osgood, Suci, & Tannenbaum, 1957; Smith & Ellsworth, 1985). Osgood et al. (1957), using the semantic differentials for verbal judgments of a wide variety of concepts (e.g., words and paintings), found pleasure-displeasure to be hierarchically organised as a fundamental dimension. A second factor that accounted for a smaller portion of total variance was arousal. This finding led the way to the formation of the motivational model that accounts for emotion's basic parameters, that being hedonic valence and arousal. Hedonic valence is seen as either pleasant (appetitive motivation) or unpleasant (defensive motivation). Arousal, on the other hand, is seen as the degree of motivational activation (Bradley et al., 2001a). Together these factors reflect the fundamental dimensions of emotion; valence determines the direction of the motivation, while arousal determines the intensity of the activation (Lang et al. 1997).

These factors are obviously influenced by many other elements such as situational, personal, and cultural divergences and cannot be seen in entirety as direct systems of activity in the motivational system. Previous studies have, nonetheless, consistently confirmed the validity of the two-factor model across languages and cultures, reflecting the motivational

foundation of affective judgements as well as biological reflexes that are associated with activation of the appetitive and defensive systems (Bradley, 2009; Bradley, Keil, & Lang, 2012; Bradley et al., 2001a; Cuthbert, Schupp, Bradley, McManis, & Lang, 1998; Ferrari, Bradley, Codispoti, & Lang, 2011; Lang & Bradley, 2010; Lang, Bradley, & Cuthbert, 1999, 2005, 2008)

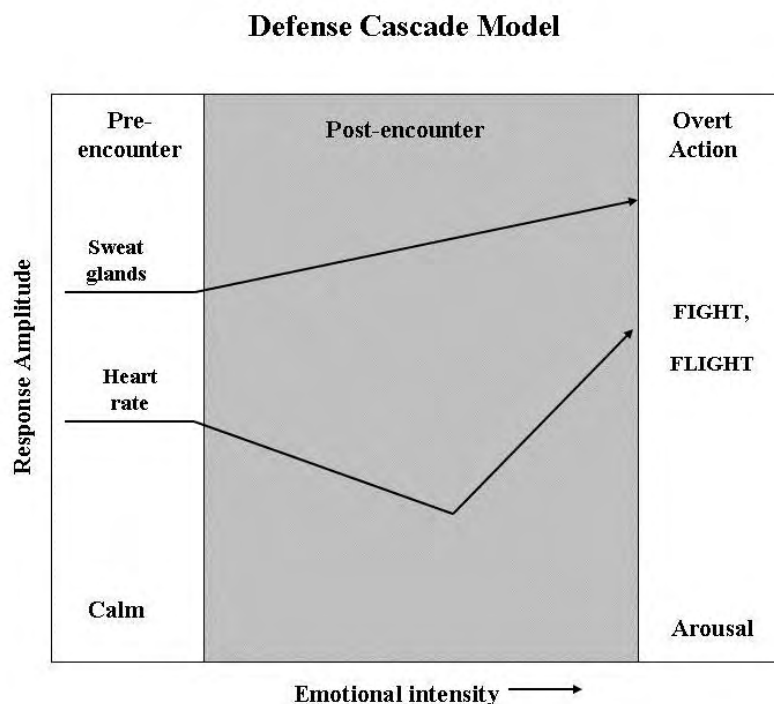
### **Defensive Motivation**

Threatening cues have been shown in animal studies to activate a neural circuit (a *defensive motivation circuit*) that is ordinarily triggered when the relevant sensory inputs activate the basolateral amygdala (BLA). Projections from this structure to other structures in the brain initiate a series of autonomic and somatic reflex behaviours. These behaviours assist the processing of the threat situation and prepare the organism for defensive behaviour (Bradley, 2009; Bradley et al., 2001a, 2012; Lang & Bradley, 2010). Responses include freezing and active flight (Fanselow, 1994), fear bradycardia (Kapp, Frysinger, Gallager, & Haselton, 1979), increase in blood pressure (Le Doux, 1990), and potentiation of the startle reflex (Davis, 2000). These behaviours are, however, subject to the proximity or imminence of the threat. Thus a distant threat would be perceived with hyperalertness, while the actual presence of the threat stimulus is more likely to result in freezing, orientating and information gathering. Passive responses are therefore more likely to be transformed to active responses with the enhancing proximity of the threat stimulus, the end result of which would be a shifting into a counter-threat defence such as flight or fight (Fanselow, 1994).

Lang et al. (1997) noted, on the basis of physiological reactions measured during picture presentation, that humans show a similar defensive response set. That is to say, in the laboratory situation, the degree to which the defensive system is activated is determined by the nature and content of, for instance, unpleasant stimulus pictures. Lang and colleagues suggest that participants reacting to unpleasant pictures in a laboratory setting are in a state similar to that of freezing animals: They are oriented to the sensory input, will process the contextual details, will retrieve the relevant information from memory and will implicitly plan for possible action.

The defence cascade model proposed by Bradley et al. (2001a), Bradley and Lang (2000), Lang (1995), and Lang et al. (1997) theoretically depicts these different patterns of change in physiological indices in response to a threat stimulus (see Figure A1). The early stages of defence are characterised by the perceptual processing of the threat. This initial post-encounter stage, when an organism is orientating to an event, is marked by classical

physiological indices such as cardiac deceleration (Graham, 1979) and a moderate increase in electrodermal activity (Vasey & Thayer, 1987). Cardiac deceleration, or fear bradycardia, is construed as an indication of heightened attention and sensory intake when the defensive or appetitive systems are alert but activation is relatively modest (Bradley 2009; Bradley et al., 2001b). During this stage there is simultaneous activation of the sympathetic and parasympathetic nervous systems (Cacioppo, Gardner, & Berntson, 1999). An increase in defence engagement can lead to orientated attention submitting to metabolic mobilisation for active defence, causing the sympathetic reflex system to override. This brings with it a further increase in electrodermal activity (Vrana, Spence, & Lang, 1988). Predator imminence, described in animal models, involves a shift in these defensive actions with the increasing presence of a threat. This change to an overt action involves a shift from cardiac deceleration to acceleration as the animal prepares for action in the form of fight or flight (Fanselow, 1994).



*Figure A1.* A schematic diagram illustrating the defence cascade model (adapted from Bradley et al., 2001a)

Defensive affective responses, similar to those predicted in the defence cascade model, have been shown to be elicited by stimulus contents that are most threatening from a

survival standpoint. Evidence of attack, mutilation or death of a member of the same species has been noted to strongly engage the defensive motivation system in animals. Primates have been shown to become agitated, fearful, and show avoidance behaviour in the presence of a representation of mutilation of the species (for instance a model of a severed monkey head; Hebb, 1949). Similarly in humans, pictures of human attack and mutilated victims of violence or disease have been shown to strongly engage the defensive system. Bradley et al. (2001a) reported significant changes in autonomic and somatic indices when participants viewed pictures of human attack and violence. These physiological responses included a large cardiac deceleration and an increase in skin conductance that is similar to moderate defence motivation activation. In the context of picture viewing, the final stage of defensive activation (i.e., fight or flight) is unlikely to be reached. Studies involving phobic subjects have, however, found cardiac acceleration and increased electrodermal reactions when subjects viewed fearful stimuli (Hamm, Cuthbert, Globisch, & Vaitl, 1997).

### **Appetitive Motivation**

An appetitive emotive state is more difficult to evoke as it depends on the degree to which a certain stimulus is viewed as attractive. For example, if the person is not hungry then a picture of food (or the actual stimulus) will not seem attractive and is hence amotivational (Lang & Bradley, 2010).

One exception to appetitive motivational stimuli is that of sexual content. Studies of mature primates have shown that viewing attractive members of the opposite sex or sexual interaction of members of other species strongly evokes an appetitive motivational state (Rolls, 2000). Bradley et al. (2001a) found that pictures involving erotic stimuli prompted the highest arousal ratings and elicited the largest skin conductance changes of any of the pleasant stimuli viewed by their participants. In addition, heart rate showed the most pronounced initial deceleration for the erotic stimuli.

Thus the defensive and appetitive motivational systems appear to induce similar patterns in physiological arousal. Both systems are associated with orientated attention and increased activation of the sympathetic and parasympathetic nervous systems. However, in spite of these similarities, the differences between the two systems extend further than the fundamental pleasure dimension.

**Differences in activation of the defensive and appetitive systems.** Early research on approach/withdrawal conflict indicates that there are potential central differences in the degree of arousal activation for positive and negative stimuli. Miller (1959) described a

pattern in which the tendency to avoid a feared stimulus as it grew nearer had a steeper gradient than the propensity to approach a desired objective as it grew closer. Thus, as each unit of arousal increases, there should be a larger change in negative valence judgements as opposed to positive valence judgements. This difference in judgements has been termed a *negativity bias* and has been consistently reported in various domains of behaviour (Cacioppo & Berntson, 1994). For instance, Kahneman and Tversky (1984) showed, in a behavioural economic study testing tenets of prospect theory, that people report more distress at the thought of losing a certain amount of money than the pleasure they would experience from gaining the same amount of money.

Approach/withdrawal conflict research has also demonstrated vital differences in activation of the motivational systems at low or near-zero levels of arousal. At distances far from an ambiguous stimulus (i.e., at low levels of arousal), animals display a stronger motivation to approach than to avoid (Miller, 1959). This suggests that the activation of arousal is characterized by a 'positivity offset' that is manifested by a tendency for weak positive (approach) motivational output at low levels of arousal. From an evolutionary perspective, a positivity offset and a negativity bias could be considered imperative for successful exploration of one's environment. Whereas the positivity offset would more likely encourage an organism to explore a natural environment and to approach novel stimuli or contexts, a negativity bias is more likely to protect an organism if the novel stimulus or context turns out to be hostile. Due to the consequences of an injurious or fatal assault on the survival of an organism, there may be an evolutionary propensity to respond more strongly to negative stimuli than to positive stimuli. The negativity bias, which triggers a stronger responsive action (such as arousal) to proximate defensive stimuli than to proximate appetitive or neutral stimuli, may therefore be considered to be a complementary, adaptive motivational organizational feature of the defensive and appetitive systems (Cacioppo & Berntson, 1994).

### **Sex Differences in Picture Viewing**

Emotion motivation theory, discussed above, suggests that the defensive and appetitive systems should have developed equally in women and men as both sexes share the common goal of survival. Nevertheless, there has been a longstanding Western-based stereotype that women are more emotional and more reactive to threatening or traumatic events than are men (Fincher & Manstead, 2000; Kret & De Gelder, 2012; Kring & Gordon, 1998). Epidemiological studies have also shown women to be at a higher risk of developing

affective disorders (Hyde, Mezulis, & Abramson, 2008, Sachs-Ericsson & Ciarlo, 2000, Nolen-Hoeksema, 2001). This predisposition suggests that women may react more strongly to aversive contexts or stimuli than would men (Alexander & Wood, 2000). It must also be noted, however, that women report more positive emotions (such as happiness and joy) in pleasant contexts. Thus women may not only react more to aversive situations or stimuli but may generally be more emotionally reactive to all situations (Alexander & Wood, 2000).

Sex differences in emotional activation could arise from biological and sociological factors that have evolved to contribute to differential emotional experience and expression. From a biological perspective, differences in physical size and strength between sexes could cause women to judge themselves as less capable of physically defending themselves in aversive situations. This is consistent with findings that women report more fear in threatening situations (Gordon & Riger, 1991). On the other hand, differences in evaluative judgements are subject to social and cultural moulding and thus suggest that these differences could also be the product of social shaping and reinforcement (Bradley et al, 2001b; Fugate, Gouzoules, & Barrett, 2009; Kret & De Gelder, 2012; LaFrance & Banaji, 1992).

Sex differences in emotional motivation system activations can also be seen with different types of stimuli. For instance, Bradley et al. (2001b) measured male and female affective reactions while they viewed pictures that varied in emotional content between unpleasant, neutral and pleasant pictures. They found that women responded more defensively to the aversive stimuli, whereas men were more aroused by appetitive pictures that contained scenes of erotica. In the case of unpleasant pictures (which featured scenes of threat and mutilation), women responded with more intense judgements of displeasure, increased facial electromyographic activity, increased fear bradycardia and increased electrodermal activity. In terms of the defence cascade model, this might be explained as demonstrating that symbolic picture cues activate the defensive system to a greater degree in women than in men.

In the case of appetitive erotic pictures, men reported more intense pleasure and arousal, and reacted with greater electrodermal activity. These reactions could again be interpreted as being influenced by biological and/or social-learning factors (Fugate et al., 2009; Kret & De Gelder, 2012). From a social-learning perspective, it is possible that Western culture (the culture in which the study was conducted) accepts or even promotes emotional expression in the context of sexual stimuli for men. Evidence of this can be seen in the numerous commercial magazines, internet sites, and movies directed at men that contain visual depictions of erotica (Bradley et al., 2001b). From a biological perspective, the

reported sex difference may be attributed to the specific gender roles that are associated with childbearing and childrearing. Women, who bear the majority of the burden of carrying and raising children, may seek non-physical attributes such as resourcefulness and commitment in a potential mate as this would ensure the survival of potential offspring and themselves. Conversely, men, who are not obligated to carry or bring up children, may seek physical (visible) attributes and relative youth in a potential mate (Buss, 1994). Thus, the differences in the roles and associated costs of sexual activity and reproduction can, in part, reflect the primacy of the physical and non-physical characteristics that men and women seek in a potential mate

### **Rationale and Hypotheses for the Pilot Study**

The primary rationale for conducting this study was to validate a set of emotionally provocative pictures that could be used in subsequent studies in my dissertation. Although much previous laboratory research into emotion and attention has used a well-established stimulus set, the International Affective Picture System (IAPS; Lang et al., 1999, 2005, 2008), I made the decision not to use pictures from the IAPS for two reasons.<sup>45</sup> Firstly, the pictures selected for this study were to be used as spatial landmarks in a virtual environment in the subsequent studies. The purpose of those landmarks is to provide spatial information in the virtual environment. Therefore, the pictures will not only serve to activate the different emotional systems but also to provide spatial information. In order for the pictures to serve these two purposes, the content must be easily identifiable, as participants will not be looking directly at the picture but rather using the pictures to find a target location (landmarks and the virtual environment tasks are described in detail in Chapter 2). The IAPS was not used because many of its emotional pictures contain scenes that are too complex and ambiguous to be comprehended at a glance. Secondly, the less complex IAPS pictures that might have been suitable for use as landmarks have been found, in previous studies, to be not emotionally provocative enough to reliably activate the defensive and appetitive systems (Bradley et al., 2001a).

Thus, for those two reasons I chose not to use pictures from the IAPS. Nevertheless, in order to ensure that the judgments for the pictures sourced in this study were comparable in

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<sup>45</sup>The IAPS is a broad set of static images based on a dimensional model of emotion. The image set contains various pictures depicting accidents, mutilations, pollution, puppies, babies, landscapes, nature, and erotic scenes, amongst others. Each of the pictures is rated on the dimensions of pleasure, arousal and dominance.

emotional qualities to the emotional pictures of the IAPS, I used the normative rating procedure used for the IAPS. In doing so, I am able to compare the ratings obtained for my picture set to the established normative picture set.

The rationale for conducting this pilot study was to obtain affective ratings for the stimuli to be used in subsequent studies. Based on the findings from previous research, I hypothesised that:

1) Pictures depicting human death, attack, mutilation and disease would activate the defensive system and would be rated as both highly unpleasant and arousing.

2) Pictures depicting content of solo and couple erotica would activate the hot appetitive system and would be judged as both pleasant and arousing.

3) A third group of pictures will act as the controls and are expected to be judged as neutral in terms of both pleasure and arousal.

4) Women would be more reactive (report more extreme judgements) to the defensive stimuli, while men would be more reactive to the appetitive stimuli.

## Methods

### Participants

Sixty-two participants between the ages of 18 and 26 years ( $M = 19.86$ ,  $SD = 1.66$ ) were recruited from the University of Cape Town undergraduate population through the Department of Psychology's Student Research Participation Program (SRPP). All received course credit in exchange for participation. Nine participants' data were discarded due to incomplete answer sheets, which left a total sample size of 53 (23 males).

### Stimulus Selection

Fifty pictures were selected from a picture set of 407 pictures gathered from various web sites on the Internet (e.g., [www.bigfoto.com](http://www.bigfoto.com), [www.rotten.com](http://www.rotten.com), [www.charonboat.com](http://www.charonboat.com), [www.drizzaro.com](http://www.drizzaro.com), [www.youngleafs.com](http://www.youngleafs.com)). The picture set was divided into three groups: 1) *hot appetitive pictures*, which were pictures that were pleasant to view (to arouse appetitive motivation), 2) *hot defensive pictures*, which were pictures that were unpleasant to view (to arouse defensive motivation), and 3) *cool pictures*, which were pictures that were neither unpleasant nor pleasant to view and did not contain an active motivational content (i.e., were neutral). Thus, I selected two sets of pictures that were on opposite sides of the spectrum in terms of pleasure and one set of pictures that was in the middle of that spectrum. The degree of arousal should, however, range for neutral to highly arousing.

The hot appetitive pictures featured content showing erotica and nudity. Pictures with this kind of content have, as mentioned above, been found to be subjectively rated as highly pleasurable and highly arousing (Lang et al., 1999, 2005, 2008). These pictures were divided into the categories erotic solo male, erotic solo female and erotic couple. Previous research has shown that pictures of erotic couples and pictures of opposite sex erotica lead to the greatest subjective ratings of pleasure and arousal, while same-sex erotica is typically subjectively rated as slightly unpleasant and unarousing (Bradley et al., 2001a, 2001b; Lang et al., 1999; 2005, 2008). Thus I hypothesised that both men and women would find the same-sex erotica to be considerably less arousing than the other erotic stimuli. Nevertheless, in order to provide sole opposite sex erotic stimuli, pictures of solo male and female erotica were included.

Hot defensive pictures featured content showing human attack, death, mutilation and disease. These pictures included content that depicted both adult and child suffering and death. Pictures containing these contents have previously been shown to have the lowest subjective rating of valence and the highest arousal ratings (Lang, Bradley, & Cuthbert, 1999, 2005, 2008). The stimuli content was limited to pictures only showing human suffering as this was predicted to induce the greatest ratings of displeasure and arousal.

Cool pictures were selected to contain unfamiliar views of common objects (such as fruit and household appliances). Pictures of this nature were selected to be rated as neither high nor low in valence. Unfamiliar views of these objects were chosen so that they would also not be rated as too low in arousal (i.e., considered familiar or mundane and thus no attention paid to the content of the picture). Thus, I selected the cool pictures on the prediction that they would be judged as neutral in terms of pleasure and arousal.

### **Apparatus**

Assessment of the pictures was done through a pen-and-paper version of the Self-Assessment Manikin (SAM; Lang, 1980). The SAM is a self-report affective rating system that uses graphic figures to assess dimensions of hedonic valence, arousal, and dominance along a 9-point scale (see Figure A6 at the end of this Appendix). The SAM scale depicts valence as ranging from a smiling, happy figure to a frowning unhappy figure. The arousal dimension is depicted as ranging from an excited, wide-eyed figure to a relaxed sleepy figure. The dominance dimension is depicted as ranging from a large figure (indicating one is in control) to a small figure (indicating one feels influenced by the content of the pictures).

Participants are instructed to select any of the five figures comprising each scale, or to select a point between any two figures. The scoring of the ratings is such that 9 signifies a high rating on each of the dimensions (i.e. high pleasure, high arousal, high dominance) and 1 represents a low rating on each of the dimensions (i.e. low pleasure, low arousal, low dominance).

Ratings obtained through the use of the SAM instrument have been compared to data collected via the relatively longer semantic differential scale devised by Russell and Mehrabian (1974). The semantic differential scale requires participants to make 18 judgements for each picture stimulus using bipolar adjective scales. The results showed exceptionally high correlations between the two scales for the factor scores of experienced pleasure (.96) and felt arousal (.95) (Bradley & Lang, 1994). The results indicate that the SAM is a relatively quick and easy way to assess the fundamental dimensions of arousal.

### **Procedure**

Males and females were run separately in groups of up to four at a time. On arrival, participants were given a consent form (see Supplement A1 at the end of this Appendix) to read and sign, and were given a chance to ask questions concerning their participation. They were then screened to ensure their willingness to view the hot appetitive and hot defensive images. The screening was done by showing the participants three sample pictures (one hot appetitive, one hot defensive, and one cool) that were not used in the study. None of the participants declined to participate after this screening phase.

After the screening phase, participants were given instruction sheets to clarify the SAM scale and the meaning of the three SAM figures. The valence dimension was explained as a way to contrast feeling completely happy, pleased, satisfied, contented, and hopeful at one extreme (a smiling figure) to feeling completely unhappy, annoyed, unsatisfied, melancholic, despaired, and bored at the other extreme (a frowning figure). The arousal dimension was explained as a way to contrast feeling totally stimulated, excited, frenzied, jittery, wide-awake, and aroused at one extreme (a shaking figure with eyes wide open) to feeling completely relaxed, calm, dull, sluggish, sleepy, and unaroused at the other extreme (a figure with closed eyes). The dominance scale was explained as a way to contrast feeling completely controlled, influenced, cared-for, awed, submissive, and guided at the one extreme (a small figure) to feeling completely controlling, influential, in control, important, dominant, and autonomous at the other extreme (a large assertive figure with folded arms). Participants were instructed to rate the pictures as honestly as possible (i.e., to indicate how

they actually felt when looking at each picture) and not to make verbal comments that might influence others making the ratings. These instructions are in line with the participant instructions for the normative rating procedure of the IAPS (Lang et al., 2005).

Following the instructions, participants were asked to practice using the SAM ratings scales on the three sample pictures used in the screening. Participants were then seated in front of a standard desktop computer, about 50 centimeters from the monitor, with a SAM answer booklet on the desk in front of them. The set of 50 images were displayed in random order using E-Prime software (Psychology Software Tools, 2002) and each participant rated the same 50 pictures. Participants were instructed to write the number of the picture (which was at the top left of the picture) and to then rate the picture by placing an “X” over the figure in each dimension that best described their feelings while viewing the picture. When they had finished rating the picture they pressed the space bar on the keyboard to go onto the next picture. Participants were told not to go on to the next picture until they had finished rating the picture that was on the screen. Following the presentation of the final picture, the answer booklets were collected and the participants were debriefed. Each rating session lasted about 30 minutes. Two participants withdrew during the rating session, as they were not able to tolerate the content of the hot defensive pictures.

## **Results**

### **Reliability**

Reliability, that is the degree to which there is agreement between repeated measurements of the same material (Howell, 2012), was assessed by calculating split-half correlations. The total participant sample was divided into two groups (i.e., participants with even subject numbers were placed into one group and those with odd subject numbers into another group). The Pearson product-moment correlations between the mean ratings of participants in each of these groups was  $r = .966$  for valence,  $r = .847$  for arousal, and  $r = .965$  for dominance.

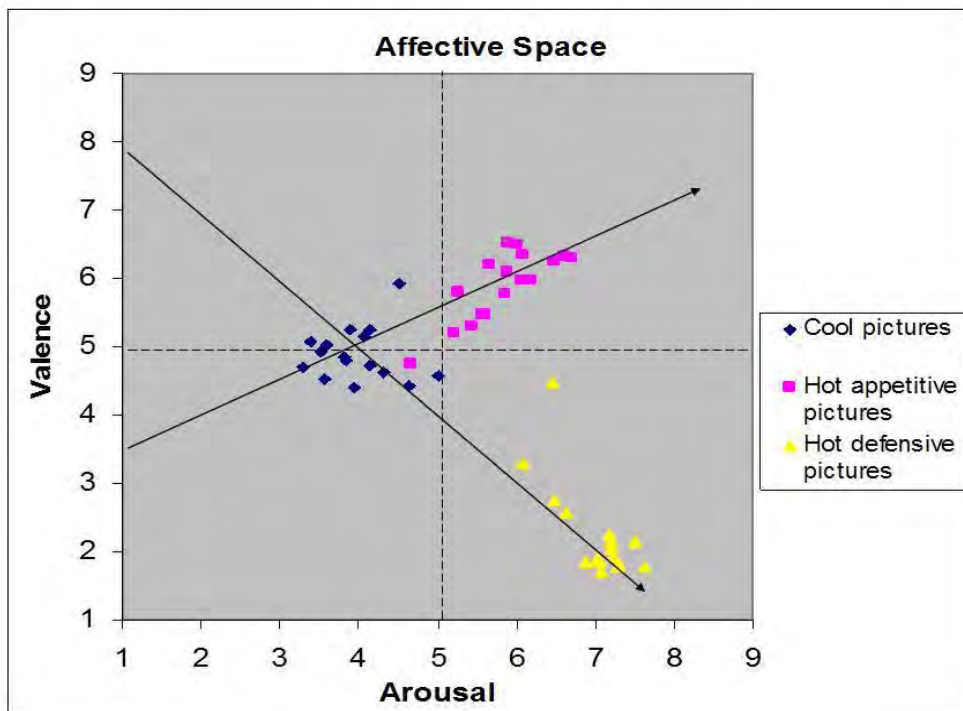
These reliability estimates are similar to those found by Lang et al. (2005) in their North American sample: the authors report split-half coefficients of .94 for both valence and arousal ratings.

### **Dimensions of Emotion**

Owing to the unequal distribution of male and female participants, each of the 23 male participants was pair matched with a female participant of the same age. The pairing

was done based on the prediction that men and women would respond differently to the appetitive and defensive pictures.

The means for the valence and arousal ratings by the matched sample for the 50 pictures used in this study are plotted in Figure A2. Due to the dominance rating typically explaining a smaller amount of the variance in affective ratings and due to valence and arousal reflecting the fundamental dimensions of emotion (Lang et al., 1997), the pictures were plotted in a two-dimensional affective space. The shape of the affective space shows a boomerang-shaped distribution of the pictures that is similar to results found previously in similar studies (Lang et al., 1999, 2005, 2008). This shape in the distribution of the pictures indicates that stimuli judged as either highly pleasant or highly unpleasant are also judged as more arousing.



*Figure A2.* A plot of the sample of 50 pictures in a two-dimensional space defined by the mean ratings of valence and arousal. *Note.* For the positive stimuli (valence > 5.00,  $n = 23$ ), intercept = 3.59 and slope = 0.41. For the negative stimuli (valence < 5.00,  $n = 27$ ), intercept = 7.89 and slope = -0.80.

To further explore the relationship between valence and arousal, the entire picture sample was dichotomised on the basis of mean valence ratings. More specifically, the 27 pictures with a mean valence rating less than 5.00 were classed as negative stimuli, and the 23 pictures with a mean valence rating of greater than 5.00 were classed as positive stimuli.

The mean valence for the negative stimuli was 3.24 ( $SD = 1.32$ ), with a range of 1.70 - 4.91. The positive stimuli had a mean valence of 5.77 ( $SD = 0.50$ ), with a range of 5.02 - 6.52.

Theories about negativity bias (Cacioppo & Berntson, 1994) propose that ratings of negative pictures should have a steeper gradient than those of positive pictures because the tendency to avoid a feared stimulus is greater than the tendency to approach an appetitive one. Moreover, the same theories predict that regression analysis should reveal a positivity offset (i.e., a greater intercept for positive stimuli than negative stimuli).

In order to compare the slopes and intercepts of both groups of stimuli and thus test these predictions, the valence ratings for the negative pictures were inverted by subtracting the valence score from 10. Regression analyses, using arousal to predict valence, were calculated separately for the positive and negative pictures. As predicted, simple regression analysis revealed a positivity offset, as shown by a greater intercept for the positive pictures (3.59 vs. 2.11). In addition, regression analyses also revealed a negativity bias, as indicated by a steeper slope for the negative stimuli (0.80 vs. 0.59). Thus the predictions of a negativity bias and a positivity offset were confirmed within the current sample.

### **Ratings of Valence, Arousal and Dominance**

The mean ratings and their standard deviations for all the pictures rated by the matched sample ( $n = 46$ ) are presented in Table A3 at the end of this Appendix. The results of the ratings are presented in terms of picture group classification. Because the ratings were made on a 9-point scale, the rating that lies in the centre (and can therefore be considered as neutral) is 5. The mean ratings and standard deviations for the cool, hot appetitive and hot defensive pictures can be seen in Table A1. A graphic display of these data can be seen in Figure A3.

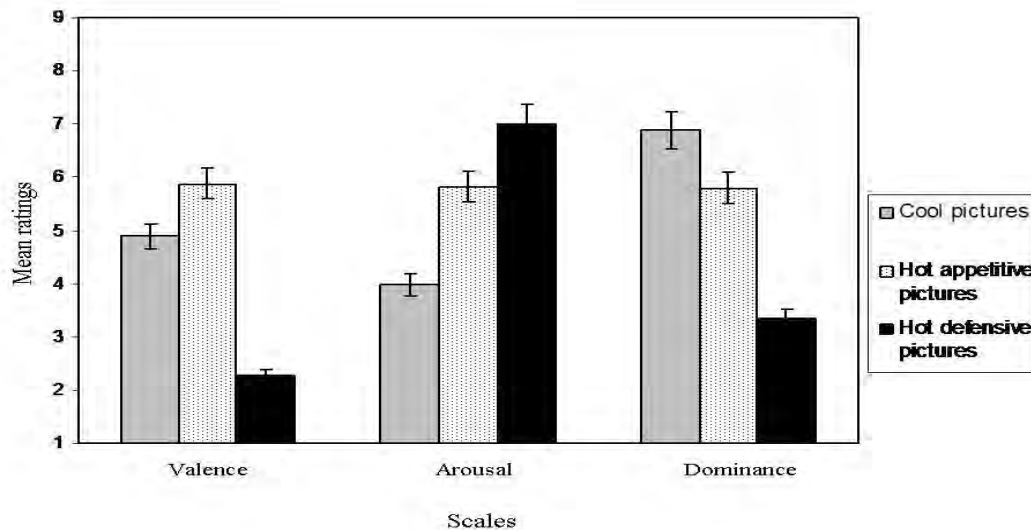
Table A1  
*Means and standard deviations of SAM rating for the cool, hot defensive and hot appetitive pictures ( $n = 46$ )*

Picture group	Valence	Arousal	Dominance
Cool	4.89 (0.39)	3.98 (0.47)	6.89 (0.32)
Hot appetitive	5.88 (0.50)	5.82 (0.51)	5.80 (0.49)
Hot defensive	2.27 (0.73)	7.02 (0.41)	3.34 (0.69)

*Note.* Means are presented with standard deviations in parentheses.

As predicted, participants found the cool pictures to be neutral in terms of pleasure but found them to be slightly below the neutral in terms of arousal. The hot defensive pictures

were, as expected, rated as low in pleasure and high in arousal, while the hot appetitive pictures were rated as fairly pleasant and arousing. Participants also found the hot defensive picture content influenced how they felt to a greater extent than the other two picture categories, as both the cool and hot appetitive picture groups had a mean rating above the midpoint of 5 on the dominance scale.



*Figure A3.* Graphs comparing the means and standard deviations for the ratings of valence, arousal and dominance. Ratings are compared between the cool, hot appetitive and hot defensive picture groups for matched sample

To determine if there was an overall difference in ratings between the three groups of pictures, statistical analyses were conducted to compare the valence, arousal, and dominance ratings between the three categories. For valence ratings, a one-way ANOVA showed a statistically significant between-categories difference,  $F(2, 47) = 187, p < .001, \eta_p^2 = .88$ . Bonferroni post-hoc analysis confirmed a statistically significant difference between all three categories ( $p < .001$  for all three comparisons). For arousal ratings, a one-way ANOVA also showed a statistically significant between-categories difference,  $F(2, 47) = 170.39, p < .001, \eta_p^2 = .87$ . Again, Bonferroni post-hoc analysis confirmed a statistically significant difference between all three categories ( $p < .001$  for all three comparisons). Lastly, for dominance ratings, a one-way ANOVA also showed a statistically significant between-categories difference,  $F(2, 47) = 195.81, p < .001, \eta_p^2 = .89$ . Again, Bonferroni post-hoc analysis confirmed a statistically significant difference between all three categories ( $p < .001$  for all three comparisons).

This relationship can be further revealed by both the distinctive significant positive linear relationship between valence and arousal for the hot appetitive pictures ( $r = .803, p < .001$ ) and the strong negative correlation between the valence and arousal ratings for the hot defensive pictures ( $r = -.744, p < .001$ ). The cool pictures, on the other hand, failed to provide a significant linear relationship between the valence and arousal ratings ( $r = .004, p = .989$ ).

These results again show that not only did the participants find the three picture groups significantly different in terms of pleasure, arousal, and dominance, but that the hot appetitive and hot defensive pictures showed a strong pairing of pleasure and arousal. Thus, the more extreme ratings of pleasure or displeasure brought with them higher ratings of arousal. The cool pictures did not show this relationship at all.

### Sex Differences in Picture Evaluation

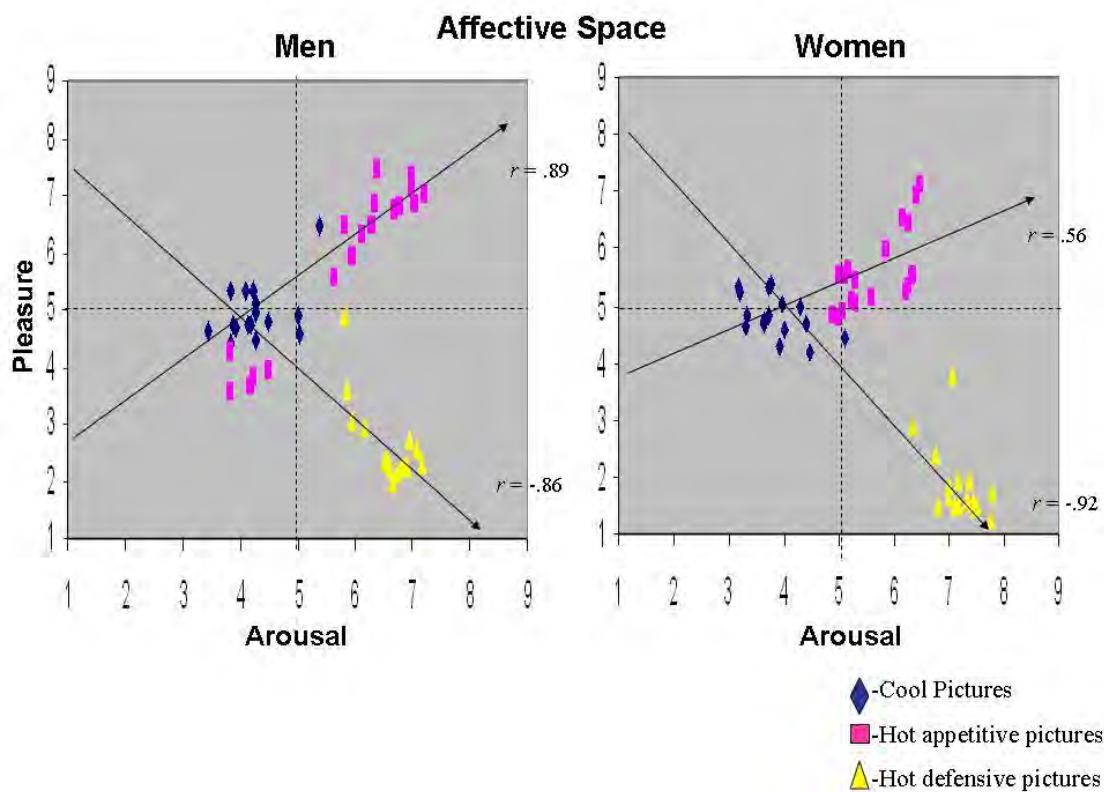
As mentioned above, sex differences have been noted in numerous studies investigating emotional motivation. In order to explore the sex differences for affective judgement within the current sample, the data were analysed separately and compared between men and women.

**Dimensions of emotion.** Figure A4 presents each of the 50 pictures rated in the study plotted, by mean valence and arousal in two-dimensional space, separately for men and women. Again the shape of the affective space shows a boomerang-shaped distribution for both sexes, indicating again that as pictures were rated as increasingly more pleasant or more unpleasant, arousal rating tended to increase as well.

As before, the sample was dichotomised on the basis of their mean valence ratings and was done separately for men and women. Pictures with a mean valence rating of below 5.00 were grouped as negative stimuli ( $n = 32$  for men,  $n = 29$  for women) while pictures with a mean valence rating of above 5.00 were grouped as positive stimuli ( $n = 18$  for men,  $n = 21$  for women). For the unpleasant pictures, women showed a slightly larger negative correlation ( $r = -.92$ ) between ratings of pleasure and arousal compared with men ( $r = -.86$ ). Furthermore, women's picture ratings projected farther into the unpleasant arousing quadrant than men (as illustrated in Figure A4). The results therefore indicate that women displayed a stronger pairing between ratings of unpleasantness and arousal than did men and that they rated the most unpleasant pictures as more arousing than did men.

For the pleasant pictures, an inverse pattern emerged. Men displayed a stronger positive correlation ( $r = .89$ ) for ratings of pleasure and arousal compared to women ( $r = .56$ ). In addition, male ratings for the pleasant pictures tended to project farther into the pleasant-

arousing quadrant than did those of women. Men consequently displayed a stronger pairing between pleasure and arousal for pleasant stimuli and also tended to find the most pleasant stimuli more arousing than did women. The results obtained for affective space between sexes are very similar to those found in similar previous studies (Bradley et al., 2001b, Lang et al., 1999, 2005, 2008).



*Figure A4.* Each of the 50 pictures rated in the study is plotted in affective space separately for men and women. *Note.* For men, positive stimuli (valence > 5.00,  $n = 18$ ), intercept = 2.83 & slope = 0.60. Negative stimuli (valence < 5.00,  $n = 32$ ), intercept = 7.40 & slope = -0.72. For women, positive stimuli (valence > 5.00,  $n = 21$ ), intercept = 3.93 & slope = 0.32. Negative stimuli (valence < 5.00,  $n = 29$ ), intercept = 8.10 & slope = -0.85

As before, regression analyses were used to compare the slopes for the positive and negative stimuli to determine if there was a negativity bias and a positivity offset for both sexes. Analyses were calculated separately for the positive and negative pictures in which arousal was used to predict valence. Regression lines can be seen in Figure A4. As might have been expected from the results described above, women showed a steeper slope (-0.85) for the negative stimuli compared with men (-0.72), while men displayed a steeper slope (0.60) for the positive stimuli compared with women (0.32). This set of data again could be interpreted as indicating that women show a greater pairing of pleasure and arousal for

negative stimuli, while men show a greater coupling of pleasure and arousal for appetitive erotic stimuli.

The predictions of a negativity bias and a positivity offset were tested separately for men and women and were again found to hold true. For women, a simple regression analysis revealed a positivity offset, as shown by a greater intercept for the positive pictures (3.93 vs. 1.90), as well as a negativity bias, as indicated by a steeper slope for the negative stimuli (0.85 vs. 0.32). Men also showed a slight positivity offset of 2.83 vs. 2.59 and a negativity bias of 0.72 vs. 0.60. These data are again consistent with the prediction that both men and women, at distances far from an ambiguous stimulus, display a stronger motivation to approach than to avoid the stimulus, but also display a stronger tendency to avoid a feared stimulus as it grows nearer (Miller, 1959).

#### **Ratings of valence, arousal and dominance of picture groups between the sexes.**

The mean ratings and their standard deviations for all the pictures rated by male and female participants are presented in Tables A4 and A5 respectively at the end of Appendix A. The overall means for the cool, hot defensive, and hot appetitive pictures for valence, arousal and dominance ratings are displayed in Table A2; the table also shows the results of *t*-tests conducted to determine if there were differences between sexes on any of the rating scales.

Table A2  
*Between sex comparisons of SAM rating for the cool, hot defensive and hot appetitive pictures (N = 53)*

Room	Scale	Male ( <i>n</i> = 23)	Female ( <i>n</i> = 30)	<i>t</i>	<i>p</i>	<i>d</i>
Cool	Valence	4.95 (0.51)	4.82 (0.37)	-0.828	.414	0.29
	Arousal	4.26 (0.51)	3.85 (0.52)	-2.234	.033	0.79
	Dominance	6.50 (0.28)	7.12 (0.41)	-4.907	<.001	1.77
Hot defensive	Valence	2.63 (0.73)	1.88 (0.65)	-3.108	.004	1.09
	Arousal	6.60 (0.43)	7.19 (0.38)	4.139	<.001	1.45
	Dominance	3.75 (0.59)	2.95 (0.76)	3.307	.002	1.18
Hot appetitive	Valence	5.89 (1.39)	5.59 (0.71)	-0.799	.430	0.27
	Arousal	5.83 (1.19)	5.65 (0.58)	-0.571	.572	0.19
	Dominance	5.65 (0.41)	6.04 (0.66)	-2.108	.043	0.71

*Note.* Means are presented with standard deviations in parentheses

As Table A2 shows, males and females differed most significantly in their ratings of the pictures classified as hot defensive. In accordance with the display of affective space, the valence ratings of women were significantly lower than those of men, while their ratings of arousal were significantly higher. Thus, women rated the hot defensive pictures as more unpleasant and more arousing than did men. Conversely, where it would be expected from

the display of affective space that men would have higher ratings than women for valence and arousal for the hot appetitive pictures, no significant difference was found. Hence, although men showed a stronger coupling between pleasure and arousal for the pleasant pictures, there was no statistically significant difference in their ratings of valence and arousal compared with women.

Another surprising result is that men tended to rate the cool neutral pictures as more arousing than did women yet there was no statistically significant difference between sexes in their ratings of valence. Although both sexes found the pictures to be in the lower half of the arousal spectrum (i.e., they found the pictures to be between neutral and non-arousing), women tended to judge these pictures as significantly less arousing compared with men.

Men and women also differed significantly in their ratings of dominance for the three picture groups. Men found both the cool and hot appetitive pictures to influence how they felt significantly more than did women, while women found the hot defensive stimuli to influence how they felt significantly more than did men. Although this result makes sense for the hot appetitive and hot defensive picture groups and falls in line with previous results found in this study (i.e., that women are more defensively reactive, while men are more appetitively reactive), it is difficult to explain, in terms of existing theory, why men found the cool pictures to influence how they felt more than women did.

**Ratings of valence, arousal and dominance of picture groups within the sexes.** In order to determine how both sexes responded to the different picture groups, a second pattern of responding to the cool, hot defensive and hot appetitive pictures was assessed separately for men and women. Figure A5 presents a graphic comparison of means and standard deviations for the three different picture groups on the valence, arousal and dominance scale. As anticipated, both men and women rated the cool, hot appetitive, and hot defensive pictures as significantly different in valence, arousal and dominance. Although the shape of the graphs are similar for both sexes, a slight difference is seen in the ratings of arousal for the hot appetitive and hot defensive pictures. Whereas women rated the hot defensive pictures as more arousing than the hot appetitive pictures,  $F(1, 47) = 78.76, p < .001, \eta_p^2 = .70$ , men tended to judge these two picture categories as being slightly more similar in terms of arousal,  $F(1, 47) = 7.81, p = .008, \eta_p^2 = .27$ . Thus although both sexes showed statistically significant differences between their ratings of arousal for the hot appetitive and hot defensive pictures, women tended to judge the picture categories as being more diverse in terms of arousal. This difference can be located in stronger ratings of arousal for the hot defensive pictures by women than by men.

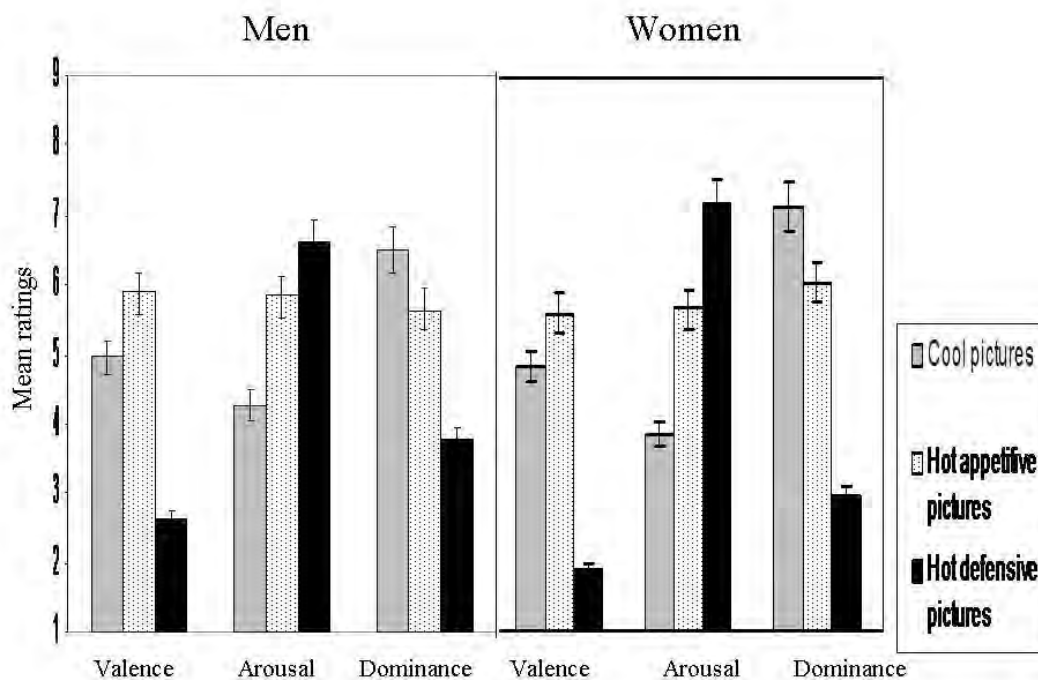


Figure A5. Graphs comparing the means and standard deviations for the ratings of valence, arousal and dominance for male and female participants.

### Discussion

The rationale behind this pilot study was to determine people's affective judgements for three groups of pictures. The first picture group contained stimuli of a neutral content; these pictures were expected to be rated as neither pleasant nor unpleasant and to carry no motivational component. The other two groups of pictures were selected because they contained an active motivational component, but on opposite extremes of emotion. One of these groups (the hot appetitive group) was predicted to be considered pleasurable and arousing and the other (the hot defensive group) was predicted to be considered unpleasant and arousing. Fifty-eight participants rated the 50 pictures on measures of pleasure, arousal and dominance using a tool commonly used in many emotional motivation studies including the International Affective Picture System (IAPS), the Self-Assessment Manikin (SAM).

Four findings from the SAM data indicate that the affective judgements found in the present sample are comparable with the IAPS. Firstly, the reliability coefficients show these ratings to be internally consistent and in line with Lang and colleagues' (2005) samples. Secondly, the ratings of pleasure and arousal plotted in two-dimensional affective space support the biphasic organisation of emotion along the hypothetical core appetitive (upper

half of the plot) and defensive (lower half of the plot) motivational systems (Lang et al., 1997). Thirdly, the association between pleasure and arousal was found to be stronger for negative stimuli than for positive stimuli. Finally, the predictions of a negativity bias and a positivity offset were confirmed within the current sample.

The ratings obtained for the cool, hot appetitive and hot defensive pictures showed the hypothesized emotional direction. As expected, the sample judged the hot appetitive pictures as being pleasurable and arousing, and found the hot defensive pictures to be to a greater degree more unpleasant and as well as more arousing. The cool pictures were, also as expected, judged as almost neutral in pleasure but were rated as being slightly unarousing or boring. This could have been due to the unequal number/distribution of arousing hot pictures compared with the cool neutral pictures. For every three pictures the participants had to rate, two of them featured content that were of an arousing nature. Thus participants could have found the content of the cool pictures rather boring compared with the numerous arousing pictures they had to rate.

The data obtained from this study are consistent with the motivational view of emotional organisation. Under this view, affective reports are determined to a significant degree by the triggering of the appetitive and defensive motive systems (Lang et al., 1997). The motive systems have been moulded through basic reflexive responses to primary reinforcers that have been shaped through evolutionary history to promote the survival of individuals and species (Rolls, 2000). Within the context of this study the unpleasant pictures invoked the activation of the defensive system, while the pleasant pictures appealed to the appetitive system. As mentioned above, affective reports have been found to correlate with activation of physiological reflexes. For instance, Bradley et al. (2001a, p. 291) report that, from affective judgements and physiological measures obtained from a sample of 95 participants, “.....in general, reports of affective arousal are closely related to the degree of motive system engagement, as defined by the autonomic and somatic reflex responses.”

Although affective judgements are to a large degree influenced by a complex social and cultural fabric, they hold within them a vital key to understanding and predicting emotional and motivational involvement.

A second pattern was found when the data were analysed separately for men and women. It was predicted that women would react more to the defensive stimuli, while men would judge the appetitive stimuli as more pleasurable and arousing. Consistent with this hypothesis, sex differences were seen to influence the shape of judgements of pleasure and arousal displayed in affective space. The ratings made by women for the unpleasant pictures

were more extreme and adhered more intimately to a steeper, more linear defence motivation vector, compared with men. Men, on the other hand, showed a steeper more linear appetitive motivation vector and rated the pleasant pictures as more pleasant and more arousing. These differences in the shape of affective shape are consistent with other previous findings, including that of Bradley and colleagues (2001b), and have also been found in affective judgements of sounds and words (Bradley & Lang, 1999a, 1999b).

Consistent with the plot of affective space, women tended to rate the hot defensive pictures as more unpleasant and more arousing than did the men. This is again in line with the hypothesis that women are more defensively reactive. Contrary to the hypothesis that men are specifically more reactive to erotic appetitive stimuli, however, there was no difference between sexes in ratings of the appetitive erotic pictures. Both sexes found the appetitive erotic pictures to be equally pleasurable and arousing. This finding is in direct contradiction to that reported by Bradley and colleagues (2001b). In attempting to explain this contradiction, one must return back to the mean ratings for the group and the individual hot appetitive pictures. As can be seen in Table A2, the amount of average deviation within the mean ratings for the hot appetitive pictures is twice as much for men in comparison to women. The source of the deviation can be seen in Figure A4. Five of the hot appetitive pictures were rated as being both unpleasant and unarousing by the male sample. These five pictures can be located to the five pictures depicting solo male erotic content (Table A4, picture numbers 3, 6, 9, 12, and 15). Same-sex erotic pictures have consistently been found to be rated as slightly unpleasant and moderately arousing and have also been found to be rated as more pleasurable and arousing by women than by men (Bradley et al., 2001a, 2001b; Lang et al., 1999, 2005, 2008). Bradley and colleagues (2001a) also reported that despite low ratings of pleasure and arousal, same-sex erotica stimuli produce changes in skin conductance, heart rate, corrugator facial electromyographic activity and startle blink magnitude that are similar to changes when participants view content that is rated as somewhat more arousing, such as pictures of opposite-sex erotica or human attack and mutilation. Thus, although men and women did not differ in their ratings of the hot appetitive pictures, men rated these pictures to greater extremes and showed stronger pairing of pleasure and arousal. Men, however, had a greater average deviation within ratings that can be attributed to the pictures containing same-sex erotica. The ratings of these pictures can be largely credited to being shaped by social learning and reinforcement (Fugate et al., 2009; Kret & De Gelder, 2012).

All evaluative judgements can be, and to a great extent are, shaped through social learning and reinforcement. Previous research has shown, however, that evaluative reports coincide with autonomic and reflex measures, which suggests that differential cue reactivity may be, to some degree, biologically determined (Bradley et al., 2001a; 2001b). The arousing pictures chosen for this study were picked to tap in to the most basic of emotional/survival responses. These pictures contained content that displayed death and mutilation on one extreme, and acts of copulation and reproductively desirable partners on the other. The findings from this initial study support the notion that the three picture groups are completely different in terms of pleasure, arousal and dominance. The pictures rated by the current sample were shown to be consistent with the rating of the IAPS and demonstrated the hypothesised direction in their emotional dimensions. Most importantly, these pictures provide a basic platform to be used in the subsequent studies reported in this dissertation.

SELF ASSESSMENT MANIKIN ©1994 PETER J. LANG




			Participant No. _____
			Session No. _____ Date _____
			Sex _____ Age _____































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Figure A6. Self Assessment Manikin (SAM) Answer Sheet.

Table A3  
*Ratings of Valence, Arousal, and Dominance for matched participant sample*

Description	Picture No.	Valence <i>Mean (SD)</i>	Arousal <i>Mean (SD)</i>	Dominance <i>Mean (SD)</i>
Cool Picture Group				
Rusted wire fence	1	4.39 (1.39)	3.93 (1.88)	6.59 (2.26)
Red insulator & wire	5	4.91 (1.30)	3.52 (1.82)	6.72 (1.99)
Thorn	8	4.41 (1.45)	4.63 (1.88)	6.50 (2.27)
Propeller	11	5.15 (1.79)	4.07 (1.85)	6.76 (2.06)
Egg, screwdriver, Pliers	14	5.24 (2.07)	3.89 (2.16)	7.04 (1.92)
Can close-up	17	5.09 (1.74)	3.39 (2.05)	7.20 (2.02)
Computer plug	20	4.80 (1.28)	3.85 (1.79)	6.98 (1.87)
Barbwire	23	4.63 (1.48)	4.33 (1.97)	6.39 (2.40)
Headphone jack	26	4.72 (1.07)	4.13 (1.88)	6.93 (2.15)
Apple with nails	29	4.59 (1.42)	5.00 (2.09)	6.22 (2.31)
Melon close-up	32	5.24 (1.97)	4.13 (2.05)	7.20 (2.37)
Broken egg	35	4.85 (1.41)	3.80 (1.94)	7.13 (1.92)
Metal loop	38	4.52 (1.28)	3.57 (1.86)	7.09 (1.82)
Aerial hinge	41	4.70 (1.23)	3.30 (1.88)	6.98 (1.89)
Computer port	44	5.02 (1.68)	3.59 (1.90)	7.30 (1.86)
Toy	47	5.91 (2.12)	4.52 (2.13)	7.15 (2.12)
Hot Defensive Picture Group				
Hung corpse	2	1.89 (1.20)	7.04 (1.62)	2.98 (1.76)
Taxi driver shotgun victim	4	2.24 (1.32)	7.17 (1.80)	3.50 (2.41)
Mutilated corpse	7	1.85 (1.21)	7.07 (1.82)	2.87 (1.73)
Dead child	10	1.91 (1.28)	7.24 (1.91)	2.87 (1.75)
Diseased child	13	1.70 (0.99)	7.09 (1.71)	3.20 (2.00)
Fingerhead	16	4.48 (1.97)	6.46 (1.63)	4.61 (2.32)
Dead man (shot in head)	19	1.80 (1.15)	7.30 (1.67)	2.83 (2.08)
Old woman (swollen neck)	22	2.74 (1.32)	6.48 (1.79)	4.15 (2.30)
Decapitated head	25	1.78 (1.21)	7.28 (1.86)	2.67 (1.93)
Shot bomber	28	1.78 (1.36)	7.63 (1.68)	2.52 (1.79)
Helicopter head	31	2.15 (1.38)	7.22 (1.69)	3.17 (2.29)
Spider thumb	34	2.59 (1.15)	6.63 (1.73)	3.63 (2.05)
Meth mouth	37	3.30 (1.59)	6.09 (1.86)	4.91 (2.23)
Woman head crush	40	2.04 (1.30)	7.22 (1.47)	2.91 (1.86)
Rape victim	43	1.85 (1.15)	6.89 (1.64)	3.30 (1.79)
Face tumor	46	2.15 (1.51)	7.50 (1.52)	3.24 (2.01)
Hot Appetitive Picture Group				
Male solo (undress)	3	5.80 (2.33)	5.26 (2.41)	6.30 (1.92)
Male solo (beach)	6	5.30 (2.59)	5.43 (2.48)	5.76 (2.23)
Male solo (waiter)	9	5.48 (2.53)	5.61 (2.40)	5.22 (2.33)
Male sole (underpants)	12	4.74 (2.17)	4.67 (2.18)	6.24 (2.07)
Male sole (behind)	15	5.20 (2.56)	5.22 (2.35)	5.65 (2.14)
Female solo (behind)	18	6.52 (1.76)	5.89 (1.83)	5.98 (2.09)
Female solo (stockings)	21	5.78 (2.24)	5.87 (2.20)	5.72 (2.22)
Female solo (blonde in towel)	24	6.50 (1.88)	6.00 (2.19)	5.59 (2.01)

Female solo (shower)	27	5.48 (2.00)	5.57 (1.92)	6.65 (1.91)
Female solo (beads)	30	5.98 (2.36)	6.17 (2.19)	5.91 (2.23)
Couple (clothed)	33	6.35 (1.66)	6.09 (1.90)	5.96 (2.17)
Couple (shower)	36	6.30 (1.82)	6.72 (1.50)	5.02 (2.11)
Couple (blonde takes off pants)	39	5.48 (1.64)	5.61 (2.14)	6.09 (2.07)
Couple (man takes off pants)	42	5.98 (1.61)	6.07 (1.64)	6.02 (1.87)
Couple (sex on desk)	45	6.33 (1.93)	6.61 (1.94)	5.37 (2.03)
Couple (blonde takes off shirt)	51	6.20 (1.57)	5.65 (1.78)	6.50 (1.96)
Couple (blonde standing)	57	6.11 (1.61)	5.89 (1.78)	5.59 (2.18)
Couple (doggy style)	60	6.24 (1.88)	6.48 (2.01)	4.78 (2.25)

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Table A4

*Ratings of Valence, Arousal and Dominance: Male participants (n = 23)*

Description	Picture No.	Valence Mean (SD)	Arousal Mean (SD)	Dominance Mean (SD)
Cool Picture Group				
Rusted wire fence	1	4.48 (1.23)	4.26 (1.68)	6.30 (2.12)
Red insulator & wire	5	4.70 (0.64)	3.91 (1.70)	6.04 (1.97)
Thorn	8	4.57 (1.59)	5.04 (1.69)	6.17 (2.52)
Propeller	11	5.30 (1.69)	4.22 (2.00)	6.43 (2.00)
Egg, screwdriver, Pliers	14	5.13 (1.87)	4.26 (1.89)	6.96 (1.99)
Can close-up	17	4.74 (1.32)	3.87 (1.74)	6.74 (1.89)
Computer plug	20	4.96 (0.98)	4.26 (1.51)	6.52 (1.86)
Barbwire	23	4.74 (1.29)	4.13 (1.66)	6.39 (2.15)
Headphone jack	26	4.78 (1.13)	4.48 (1.68)	6.35 (2.10)
Apple with nails	29	4.87 (1.33)	5.00 (1.78)	6.09 (2.19)
Melon close-up	32	5.35 (1.34)	4.09 (1.81)	6.83 (2.23)
Broken egg	35	4.74 (1.54)	4.17 (1.70)	6.61 (2.02)
Metal loop	38	4.39 (1.31)	3.83 (1.75)	6.70 (1.89)
Aerial hinge	41	4.61 (1.12)	3.43 (1.83)	6.57 (1.75)
Computer port	44	5.35 (1.58)	3.83 (2.01)	6.96 (1.74)
Toy	47	6.48 (1.86)	5.39 (1.92)	6.39 (2.27)
Hot Defensive Picture Group				
Hung corpse	2	2.35 (1.23)	6.57 (1.62)	3.52 (1.90)
Taxi driver shotgun victim	4	2.74 (1.25)	6.96 (1.55)	3.57 (1.83)
Mutilated corpse	7	2.26 (1.42)	6.91 (1.78)	3.35 (1.87)
Dead child	10	2.26 (1.45)	6.87 (1.84)	3.26 (1.60)
Diseased child	13	1.96 (1.11)	6.65 (1.90)	3.30 (2.03)
Fingerhead	16	4.87 (1.82)	5.83 (1.47)	5.04 (2.03)
Dead man (shot in head)	19	2.13 (1.29)	6.74 (1.86)	3.61 (2.23)
Old woman (swollen neck)	22	2.96 (1.22)	6.17 (1.85)	4.26 (2.07)
Decapitated head	25	2.26 (1.39)	6.83 (1.77)	3.57 (2.25)
Shot bomber	28	2.30 (1.66)	7.17 (1.99)	2.96 (1.97)
Helicopter head	31	2.26 (1.45)	6.61 (1.70)	3.48 (2.21)
Spider thumb	34	3.04 (0.88)	5.96 (1.66)	4.35 (1.99)
Meth mouth	37	3.61 (1.34)	5.87 (1.84)	4.91 (1.88)
Woman head crush	40	2.35 (1.37)	6.52 (2.11)	3.39 (1.99)
Rape victim	43	2.22 (1.28)	6.87 (1.69)	3.78 (1.76)
Face tumor	46	2.57 (1.78)	7.09 (1.31)	3.61 (1.88)
Hot Appetitive Picture Group				
Male solo (undress)	3	4.26 (2.12)	3.83 (2.15)	6.30 (2.03)
Male solo (beach)	6	3.83 (2.46)	4.22 (2.37)	5.48 (2.02)
Male solo (waiter)	9	3.91 (2.15)	4.48 (2.29)	4.96 (2.08)
Male solo (underpants)	12	3.52 (1.78)	3.83 (2.06)	5.83 (2.15)
Male solo (behind)	15	3.65 (2.33)	4.17 (2.17)	5.65 (1.94)
Female solo (behind)	18	7.43 (1.65)	6.39 (1.70)	5.48 (2.09)
Female solo (stockings)	21	6.78 (2.11)	6.78 (1.65)	5.22 (2.04)
Female solo (blonde in towel)	24	7.30 (1.46)	7.00 (1.62)	5.57 (1.97)

Female solo (shower)	27	5.91 (2.11)	5.96 (1.89)	6.61 (1.67)
Female solo (beads)	30	7.00 (1.98)	7.22 (1.76)	5.61 (2.27)
Couple (clothed)	33	6.30 (1.96)	6.13 (1.98)	5.96 (2.10)
Couple (shower)	36	6.83 (1.85)	7.04 (1.58)	5.22 (2.13)
Couple (blonde takes off pants)	39	5.57 (1.67)	5.65 (2.12)	5.87 (2.01)
Couple (man takes off pants)	42	6.48 (1.47)	6.30 (1.43)	5.61 (1.92)
Couple (sex on desk)	45	7.13 (1.36)	7.00 (1.73)	5.30 (1.92)
Couple (blonde takes off shirt)	51	6.48 (1.34)	5.83 (1.77)	6.17 (2.01)
Couple (blonde standing)	57	6.83 (1.30)	6.35 (1.40)	5.52 (2.21)
Couple (doggy style)	60	6.74 (1.54)	6.70 (1.55)	5.39 (2.04)

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Table A5

*Ratings of Valence, Arousal and Dominance: Female participants (n = 30)*

Description	Picture No.	Valence <i>Mean (SD)</i>	Arousal <i>Mean (SD)</i>	Dominance <i>Mean (SD)</i>
Cool Picture Group				
Rusted wire fence	1	4.30 (1.58)	3.93 (1.89)	6.63 (2.44)
Red insulator & wire	5	5.33 (1.81)	3.17 (1.82)	7.30 (1.82)
Thorn	8	4.17 (1.39)	4.47 (2.05)	6.53 (2.19)
Propeller	11	5.03 (1.97)	3.97 (1.67)	7.10 (2.02)
Egg, screwdriver, Pliers	14	5.37 (2.08)	3.77 (2.27)	7.07 (1.91)
Can close-up	17	5.23 (1.96)	3.20 (2.14)	7.33 (2.12)
Computer plug	20	4.67 (1.56)	3.63 (1.81)	7.27 (1.87)
Barbwire	23	4.67 (1.63)	4.40 (2.14)	6.43 (2.71)
Headphone jack	26	4.57 (1.41)	4.00 (1.98)	7.53 (2.01)
Apple with nails	29	4.43 (1.55)	5.10 (2.20)	6.30 (2.45)
Melon close-up	32	5.00 (2.33)	4.30 (2.07)	7.47 (2.34)
Broken egg	35	4.83 (1.56)	3.73 (2.16)	7.27 (2.13)
Metal loop	38	4.63 (1.33)	3.30 (1.91)	7.37 (1.75)
Aerial hinge	41	4.83 (1.58)	3.33 (1.95)	7.27 (1.96)
Computer port	44	4.73 (1.70)	3.63 (1.85)	7.37 (2.16)
Toy	47	5.30 (2.26)	3.73 (1.98)	7.63 (1.77)
Hot Defensive Picture Group				
Hung corpse	2	1.50 (0.97)	7.17 (1.80)	2.57 (1.63)
Taxi driver shotgun victim	4	1.83 (1.21)	7.00 (2.35)	3.47 (2.85)
Mutilated corpse	7	1.50 (0.90)	7.10 (2.01)	2.53 (1.61)
Dead child	10	1.60 (1.10)	7.33 (2.06)	2.53 (1.74)
Diseased child	13	1.50 (0.82)	7.50 (1.41)	3.30 (2.12)
Fingerhead	16	3.77 (2.06)	7.07 (1.55)	4.00 (2.41)
Dead man (shot in head)	19	1.57 (1.04)	7.43 (2.11)	2.17 (1.72)
Old woman (swollen neck)	22	2.40 (1.33)	6.77 (1.76)	4.00 (2.35)
Decapitated head	25	1.43 (0.97)	7.47 (2.18)	1.97 (1.19)
Shot bomber	28	1.23 (0.63)	7.77 (1.70)	2.20 (1.63)
Helicopter head	31	1.93 (1.23)	7.37 (1.99)	2.90 (2.35)
Spider thumb	34	1.97 (1.22)	7.17 (1.66)	2.73 (1.76)
Meth mouth	37	2.87 (1.66)	6.33 (1.81)	4.70 (2.58)
Woman head crush	40	1.67 (1.15)	7.00 (1.82)	2.50 (1.66)
Rape victim	43	1.50 (0.94)	6.80 (1.83)	2.80 (1.71)
Face tumor	46	1.77 (1.04)	7.80 (1.58)	2.90 (2.19)
Hot Appetitive Picture Group				
Male solo (undress)	3	7.10 (1.42)	6.47 (1.68)	6.40 (1.83)
Male solo (beach)	6	6.40 (1.81)	6.27 (1.91)	6.13 (2.39)
Male solo (waiter)	9	6.93 (1.70)	6.40 (1.99)	5.80 (2.46)
Male sole (underpants)	12	5.60 (1.87)	5.17 (2.10)	6.60 (2.09)
Male sole (behind)	15	6.50 (1.83)	6.17 (1.91)	5.73 (2.30)
Female solo (behind)	18	5.40 (1.43)	5.30 (1.73)	6.50 (2.13)
Female solo (stockings)	21	4.83 (1.82)	4.90 (2.23)	6.20 (2.27)
Female solo (blonde in towel)	24	5.53 (1.85)	5.00 (2.08)	5.83 (2.13)
Female solo (shower)	27	4.80 (1.83)	5.00 (1.80)	6.87 (2.18)
Female solo (beads)	30	4.87 (2.21)	5.07 (1.96)	6.23 (2.19)

Couple (clothed)	33	5.97 (1.63)	5.87 (1.80)	6.07 (2.23)
Couple (shower)	36	5.50 (1.80)	6.33 (1.32)	5.00 (2.13)
Couple (blonde takes off pants)	39	5.03 (1.79)	5.30 (2.14)	6.57 (2.05)
Couple (man takes off pants)	42	5.10 (1.75)	5.60 (1.73)	6.30 (1.99)
Couple (sex on desk)	45	5.23 (2.08)	6.23 (1.92)	5.30 (2.09)
Couple (blonde takes off shirt)	51	5.50 (1.85)	5.10 (1.90)	6.97 (1.83)
Couple (blonde standing)	57	5.07 (1.64)	5.23 (1.94)	5.87 (2.05)
Couple (doggy style)	60	5.30 (2.25)	6.27 (2.26)	4.33 (2.37)

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***Informed Consent to Participate in Research and  
Authorization for Collection, Use, and Disclosure  
of Cognitive Performance and Other Personal Data***

You are being asked to take part in a research study. This form provides you with information about the study and seeks your authorization for the collection, use and disclosure of your cognitive performance data, as well as other information necessary for the study. The Principal Investigator (the person in charge of this research) or a representative of the Principal Investigator will also describe this study to you and answer all of your questions. Your participation is entirely voluntary. Before you decide whether or not to take part, read the information below and ask questions about anything you do not understand. By participating in this study you will not be penalized or lose any benefits to which you would otherwise be entitled.

**1. Name of Participant ("Study Subject")**

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**2. Title of Research Study**

The effects of emotional arousal on spatial learning and memory

**3. Principal Investigator and Telephone Number(s)**

Kevin G. F. Thomas, Ph.D.  
Senior Lecturer  
Department of Psychology  
University of Cape Town  
021-650-4608

Christopher du Plooy (Ph.D. candidate)  
Department of Psychology  
University of Cape Town  
082-594-9939

**4. Source of Funding or Other Material Support**

None.

**5. What is the purpose of this research study?**

The purpose of this research is to collect information about how people find their way around different kinds of environments under different conditions of arousal.

**6. What will be done if you take part in this research study?**

In this experiment:

You will have to evaluate a series of pictures on a three-item scale.

OR

You will be administered a series of cognitive tests. These tests measure certain aspects of memory and spatial abilities, as well as general cognitive functioning. You will also be asked to complete some short questionnaires. In addition, you will be fitted with a device that measures physiological arousal, and we will take two saliva samples to acquire hormonal measures.

After the experimental session is over, you will be informed in detail about the design of the study and the research questions we hope to answer with this study. You will also have the opportunity to ask questions and to thus learn more about psychological research.

If you have any questions now or at any time during the study, you may contact the Principal Investigator listed in #3 of this form.

**7. If you choose to participate in this study, how long will you be expected to participate in the research?**

The experiment consists of one session, which should not last longer than 90 minutes. If at any time during the experiment you find any of the procedures uncomfortable, you are free to discontinue your participation without penalty.

**8. How many people are expected to participate in the research?**

100

**9. What are the possible discomforts and risks?**

There are no known risks associated with participation in this study. One possible discomfort you may experience is with the graphic content of the pictures you will see during testing. In order not to cause you too much distress, we will show you a sample of the type of pictures you will encounter in the testing session and you will have the choice to continue with the study. If after the study you still feel distressed, we will talk with you and give a referral for care if necessary.

Another possible discomfort you may encounter is slight fatigue. If you become tired during any of the paper-and-pencil or computer-based tests or questionnaires, you can take a break. You will be allowed to take breaks whenever you want to. A further possible source of discomfort is that you may find out that some of your thinking and memory abilities are worse than you expected, and this may cause some sadness or distress. Again, if this happens, we will talk with you and give a referral for care if necessary.

If you wish to discuss the information above or any discomforts you may experience, you may ask questions now or call the Principal Investigator listed on the front of this form.

**10. What are the possible benefits to you?**

You may or may not personally benefit from participating in this study. Participation in this study may, however, improve your mental test performance due to training and practice.

**11. What are the possible benefits to others?**

The information from this study may help improve our understanding of spatial abilities and other cognitive processing in adults. Additionally, this research will allow us to gather information about the performance of healthy adults on the administered tests. This research can then be applied to people who have experienced a neurological injury or other change in brain functioning, in that it may help (a) identify people who may have problems with memory and spatial processing, and (b) improve treatment of people who have experienced such injuries or changes in functioning.

**12. If you choose to take part in this research study, will it cost you anything?**

Participating in this study will not cost you anything.

**13. Will you receive compensation for taking part in this research study?**

You will receive no compensation for taking part in this study.  
Information already collected may be used.

**14. Once personal and performance information is collected, how will it be kept secret (confidential) in order to protect your privacy?**

Information collected will be stored in locked filing cabinets or in computers with security passwords. Only certain people have the right to review these research records. These people include the researchers for this study and certain University of Cape Town officials. Your research records will not be released without your permission unless required by law or a court order.

**15. What information about you may be collected, used and shared with others?**

This information gathered from you will be demographic information, records of your performance on cognitive tests. If you agree to be in this research study, it is possible that some of the information collected might be copied into a "limited data set" to be used for other research purposes. If so, the limited data set may only include information that does not directly identify you. For example, the limited data set cannot include your name, address, telephone number, ID number, or any other photographs, numbers, codes, or so forth that link you to the information in the limited data set.

**16. How will the researcher(s) benefit from your being in the study?**

In general, presenting research results helps the career of a scientist. Therefore, the Principal Investigator and others attached to this research project may benefit if the results of this study are presented at scientific meetings or in scientific journals.

## 17. Signatures

As a representative of this study, I have explained to the participant the purpose, the procedures, the possible benefits, and the risks of this research study;; and how the participant's performance and other data will be collected, used, and shared with others:

\_\_\_\_\_  
Signature of Person Obtaining Consent and Authorization

\_\_\_\_\_  
Date

You have been informed about this study's purpose, procedures, possible benefits, and risks; and how your performance and other data will be collected, used and shared with others. You have received a copy of this form. You have been given the opportunity to ask questions before you sign, and you have been told that you can ask other questions at any time.

You voluntarily agree to participate in this study. You hereby authorize the collection, use and sharing of your performance and other data. By signing this form, you are not waiving any of your legal rights.

\_\_\_\_\_  
Signature of Person Consenting and Authorizing

\_\_\_\_\_  
Date

Please indicate below if you would like to be notified of future research projects conducted by our research group:

\_\_\_\_\_ (initial) Yes, I would like to be added to your research participation pool and be notified of research projects in which I might participate in the future.

Method of contact:

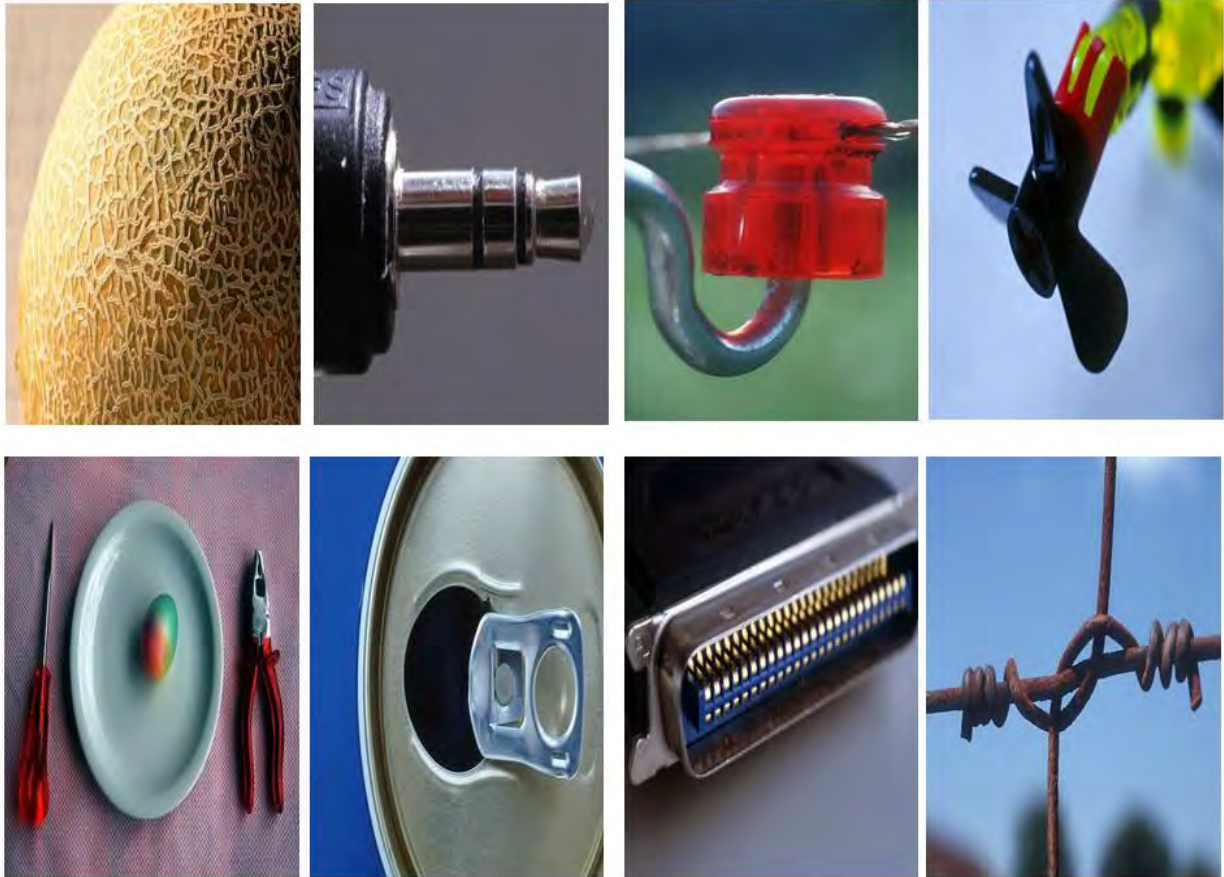
Phone number: \_\_\_\_\_

E-mail address: \_\_\_\_\_

Mailing address: \_\_\_\_\_

\_\_\_\_\_  
\_\_\_\_\_

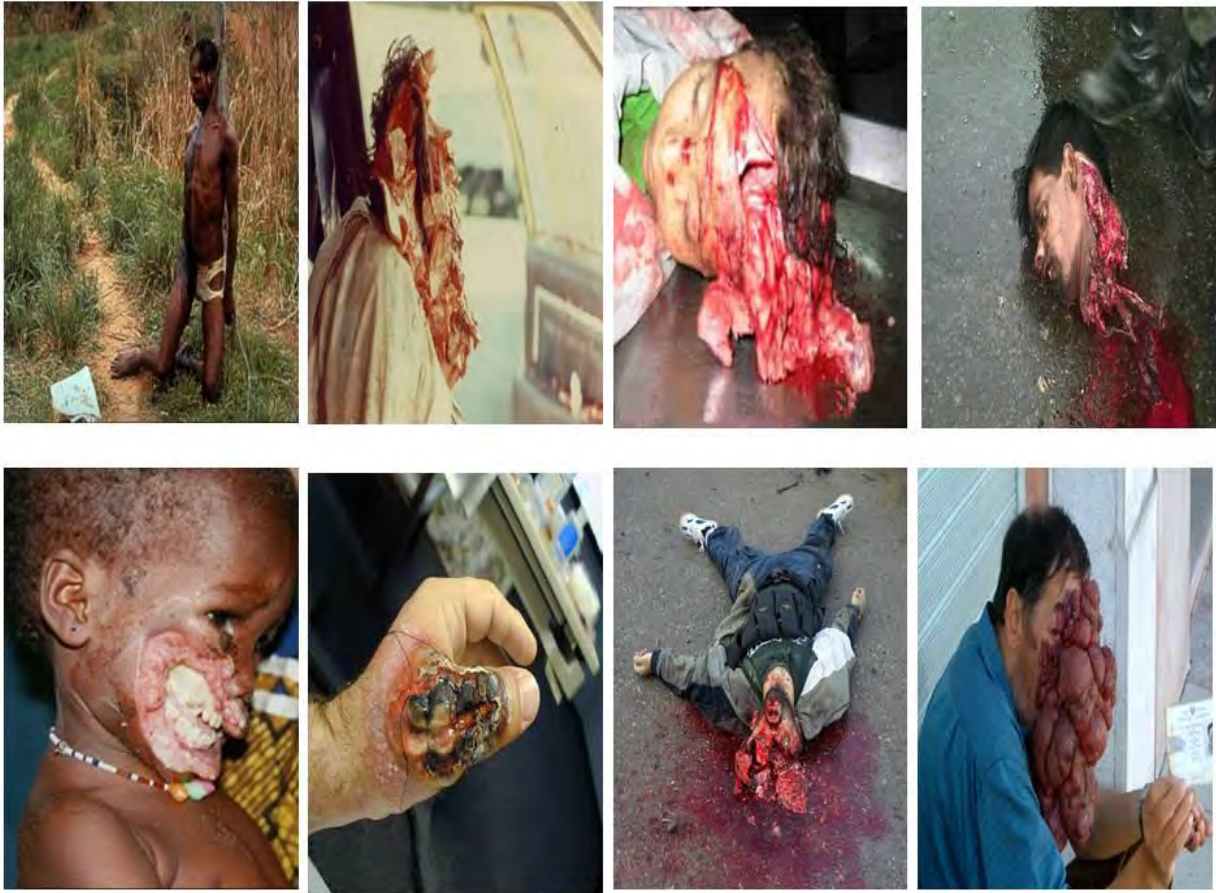
**APPENDIX B:  
Images in the Cool, Hot Appetitive and Hot Defensive CG Arena Rooms**



*Figure B1.* The eight neutral images that featured as landmarks in the Cool CG Arena room. Please note that the contents of the images in this figure might be distorted due to the uniform shape of the presented images.



*Figure B2.* The eight positively arousing images that featured as landmarks in the Hot Appetitive CG Arena room. Please note that the contents of the images in this figure might be distorted due to the uniform shape of the presented images.



*Figure B3.* The eight negatively arousing images that featured as landmarks in the Hot Defensive CG Arena room. Please note that the contents of the images in this figure might be distorted due to the uniform shape of the presented images.

**APPENDIX C:**  
**Dimensions and Parameters for the CG Arena Rooms used In Study A, Study 1 And Study 2**

**General Room Parameters:**

32 Frames per Second: 1 sec intermission length

Teleport Sound: Game 22\_SSO1.wav

Target Sound: 136.wav

Timers: Trial 120 sec Target: 20 sec Probe: 45 sec

<b>Rooms</b>	Width: 100	Depth: 100	Height: 22.5	
<b>Arena Wall</b>	Height: 5.00	Radius: 40	Number of sides: 30	
<b>User</b>	Height: 5.00	Move: 0.50	Turn Quantum: 5.00	Field of View: 90

**Cool Room Parameters and Dimensions:**

<i>North Wall</i>	<i>East Wall</i>	<i>South Wall</i>	<i>West Wall</i>
Solid fill <sup>46</sup> : Black	Solid fill: Black	Solid fill: Black	Solid fill: Black
<b>Object 1</b> Texture <sup>47</sup> : Wire-fence	<b>Object 3</b> Texture: Audio-jack	<b>Object 1</b> Texture: Egg on plate	<b>Object 3</b> Texture: Propeller
Object <sup>48</sup> : 30 x 20	Object 1: 25 x 20	Object: 30 x 20	Object: 25 x 20
Distance <sup>49</sup> : 60.5, 12, 0	Distance <sup>50</sup> : 47.5, 12, 10	Distance <sup>51</sup> : 55, 12, 0	Distance <sup>52</sup> : 47.5, 12, 0
	<b>Object 2</b> Texture: Close-up can		<b>Object 2</b> Texture: Red object
	Object: 15 x 20		Object: 15 x 20
	Distance: 22, 12, 0		Distance: 22, 12, 0
	<b>Object 1</b> Texture: Melon close-up		<b>Object 1</b> Texture: Cable
	Object: 15 x 20		Object: 15 x 20
	Distance: 72, 12, 0		Distance: 72, 12, 0

<sup>46</sup> Solid fill refers to the color of the wall

<sup>47</sup> Texture refers to the picture or landmark

<sup>48</sup> Object refers to the Width x Height of the picture

<sup>49</sup> Distance on the North Wall in relation to: West Wall, Floor, North Wall

<sup>50</sup> Distance on the East Wall in relation to: North Wall, Floor, East Wall

<sup>51</sup> Distance on the South Wall in relation to: East Wall, Floor, South Wall

<sup>52</sup> Distance on the West Wall in relation to: South Wall, Floor, West Wall

**Hot Defensive Room Parameters and Dimensions:**

<i>North Wall</i>	<i>East Wall</i>	<i>South Wall</i>	<i>West Wall</i>
Solid fill: Black	Solid fill: Black	Solid fill: Black	Solid fill: Black
<b>Object 1</b> Texture: Head	<b>Object 3</b> Texture: Cab-driver	<b>Object 1</b> Texture: Tumor	<b>Object 3</b> Texture: Head smashed
Object: 30 x 20	Object: 30 x 20	Object: 30 x 20	Object : 25 x 20
Distance: 50, 10, 00	Distance: 50, 10, 1	Distance: 55, 13.5, 0	Distance:47.5, 12, 0
	<b>Object 2</b> Texture: War corpse		<b>Object 2:</b> Texture: Deformed child
	Object: 15 x20		Object: 15 x 20
	Distance: 22, 12, 0		Distance: 22, 12, 0
	<b>Object 1</b> Texture: Dead child		<b>Object 1:</b> Texture: Infected hand
	Object: 15 x 20		Object: 15 x 20
	Distance: 72, 12, 0		Distance: 72, 12, 0

**Hot Appetitive Room Parameters and Dimensions:**

<i>North Wall</i>	<i>East Wall</i>	<i>South Wall</i>	<i>West Wall</i>
Solid fill: Black	Solid fill: Black	Solid fill: Black	Solid fill: Black
<b>Object 1</b> Texture: Shower couple	<b>Object 3</b> Texture: Female solo	<b>Object 1</b> Texture: Sex on desk couple	<b>Object 3</b> Texture: Male solo
Object: 30 x 20	Object 1: 25 x 20	Object: 30 x 20	Object: 25 x 20
Distance: 60.5, 12, 0	Distance: 47.5, 12, 1	Distance:55, 12, 0	Distance: 47.5, 12, 0
	<b>Object 2</b> Texture: Clothed couple		<b>Object 2</b> Texture: Doggy-style couple
	Object: 15 x 20		Object: 15 x 20
	Distance: 22, 12, 0		Distance: 22, 12, 0
	<b>Object 1</b> Texture: Blonde standing		<b>Object 1</b> Texture: Undress couple
	Object: 15 x 20		Object: 15 x 20
	Distance: 72, 12, 0		Distance:72, 12, 0

**APPENDIX D:**  
**Start and Target Locations in the CG Arena for Study A, Study 1 and Study 2**

Table D1

*Start and target locations for the Acquisition Phase in Study A*

Trial	Direction	Start Locations	Target Location	Target Size
Trial 1*	W	2, 50, 270 <sup>53</sup>	33.25, 33.25 <sup>54</sup>	6.5 x 6.5 <sup>55</sup>
Trial 2	S	50, 2, 00	33.25, 33.25	6.5 x 6.5
Trial 3	E	99, 50, 90	33.25, 33.25	6.5 x 6.5
Trial 4	N	50, 95, 180	33.25, 33.25	6.5 x 6.5
Trial 5	W	2, 50, 270	33.25, 33.25	6.5 x 6.5
Trial 6	S	50, 2, 00	33.25, 33.25	6.5 x 6.5
Trial 7	E	99, 50, 90	33.25, 33.25	6.5 x 6.5
Trial 8**	Random		Absent target	
Trial 9*	S	50, 2, 00	33.25, 33.25	6.5 x 6.5
Trial 10	E	99, 50, 90	33.25, 33.25	6.5 x 6.5
Trial 11	N	50, 95, 180	33.25, 33.25	6.5 x 6.5
Trial 12	W	2, 50, 270	33.25, 33.25	6.5 x 6.5
Trial 13	S	50, 2, 00	33.25, 33.25	6.5 x 6.5
Trial 14	E	99, 50, 90	33.25, 33.25	6.5 x 6.5
Trial 15	N	50, 95, 180	33.25, 33.25	6.5 x 6.5
Trial 16	Random		Absent target	
Trial 17*	E	99, 50, 90	33.25, 33.25	6.5 x 6.5
Trial 18	N	50, 95, 180	33.25, 33.25	6.5 x 6.5
Trial 19	W	2, 50, 270	33.25, 33.25	6.5 x 6.5
Trial 20	S	50, 2, 00	33.25, 33.25	6.5 x 6.5
Trial 21	E	99, 50, 90	33.25, 33.25	6.5 x 6.5
Trial 22	N	50, 95, 180	33.25, 33.25	6.5 x 6.5
Trial 23	W	2, 50, 270	33.25, 33.25	6.5 x 6.5
Trial 24	Random		Absent target	

*Note:* \* = Trial 1 in new room. \*\* = Probe Trial

<sup>53</sup> Width, Depth, Orientation

<sup>54</sup> West Wall, South Wall

<sup>55</sup> Width x Height

Table D2  
*Start and target locations for the Acquisition Phase in Study 1 and Study 2*

Trial	Direction	Start Location	Target Location	Target Size
Trial 1*	W	2, 50, 90 <sup>56</sup>	33.25, 33.25 <sup>57</sup>	6.5 x 6.5 <sup>58</sup>
Trial 2	S	50, 2, 180	33.25, 33.25	6.5 x 6.5
Trial 3	E	99, 50, 270	33.25, 33.25	6.5 x 6.5
Trial 4	N	50, 95, 0	33.25, 33.25	6.5 x 6.5
Trial 5	W	2, 50, 90	33.25, 33.25	6.5 x 6.5
Trial 6	S	50, 2, 180	33.25, 33.25	6.5 x 6.5
Trial 7*	S	50, 2, 180	33.25, 33.25	6.5 x 6.5
Trial 8	E	99, 50, 270	33.25, 33.25	6.5 x 6.5
Trial 9	N	50, 95, 0	33.25, 33.25	6.5 x 6.5
Trial 10	W	2, 50, 90	33.25, 33.25	6.5 x 6.5
Trial 11	S	50, 2, 180	33.25, 33.25	6.5 x 6.5
Trial 12	E	99, 50, 270	33.25, 33.25	6.5 x 6.5
Trial 13*	E	99, 50, 270	33.25, 33.25	6.5 x 6.5
Trial 14	N	50, 95, 0	33.25, 33.25	6.5 x 6.5
Trial 15	W	2, 50, 90	33.25, 33.25	6.5 x 6.5
Trial 16	S	50, 2, 180	33.25, 33.25	6.5 x 6.5
Trial 17	E	99, 50, 270	33.25, 33.25	6.5 x 6.5
Trial 18	N	50, 95, 0	33.25, 33.25	6.5 x 6.5

Note: \* = Trial 1 in new room

Table D3  
*Start and Target Locations for the Recall Phase in Study 1 and Study 2*

Trial	Direction	Location	Target Location	Target Size
Trial 1*	E	99, 50, 270 <sup>59</sup>	33.25, 33.25 <sup>60</sup>	6.5 x 6.5 <sup>61</sup>
Trial 2**	Random		Absent target	
Trial 3*	N	50, 95, 0	33.25, 33.25	6.5 x 6.5
Trial 4**	Random		Absent target	
Trial 5*	W	2, 50, 90	33.25, 33.25	6.5 x 6.5
Trial 6**	Random		Absent target	

Note: \* = Recall Trial in each room. \*\* = Probe Trial

<sup>56</sup> Width, Depth, Orientation

<sup>57</sup> West Wall, South Wall

<sup>58</sup> Width x Height

<sup>59</sup> Width, Depth, Orientation

<sup>60</sup> West Wall, South Wall

<sup>61</sup> Width x Height

**APPENDIX E:  
Cool, Hot Appetitive and Hot Defensive Distractor Images in the Object Recognition  
Task (ORT)**



*Figure E1.* The eight neutral images that featured as distractor images in the Cool CG Arena room Object Recognition Task. Please note that the contents of the images in this figure might be distorted due to the uniform shape of the presented images.

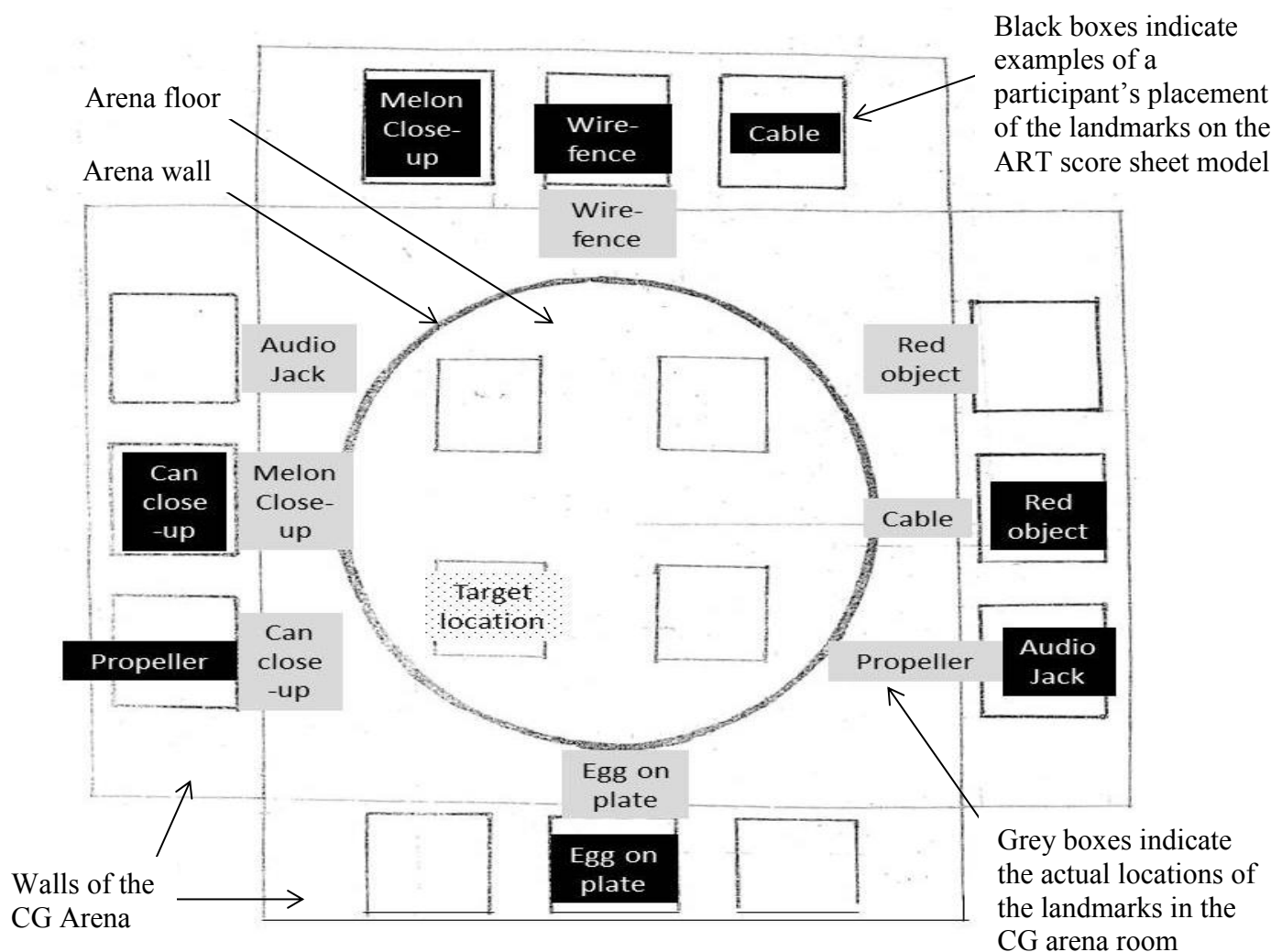


*Figure E2.* The eight positively arousing images that featured as distractor images in the Hot Appetitive CG Arena room Object Recognition Task. Please note that the contents of the images in this figure might be distorted due to the uniform shape of the presented images.



*Figure E3.* The eight negatively arousing images that featured as distractor images in the Hot Defensive CG Arena room Object Recognition Task. Please note that the contents of the images in this figure might be distorted due to the uniform shape of the presented images.

**APPENDIX F:  
Example of Arena Reconstitution Task Score Sheet**



*Figure F1.* Worked example of an Arena Reconstitution Task (ART) displacement score sheet for the Cool CG Arena room. Black boxes indicate where the participant placed the laminated pictures on the ART score sheet model (i.e., together, they indicate the participant's recollection of the spatial layout of the Cool room). Grey boxes indicate the actual locations of the landmarks (pictures) in the Cool room. The names in the black and grey boxes (e.g., *propeller*) refer to the names of the landmarks.

The following is a worked example for calculating a displacement score: Each square (i.e., each Velcro strip in the model) represents a possible location for a landmark (picture) in the CG Arena room. A displacement score for each picture (the black boxes in Figure F1) is calculated by counting the minimum number of locations (distance) it is from its actual location in the CG Arena (grey boxes in Figure F1). The total ART score is the sum of the displacement distances (in this example, the score is 16). Table F1 shows the calculation.

Table F1

*Worked Example for Calculating an ART Displacement Score from Figure F1.*

Landmark name	Displacement score
Egg on plate	0
Can close-up	1
Melon close-up	2
Audio jack	6
Wire-fence	0
Red object	1
Cable	2
Propeller	4
Total	16

**APPENDIX G:  
Informed Consent Form for Study A**

***Informed Consent to Participate in Research and  
Authorization for Collection, Use, and Disclosure  
of Cognitive Performance and Other Personal Data***

You are being asked to take part in a research study. This form provides you with information about the study and seeks your authorization for the collection, use and disclosure of your cognitive performance data, as well as other information necessary for the study. The Principal Investigator (the person in charge of this research) or a representative of the Principal Investigator will also describe this study to you and answer all of your questions. Your participation is entirely voluntary. Before you decide whether or not to take part, read the information below and ask questions about anything you do not understand. By participating in this study you will not be penalized or lose any benefits to which you would otherwise be entitled.

**18. Name of Participant ("Study Subject")**

---

**19. Title of Research Study**

The effects of arousal on visual-spatial cognition

**20. Principal Investigator and Telephone Number(s)**

Kevin G. F. Thomas, Ph.D.  
Senior Lecturer  
Department of Psychology  
University of Cape Town  
021-650-4608

Christopher du Plooy (Ph.D. candidate)  
Department of Psychology  
University of Cape Town  
082-594-9939

**21. What is the purpose of this research study?**

The purpose of this research is to collect information about how people find their way around different kinds of environments under different conditions of arousal and stress.

**22. What will be done if you take part in this research study?**

This study requires you to take part a 90 minute research study. In that session you will be required to complete a number of cognitive tasks. These tasks measure certain aspects of

memory and spatial abilities, as well as general cognitive functioning. You will also be asked to complete a short demographic questionnaire and attitude questionnaires.

After the experimental session is over, you will be informed in detail about the design of the study and the research questions we hope to answer with this study. You will also have the opportunity to ask questions and to thus learn more about psychological research.

If you have any questions now or at any time during the study, you may contact the Principal Investigator listed in #3 of this form.

This study has been approved by the Research Ethics Committee of the Faculty of Health Sciences of the University of Cape Town and you should feel free to contact Professor Marc Blockman, chairperson of the committee (021 4066496), if you have any concerns about your rights and welfare as a research participant.

**23. If you choose to participate in this study, how long will you be expected to participate in the research?**

The experiment consists of one session, which should not last longer than 90 minutes in total. If at any time during the experiment you find any of the procedures uncomfortable, you are free to discontinue your participation without penalty.

**24. How many people are expected to participate in the research?**

24

**25. What are the possible discomforts and risks?**

There are no known risks associated with participation in this study. One possible discomfort you may experience is with the graphic content of the pictures you will see during testing. In order not to cause you too much distress, we will show you a sample of the type of pictures you will encounter in the testing session and you will have the choice to continue with the study. If after the study you still feel distressed, we will talk with you and give a referral for care if necessary.

Another possible discomfort you may encounter is slight fatigue. If you become tired during any of the paper-and-pencil or computer-based tests or questionnaires, you can take a break. You will be allowed to take breaks whenever you want to. A further possible source of discomfort is that you may find out that some of your thinking and memory abilities are worse than you expected, and this may cause some sadness or distress. Again, if this happens, we will talk with you and give a referral for care if necessary.

If you wish to discuss the information above or any discomforts you may experience, you may ask questions now or call the Principal Investigator listed on the front of this form.

**26. What are the possible benefits to you?**

You may or may not personally benefit from participating in this study. Participation in this study may, however, improve your mental test performance due to training and practice.

**27. What are the possible benefits to others?**

One major benefit of this study is that scientists, and society in general, will have better understanding of the effects of arousal on cognitive functioning. This knowledge can then be applied to many different individuals and situations, including students who are taking exams, business managers who have to present to their boards, and so on.

The information from this study may also help improve our understanding of spatial abilities and other cognitive processing in adults under conditions of arousal. Additionally, this research will allow us to gather information about the performance of healthy adults on the administered tests. This research can then be applied to people who have experienced a neurological injury or other change in brain functioning, in that it may help (a) identify people who may have problems with memory and spatial processing, and (b) improve treatment of people who have experienced such injuries or changes in functioning.

**28. If you choose to take part in this research study, will it cost you anything?**

Participating in this study will not cost you anything.

**29. Will you receive compensation for taking part in this research study?**

You will receive no compensation for taking part in this study. Information already collected may be used.

**30. Once personal and performance information is collected, how will it be kept secret (confidential) in order to protect your privacy?**

Information collected will be stored in locked filing cabinets or in computers with security passwords. Only certain people have the right to review these research records. These people include the researchers for this study and certain University of Cape Town officials. Your research records will not be released without your permission unless required by law or a court order.

**31. What information about you may be collected, used and shared with others?**

This information gathered from you will be demographic information, records of your performance on cognitive tests. If you agree to be in this research study, it is possible that some of the information collected might be copied into a "limited data set" to be used for other research purposes. If so, the limited data set may only include information that does not directly identify you. For example, the limited data set cannot include your name, address, telephone number, ID number, or any other photographs, numbers, codes, or so forth that link you to the information in the limited data set.

**32. How will the researcher(s) benefit from your being in the study?**

In general, presenting research results helps the career of a scientist. Therefore, the Principal Investigator and others attached to this research project may benefit if the results of this study are presented at scientific meetings or in scientific journals. This study is being undertaken for the Principal Investigator's Doctorial degree.

### 33. Signatures

As a representative of this study, I have explained to the participant the purpose, the procedures, the possible benefits, and the risks of this research study;; and how the participant's performance and other data will be collected, used, and shared with others:

\_\_\_\_\_  
Signature of Person Obtaining Consent and Authorization

\_\_\_\_\_  
Date

You have been informed about this study's purpose, procedures, possible benefits, and risks; and how your performance and other data will be collected, used and shared with others. You have received a copy of this form. You have been given the opportunity to ask questions before you sign, and you have been told that you can ask other questions at any time.

You voluntarily agree to participate in this study. You hereby authorize the collection, use and sharing of your performance and other data. By signing this form, you are not waiving any of your legal rights.

\_\_\_\_\_  
Signature of Person Consenting and Authorizing

\_\_\_\_\_  
Date

Please indicate below if you would like to be notified of future research projects conducted by our research group:

\_\_\_\_\_ (initial) Yes, I would like to be added to your research participation pool and be notified of research projects in which I might participate in the future.

Method of contact:

Phone number: \_\_\_\_\_

E-mail address: \_\_\_\_\_

Mailing address: \_\_\_\_\_

\_\_\_\_\_

**APPENDIX H:  
Demographic Questionnaire**

1. Age: \_\_\_\_\_

2. Sex (circle one):                      Male                      Female

3. Handedness (circle one):              Left                      Right                      Ambidextrous

4. Sexual orientation (circle one):      Heterosexual      Homosexual      Bisexual              Other

4. Have you ever experienced a head injury?

(e.g., being hit on the head with an object and then losing consciousness)      YES                      NO

5. Have you ever had any neurological problems?    YES                      NO

6. Do you have any problems with dizziness or motion sickness?                              YES                      NO

7. Are you currently taking any prescription medication?                                      YES                      NO

7a. If yes, what medication(s)?  
\_\_\_\_\_

8. Do you have any allergies?    YES                      NO

8a. If yes, what allergies?  
\_\_\_\_\_

8. How often do you use a computer?

(Please tick the corresponding box)

Never	A few times a year	About once a month	About once a week	Every day
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9. How much experience have you had with computers?

(Please tick the corresponding box)

None at all	A few hours total	20 -50 hours	50 -100 hours	Several hundred hours
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10. Have you had any experience with (visited) the web sites [www.rotten.com](http://www.rotten.com) or [www.charonboat.com](http://www.charonboat.com)?                      YES                      NO

10a. If yes, how many times have you visited the websites and how long ago?  
\_\_\_\_\_

11. Education (highest degree or grade completed): \_\_\_\_\_

*ONLY COMPLETE QUESTIONS 12-14 IF YOU HAVE COMPLETED MATRIC*

12. Did you matriculate from a public high school or a private high school (circle one)?

Public

Private

**13. What is the name of the school from which you matriculated?**

\_\_\_\_\_

**14. Did you attend any other high school before matriculation?**

YES

NO

13a. If yes, what is the name of that school?

\_\_\_\_\_

13b. Until which grade did you attend that school?

\_\_\_\_\_

**APPENDIX I:  
Informed Consent Form for Study B and Study 1**

***Informed Consent to Participate in Research and  
Authorization for Collection, Use, and Disclosure  
of Cognitive Performance and Other Personal Data***

You are being asked to take part in a research study. This form provides you with information about the study and seeks your authorization for the collection, use and disclosure of your cognitive performance data, as well as other information necessary for the study. The Principal Investigator (the person in charge of this research) or a representative of the Principal Investigator will also describe this study to you and answer all of your questions. Your participation is entirely voluntary. Before you decide whether or not to take part, read the information below and ask questions about anything you do not understand. By participating in this study you will not be penalized or lose any benefits to which you would otherwise be entitled.

**34. Name of Participant ("Study Subject")**

---

**35. Title of Research Study**

The effects of stress on visual-spatial cognition

**36. Principal Investigator and Telephone Number(s)**

Kevin G. F. Thomas, Ph.D.  
Senior Lecturer  
Department of Psychology  
University of Cape Town  
021-650-4608

Christopher du Plooy (Ph.D. candidate)  
Department of Psychology  
University of Cape Town  
082-594-9939

**37. What is the purpose of this research study?**

The purpose of this research is to collect information about how people find their way around different kinds of environments under different conditions of arousal and stress.

**38. What will be done if you take part in this research study?**

This study requires you to take part in two research sessions on two consecutive days. On the first day you will be required to complete a number of memory-based tasks. On the second day you may be required to complete a 10-minute presentation and submerge your arm in water, which will be followed by another series of memory based tasks.

Throughout the study your levels of stress will be assessed through the collection of heart rate measurements and saliva samples with the aid of a cotton swab. These saliva samples will be used to analyse levels of salivary cortisol.

After the experimental session is over, you will be informed in detail about the design of the study and the research questions we hope to answer with this study. You will also have the opportunity to ask questions and to thus learn more about psychological research.

If you have any questions now or at any time during the study, you may contact the Principal Investigator listed in #3 of this form.

This study has been approved by the Research Ethics Committee of the Faculty of Health Sciences of the University of Cape Town and you should feel free to contact Professor Marc Blockman, chairperson of the committee (021 4066496), if you have any concerns about your rights and welfare as a research participant.

**39. If you choose to participate in this study, how long will you be expected to participate in the research?**

The experiment consists of two sessions, which should not last longer than 180 minutes in total. If at any time during the experiment you find any of the procedures uncomfortable, you are free to discontinue your participation without penalty.

**40. How many people are expected to participate in the research?**

60

**41. What are the possible discomforts and risks?**

There are no known risks associated with participation in this study. One possible discomfort you may experience is with the graphic content of the pictures you will see during testing. In order not to cause you too much distress, we will show you a sample of the type of pictures you will encounter in the testing session and you will have the choice to continue with the study. If after the study you still feel distressed, we will talk with you and give a referral for care if necessary.

Another possible discomfort you may encounter is slight fatigue. If you become tired during any of the paper-and-pencil or computer-based tests or questionnaires, you can take a break. You will be allowed to take breaks whenever you want to. A further possible source of discomfort is that you may find out that some of your thinking and memory abilities are worse than you expected, and this may cause some sadness or distress. Again, if this happens, we will talk with you and give a referral for care if necessary.

A final possible discomfort is that if you are one of the participants selected to complete the 20-minute presentation, you may be placed in a mildly stressful situation involving public speaking

If you wish to discuss the information above or any discomforts you may experience, you may ask questions now or call the Principal Investigator listed on the front of this form.

**42. What are the possible benefits to you?**

You may or may not personally benefit from participating in this study. Participation in

this study may, however, improve your mental test performance due to training and practice.

**43. What are the possible benefits to others?**

One major benefit of this study is that scientists, and society in general, will have better understanding of the effects of stress on cognitive functioning. This knowledge can then be applied to many different individuals and situations, including students who are taking exams, business managers who have to present to their boards, and so on.

The information from this study may also help improve our understanding of spatial abilities and other cognitive processing in adults under conditions of stress. Additionally, this research will allow us to gather information about the performance of healthy adults on the administered tests. This research can then be applied to people who have experienced a neurological injury or other change in brain functioning, in that it may help (a) identify people who may have problems with memory and spatial processing, and (b) improve treatment of people who have experienced such injuries or changes in functioning.

**44. If you choose to take part in this research study, will it cost you anything?**

Participating in this study will not cost you anything.

**45. Will you receive compensation for taking part in this research study?**

You will receive no compensation for taking part in this study. Information already collected may be used.

**46. Once personal and performance information is collected, how will it be kept secret (confidential) in order to protect your privacy?**

Information collected will be stored in locked filing cabinets or in computers with security passwords. Only certain people have the right to review these research records. These people include the researchers for this study and certain University of Cape Town officials. Your research records will not be released without your permission unless required by law or a court order.

**47. What information about you may be collected, used and shared with others?**

This information gathered from you will be demographic information, records of your performance on cognitive tests. If you agree to be in this research study, it is possible that some of the information collected might be copied into a "limited data set" to be used for other research purposes. If so, the limited data set may only include information that does not directly identify you. For example, the limited data set cannot include your name, address, telephone number, ID number, or any other photographs, numbers, codes, or so forth that link you to the information in the limited data set.

**48. How will the researcher(s) benefit from your being in the study?**

In general, presenting research results helps the career of a scientist. Therefore, the Principal Investigator and others attached to this research project may benefit if the

results of this study are presented at scientific meetings or in scientific journals. This study is being undertaken for the Principal Investigator's Doctorial degree.

#### 49. Signatures

As a representative of this study, I have explained to the participant the purpose, the procedures, the possible benefits, and the risks of this research study;; and how the participant's performance and other data will be collected, used, and shared with others:

\_\_\_\_\_  
Signature of Person Obtaining Consent and Authorization

\_\_\_\_\_  
Date

You have been informed about this study's purpose, procedures, possible benefits, and risks; and how your performance and other data will be collected, used and shared with others. You have received a copy of this form. You have been given the opportunity to ask questions before you sign, and you have been told that you can ask other questions at any time.

You voluntarily agree to participate in this study. You hereby authorize the collection, use and sharing of your performance and other data. By signing this form, you are not waiving any of your legal rights.

\_\_\_\_\_  
Signature of Person Consenting and Authorizing

\_\_\_\_\_  
Date

Please indicate below if you would like to be notified of future research projects conducted by our research group:

\_\_\_\_\_ (initial) Yes, I would like to be added to your research participation pool and be notified of research projects in which I might participate in the future.

Method of contact:

Phone number: \_\_\_\_\_

E-mail address: \_\_\_\_\_

Mailing address: \_\_\_\_\_

\_\_\_\_\_

\_\_\_\_\_

**APPENDIX J:  
Cortisol Responders versus Control Participant Analyses**

**Cortisol Responders vs. Control Participants**

The following series of analyses compared those participants in the Stress groups who could be classified as cortisol responders (that is, the participants who showed a 2 nmol/l increase, relative to their individual baseline, in cortisol levels either 5 or 35 minutes after the manipulation ended) to control participants. The final size of the responder groups were 11 in the Stress Male group, and 9 in the Stress Female group. The subset of analyses presented below examined group differences in cortisol response, CG Arena performance, and VPA performance. Statistical analysis of the responder groups versus the control groups mirrors the whole-group analysis presented above.

**Physiological stress measures: Salivary cortisol.** Due to violation of the assumptions of normality and sphericity, it was necessary for to perform transformations on the data. Log transformations corrected for the violation of normality. In order to account for the violation of sphericity,  $\chi^2(2) = 9.78, p = .008$ , it was necessary to use a Greenhouse-Geisser degrees of freedom correction ( $\epsilon = 0.84$ ). Table J1 shows the descriptive statistics for the cortisol levels for the Stress responder and Control groups.

Table J1

*Descriptive Statistics for cortisol levels across the testing session on Day 2 (N = 50)*

Measure	Stress Group Responders		Control Group	
	Males (n = 11)	Females (n = 9)	Males (n = 15)	Females (n = 15)
CORT <sub>B</sub>	3.93 (1.39)	3.44 (1.71)	4.14 (3.07)	4.96 (7.14)
CORT <sub>1</sub>	7.46 (1.95)	6.53 (3.50)	3.48 (2.36)	3.33 (3.38)
CORT <sub>2</sub>	9.84 (7.04)	10.14 (9.09)	2.43 (1.72)	2.50 (2.30)

*Note.* Mean scores are provided with standard deviations in parentheses. Cortisol levels are measured in nanomoles per litre (nmol/l). Where cortisol levels for a participant were indicated to be < 0.50 nmol/l, 0.45 nmol/l was used as an estimate.

Repeated measures analysis showed significant main effects of Time,  $F(1.67, 76.96) = 3.93, p = .030, \eta_p^2 = .08$ , and Experimental Condition,  $F(1, 46) = 19.66, p < .001, \eta_p^2 = .30$ , in the absence of a significant main effect of Sex,  $p = .395$ . In addition, a statistically significant interaction effect was present between the Experimental Condition and the Time,  $F(1.67, 76.96) = 30.45, p < .001, \eta_p^2 = .40$ , in the absence of an Experimental Condition x Sex interaction,  $p = .718$ , Sex x Time interaction,  $p = .461$ , or Experimental Condition x Sex

x Time interaction,  $p = .985$ . Therefore, these results showed that the Experimental Condition (Stress group,  $M = 6.90$ ,  $SD = 4.01$ ; Control group,  $M = 3.47$ ,  $SD = 3.43$ ) and the Time both had an effect on participants' cortisol levels. Figure J1 shows the fluctuations in cortisol levels for each Experimental Condition across Time.

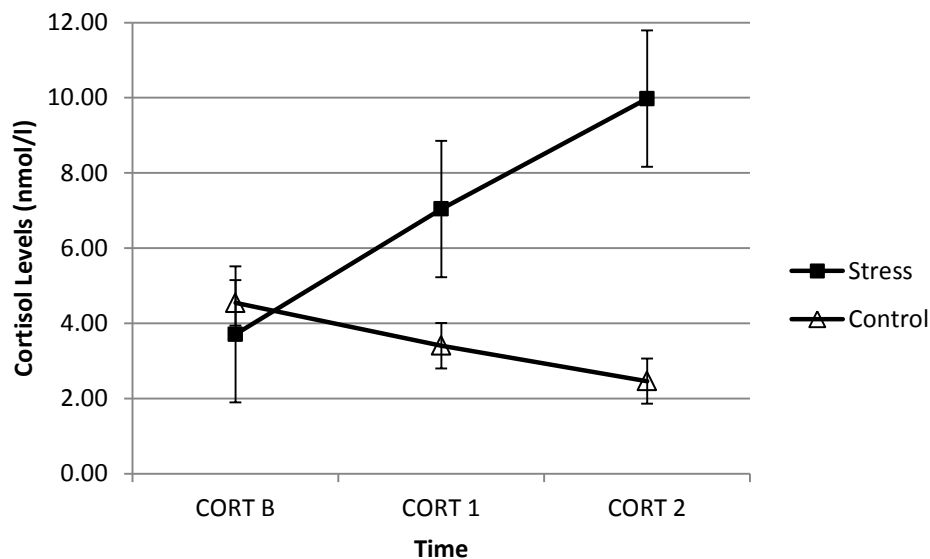


Figure J1. Changes in cortisol levels on Day 2 for the combined Stress-responders and combined Control groups. Error bars indicate standard error of means.

Within-group analysis across time points showed that the Stress group displayed a consistent significant increase in cortisol levels from CORT<sub>B</sub> ( $M = 3.70$ ,  $SD = 1.52$ ) to CORT<sub>1</sub> ( $M = 7.04$ ,  $SD = 2.72$ ;  $F(1, 19) = 19.35$ ,  $p = .001$ ,  $\eta_p^2 = .51$ ), and a further increase by CORT<sub>2</sub> ( $M = 9.98$ ,  $SD = 7.80$ ;  $F(1, 19) = 37.54$ ,  $p = .001$ ,  $\eta_p^2 = .66$ ) in comparison to CORT<sub>B</sub>. The Control group showed the same pattern described in the whole-group analysis above. That is, a non-significant decrease in cortisol levels from CORT<sub>B</sub> ( $M = 4.55$ ,  $SD = 5.42$ ) to CORT<sub>1</sub> levels ( $M = 3.41$ ,  $SD = 2.87$ ;  $p = .126$ ). By the CORT<sub>2</sub> ( $M = 2.46$ ,  $SD = 1.99$ ), participants' cortisol levels in the control group were significantly lower than at CORT<sub>B</sub>,  $F(1, 28) = 74.50$ ,  $p < .001$ ,  $\eta_p^2 = .73$ . Thus, analysis of cortisol responders showed the same within-group pattern that was seen in the whole-group analysis, except that the responder groups showed a sharper increase in cortisol. The greater increase seen in the select responder group is indicative of a more successful experimental manipulation, as the intended result of the experimental manipulation was to increase cortisol levels in the Stress groups.

Between-group analysis showed that at  $CORT_B$  there were no significant main effects for the Experimental Condition,  $p = .501$ , or for Sex,  $p = .899$ , nor was there a significant interaction between the Experimental Condition and Sex,  $p = .608$ . Thus, there were no significant differences in cortisol levels between the groups at the start of the testing session.

Analysis of  $CORT_1$  data showed a significant main effect of Experimental Condition,  $F(1, 50) = 18.87, p < .001, \eta_p^2 = .29$ , in the absence of a main effect of Sex,  $p = .516$ , or an Experimental Condition x Sex interaction effect,  $p = .637$ . At this Time, the Stress groups ( $M = 7.04, SD = 2.72$ ) showed significantly raised cortisol levels in comparison to the Control groups ( $M = 3.41, SD = 2.87$ ).

Analysis of cortisol levels at  $CORT_2$  showed a significant main effect of Experimental Condition,  $F(1, 50) = 24.45, p < .001, \eta_p^2 = .35$ , in the absence of a significant main effect of Sex,  $p = .906$ , and Experimental Condition x Sex interaction,  $p = .939$ . The participants in the Stress groups ( $M = 9.97, SD = 7.80$ ) continued to show significantly higher cortisol than the control groups ( $M = 2.46, SD = 1.99$ ).

Thus, analysis of the responder group's cortisol levels showed the same pattern that was seen in the whole-group analysis. The only differences seen in the sub-group analysis was a greater cortisol increase due to the exclusion of the cortisol non-responders.

**CG Arena. Acquisition phase: Trial 6.** Table J2 provides descriptive statistics for each group on Trial 6 in each of the CG Arena rooms.

Table J2

*Descriptive Statistics for each of the Experimental Groups' path length on Trial 6 in each CG Arena room (N = 50)*

Room	Stress Group Responders		Control Group	
	Males (n = 11)	Females (n = 9)	Males (n = 15)	Females (n = 15)
Cool room T6	18.27 (21.90)	73.63 (60.89)	112.06 (226.14)	44.58 (50.14)
Hot Appetitive room T6	47.12 (95.61)	136.98 (162.92)	86.72 (157.00)	55.77 (97.99)
Hot Defensive room T6	27.43 (38.13)	91.97 (155.84)	96.62 (144.27)	51.70 (52.51)

*Note.* Data are  $M$  ( $SD$ ) for deviation from optimal path length.

Due to violation of the assumption of sphericity,  $\chi^2(2) = 7.68, p = .021$ , it was once again necessary to use a Greenhouse-Geisser degrees of freedom correction ( $\epsilon = 0.86$ ). Analysis of performance across the three CG rooms did not show significant main effects of Room,  $p = .516$ , Experimental Condition,  $p = .758$  or Sex,  $p = .694$ . There was, however, a significant

interaction effect seen between Experimental Condition x Sex ,  $F(1, 56) = 4.43$ ,  $p = .041$ ,  $\eta_p^2 = .09$ , in the absence of a Room x Experimental Condition interaction,  $p = .330$ , a Room x Sex interaction,  $p = .595$ , or Room x Experimental Condition x Sex interaction,  $p = .969$ .

Thus, analysis of Trial 6 across the three CG Arena rooms revealed a significant interaction effect between Experimental Condition and Sex. Across the three rooms, the Stress Male group showed the shortest average path length ( $M = 30.94$ ,  $SD = 51.88$ ), followed by the Control Female group ( $M = 50.69$ ,  $SD = 66.88$ ), the Control Male group ( $M = 98.47$ ,  $SD = 175.80$ ) and lastly the Stress Female group ( $M = 100.86$ ,  $SD = 129.55$ ). Despite a significant interaction effect being reported in the repeated measures ANOVA model, results of Bonferroni pairwise comparisons failed to detect a significant difference between groups (all  $p$  values  $< .500$ ).

A final set of analyses aimed to determine whether all groups learned the location of the target with relatively equal efficiency in each of three CG Arena rooms. Analysis of the Cool room did not show significant main effects of Experimental Condition,  $p = .343$  or Sex,  $p = .819$ . There was no significant interaction effect between Experimental Condition and Sex,  $p = .084$ .

Analysis of the Hot Appetitive room did not show significant main effects of Experimental Condition,  $p = .639$ , or Sex,  $p = .483$ , nor was there a significant interaction effect between Experimental Condition and Sex,  $p = .090$ .

Lastly, analysis of the Hot Defensive room again failed to show significant main effects of Experimental Condition,  $p = .639$ , or Sex,  $p = .750$ , nor was there a significant interaction effect between Experimental Condition and Sex,  $p = .081$ .

Thus, no significant between-group differences were seen on any of the three CG arena trials. These results indicate that all the groups learned the location of the target with relatively equal efficiency in each of three CG Arena rooms. However, due to the significant between-group interaction reported in the repeated measures ANOVA model, analysis of the recall trials should be viewed with caution due to the chance of some groups (i.e., the Stress Male and Control Female) showing superior performance in the acquisition trials.

**Recall Phase: Recall trial.** Table J3 provides descriptive statistics for the experimental groups on the recall trial in each of the CG Arena rooms. Figure J2 depicts the data graphically. Repeated measures analysis did not yield significant main effects of Room,  $p = .908$ , Experimental Condition,  $p = .232$ , or Sex,  $p = .790$ , nor were significant interaction effects seen between Room x Sex,  $p = .114$ , Room x Experimental Condition,  $p = .397$ ,

Experimental Condition x Sex,  $p = .774$ , or Room x Experimental Condition x Sex,  $p = .463$ . Thus, analysis did not show any significant differences within- or between-groups on the recall trial across the CG Arena rooms.

The second set of analyses aimed to examine between-group differences in each of three CG Arena rooms more closely. Analysis of the Cool room revealed a violation of the assumption of homogeneity of variances. However, due to ANOVA being a robust test, I continued with analysis. Analysis of the Cool room did not show significant main effects of Experimental Condition,  $F(1, 47) = 3.93$ ,  $p = .053$ ,  $\eta_p^2 = .08$ , or Sex,  $p = .312$ , nor was there a significant interaction effect between the Experimental Condition and Sex,  $p = .452$ . Interestingly, the main effect of Experimental Condition bordered on the significance level. Despite not being statistically significant, the stress groups ( $M = 130.93$ ,  $SD = 152.97$ ) showed a shorter path length than the Control groups ( $M = 261.73$ ,  $SD = 249.16$ ) in this particular CG Arena room.

Table J3

*Descriptive Statistics for each of the Experimental Groups' recall performance in/of the CG Arena rooms (N = 50)*

	Stress Group Responders		Control Group	
	Males ( $n = 11$ )	Females ( $n = 9$ )	Males ( $n = 15$ )	Females ( $n = 15$ )
<b>Cool Room</b>				
Recall Trial	83.63 (114.61)	194.00 (180.75)	253.57 (258.80)	269.89 (247.95)
Dwell Time	62.56 (20.05)	64.37 (17.61)	65.32 (25.96)	70.19 (24.35)
ART Score	23.42 (6.04)	21.22 (7.34)	20.47 (7.72)	22.53 (5.82)
ORT $d'$ score	1.27 (0.71)	1.17 (0.80)	1.33 (0.65)	1.15 (0.88)
<b>Hot Appetitive Room</b>				
Recall Trial	152.94 (248.25)	261.63 (275.87)	218.89 (231.44)	244.36 (225.76)
Dwell time	62.28 (17.17)	60.76 (21.20)	61.90 (20.20)	61.80 (23.37)
ART Score	16.67 (4.79)	20.89 (6.19)	22.40 (4.98)	22.80 (5.93)
ORT $d'$ score	1.56 (0.85)	1.60 (0.75)	1.90 (0.62)	1.67 (0.70)
<b>Hot Defensive Room</b>				
Recall Trial	273.65 (311.50)	129.24 (80.34)	239.13 (266.62)	194.48 (233.28)
Dwell Time	58.91 (29.34)	69.57 (18.63)	59.32 (21.41)	62.99 (29.53)
ART Score	20.57 (5.48)	21.57 (5.61)	21.80 (5.00)	17.73 (7.23)
ORT $d'$ score	1.70 (0.81)	1.67 (0.62)	2.02 (0.61)	1.75 (0.69)

*Note.* Data are  $M$  ( $SD$ ). The variable Recall Trial represents deviations from the optimal path length.

Analysis of the Hot Appetitive room did not show significant main effects of Experimental Condition,  $p = .727$ , or Sex,  $p = .338$ , nor was there a significant interaction effect between the Experimental Condition and Sex,  $p = .551$ .

Lastly, analysis of the Hot Defensive room again revealed a violation of the assumption of homogeneity of variances. However, due to ANOVA being a robust test, I continued with analysis. Analysis again failed to show significant main effects of Experimental Condition,  $p = .829$ , or Sex,  $p = .188$ . Nor was there a significant interaction effect between the Experimental Condition and Sex,  $p = .485$ .

Thus, no significant between-group differences were seen in any of the three CG arena rooms on the recall trial on day 2. However, the Stress responder groups showed a shorter path length in the Cool room that was almost statistically significant. Other than this near significant result, the findings on the recall trial for the responder analyses echoed those seen in the whole-group analysis.

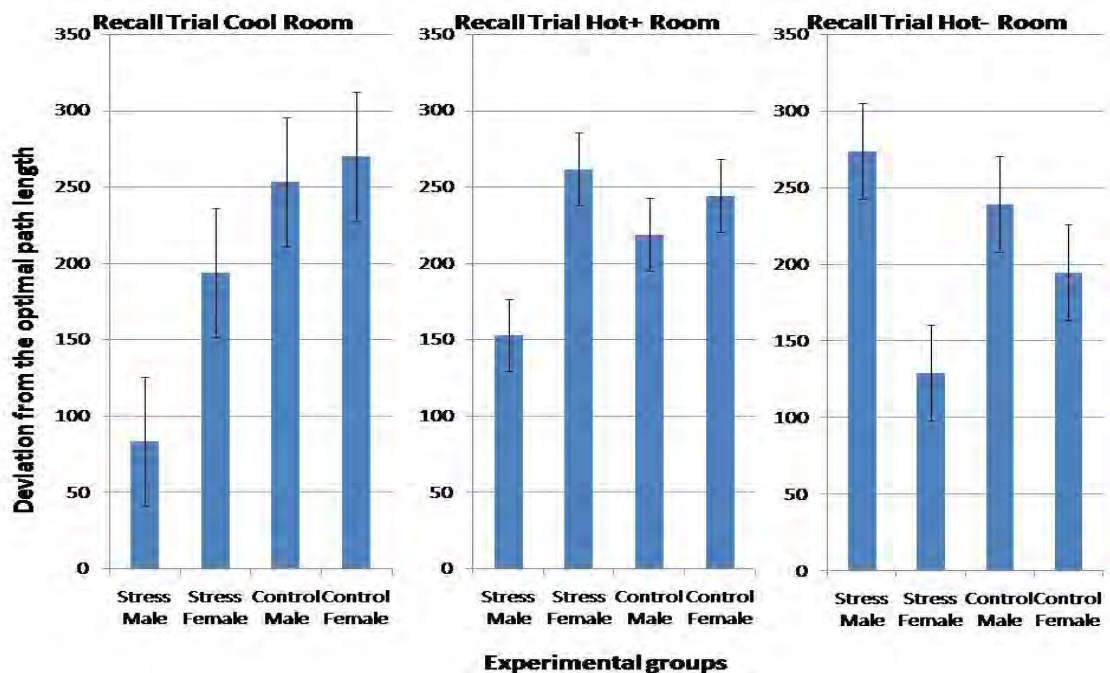


Figure J2. Mean deviation from the optimal path length for the recall trial in the Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. Error bars indicate standard error of means.

**Dwell time.** Table J3 provides descriptive statistics for each group on the Probe Trial in each of the CG Arena rooms, while Figure J3 displays this data graphically.

Repeated measures analysis did not show significant main effects of Room,  $p = .628$ , Experimental Condition,  $p = .910$ , or Sex,  $p = .478$ . No significant interaction effects were seen between Room x Experimental Condition,  $p = .628$ , Room x Sex,  $p = .639$ , Experimental Condition x Sex,  $p = .927$ , or Room x Experimental Condition x Sex,  $p = .815$ . Thus, analysis did not show any significant differences within- or between-groups on dwell time across the CG Arena rooms.

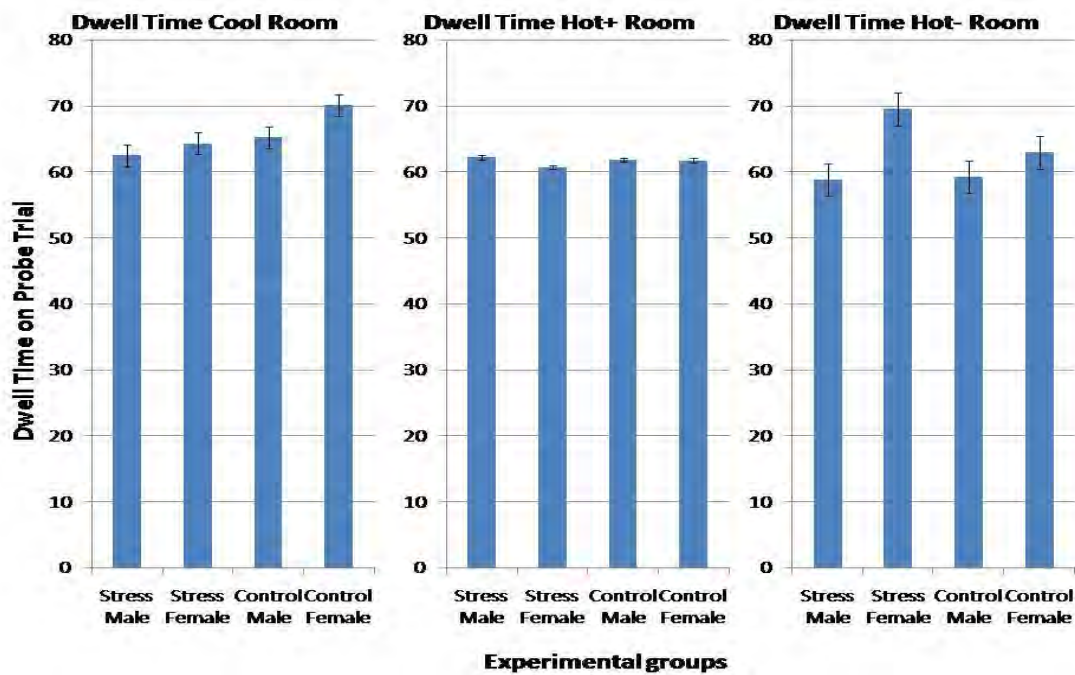


Figure J3. Mean deviation from the optimal path length for dwell time in Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. Error bars indicate standard error of means.

In order to look more closely at the between-group differences of dwell time, each of the three CG Arena rooms was analysed separately. Analysis of the Cool room did not show significant main effects of Experimental Condition,  $p = .516$ , or Sex,  $p = .613$ . There was no significant interaction effect between the Experimental Condition and Sex,  $p = .816$ .

Analysis of the Hot Appetitive room did not show significant main effects of Experimental Condition,  $p = .956$ , or Sex,  $p = .891$ , nor was there a significant Experimental Condition x Sex,  $p = .906$  interaction.

Consistent with the previous two rooms, analysis of the Hot Defensive room did not show significant main effects of Experimental Condition,  $p = .676$ , or Sex,  $p = .334$ , nor was there a significant interaction effect between Experimental Condition and Sex,  $p = .637$ .

Thus, no significant between-group differences for dwell time were seen in any of the three CG arena room on Day 2. These results are consistent with those from the whole-group analysis.

**ORT Score.** Table J3 provides descriptive statistics for each group ORT  $d'$  Prime scores for each of the CG Arena rooms, while Figure J4 depicts this data graphically.

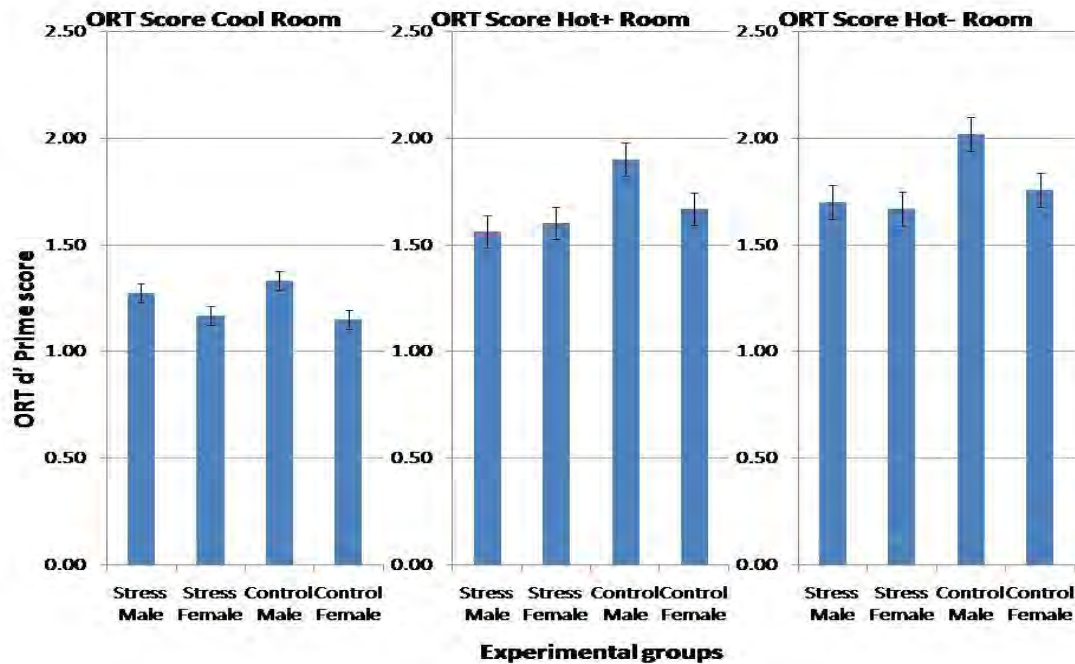


Figure J4. Mean ORT  $d'$  Prime scores for the Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. Error bars indicate standard error of means.

Repeated measures analysis showed a significant main effect of Room  $F(2, 94) = 15.19, p < .001, \eta_p^2 = .25$ , in the absence of significant main effects of Experimental Condition,  $p = .402$ , or Sex,  $p = .466$ . There were no significant interaction effects between Room x Experimental Condition,  $p = .611$ , Room x Sex,  $p = .963$ , Experimental Condition x Sex,  $p = .599$ , or Room x Experimental Condition x Sex,  $p = .890$ . Therefore, the only significant within-group effect observed was for Room. The participants, regardless of Experimental Condition and Sex, showed better recognition for the pictures in the Hot Defensive room ( $M = 1.80, SD = 0.60$ ) than the Hot Appetitive room ( $M = 1.70, SD = 0.72$ ) and showed poorest recognition for the Cool room ( $M = 1.24, SD = 0.75$ ). The results from the Bonferroni pairwise comparisons showed a significant difference between ORT scores for the Hot Defensive room and the Cool room,  $p < .001$ , and a significant difference between the

Hot Appetitive room and the Cool room,  $p = .001$ . However, there was no significant difference between the Hot Defensive room and the Hot Appetitive room,  $p = .794$ .

A second set of analyses was conducted in order to determine whether between-group differences were apparent for recognition of the pictures in each of the CG Arena rooms. Analysis of the Cool room did not show significant main effects of Experimental Condition,  $p = .933$ , or Sex,  $p = .516$ . There was no significant interaction effect between Experimental Condition and Sex,  $p = .863$ .

Analysis of the Hot Appetitive room did not show significant main effects of Experimental Condition,  $p = .334$ , or Sex,  $p = .650$ . There was no significant interaction effect between Experimental Condition and Sex,  $p = .515$ .

Analysis of the Hot Defensive room did not show significant main effects of Experimental Condition,  $p = .306$ , or Sex,  $p = .457$ . There also was not a significant interaction effect between Experimental Condition and Sex,  $p = .560$ .

Therefore, analyses of ORT scores indicate that all the participants' recognition of the pictures, which were in the CG Arena, were better for the arousing stimuli, irrespective of the valence of the picture. No between-group differences were seen for recognition of the pictures in any of the rooms. These results are again consistent with the whole-group analysis.

**ART Score.** Table J3 provides descriptive statistics for each groups' ART displacement scores for each of the CG Arena rooms, while Figure J5 depicts these data graphically.

Repeated measures analysis did not show significant main effects of Room,  $p = .453$ , Experimental Condition,  $p = .591$ , or Sex,  $p = .837$ . There were no significant interaction effects seen between Room x Experimental Condition,  $p = .074$ , Room x Sex,  $p = .279$ , Experimental Condition x Sex,  $p = .462$ , or Room x Experimental Condition x Sex,  $p = .135$ . Thus, analysis did not show any significant differences within- or between-groups for ART scores across the CG Arena rooms.

Between-group analysis of the Cool room ART scores did not show significant main effects of Experimental Condition,  $p = .673$ , or Sex,  $p = .974$ . There was no significant interaction effect between Experimental Condition and Sex,  $p = .276$ .

Analysis of the Hot Appetitive room showed a significant main effect of Experimental Condition,  $F(1, 47) = 5.99$ ,  $p = .018$ ,  $\eta_p^2 = .11$ , in the absence of a main effect of Sex,  $p = .146$ , or a significant interaction effect between Experimental Condition and Sex,  $p = .227$ .

As with the whole-group analysis, the Stress group ( $M = 18.46$ ,  $SD = 5.71$ ) showed a better recall of the spatial layout of the pictures in the Hot Appetitive room than the Control group ( $M = 22.60$ ,  $SD = 5.39$ ) did. However, the effect size for the difference was greater for the responder group ( $\eta_p^2 = .11$ ) in comparison to whole-group ( $\eta_p^2 = .08$ ).

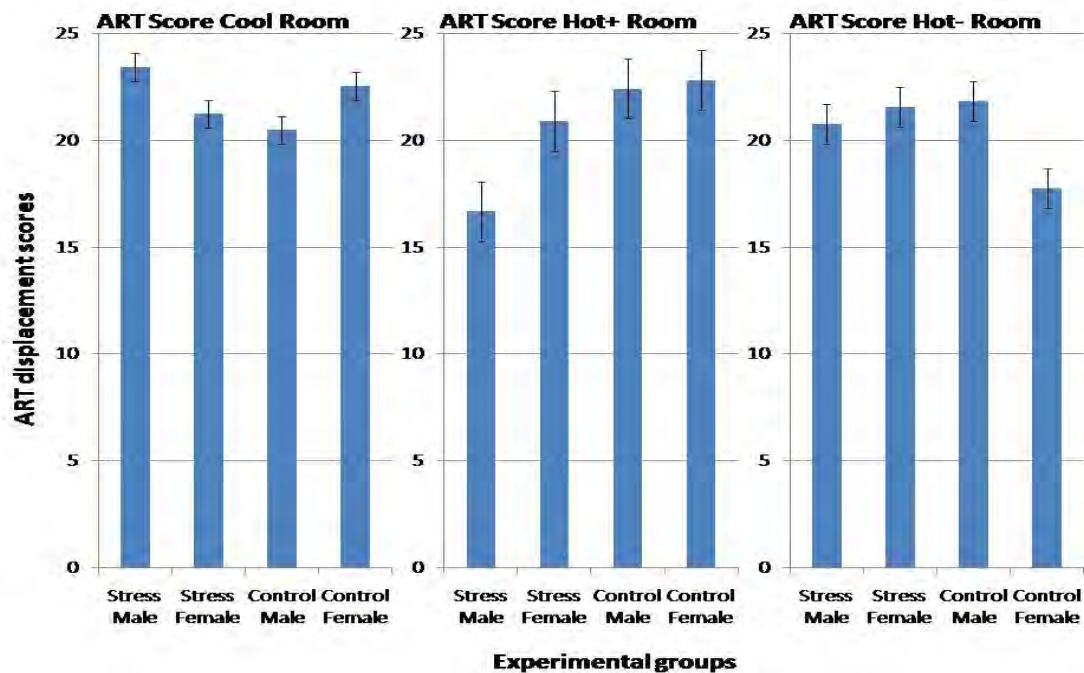


Figure J5. Mean ART displacement scores for the Cool, Hot Appetitive (Hot+) and Hot Defensive (Hot-) CG Arena rooms. Error bars indicate standard error of means.

Finally, analysis of Hot Defensive room failed to show significant main effects of Experimental Condition,  $p = .420$ , or Sex,  $p = .343$ , nor was there a significant interaction effect between Experimental Condition and Sex,  $p = .159$ .

Therefore, between-group analysis only showed a significant difference for the Hot Appetitive room. As was the case with the whole-group analysis, the stress group showed better memory for the spatial layout of the Hot Appetitive room than the control group did. However, the effect size for this difference was greater for the responder group relative to the whole group.

**Verbal Paired Associates Test. Day 1: Immediate recall trials.** Descriptive data for all VPA trials can be seen in Table J4, while Figure J6 displays these data graphically.

Repeated measures analysis showed a significant main effect of Trial,  $F(1, 47) = 166.23$ ,  $p < .001$ ,  $\eta_p^2 = .78$ , in the absence of significant main effects of Experimental Condition,  $p = .557$ , and Sex,  $p = .933$ . There were no significant interaction effects between

Trial x Experimental Condition,  $p = .146$ , Trial x Sex,  $p = .384$ , Experimental Condition x Sex,  $p = .357$ , or Trial x Experimental Condition x Sex,  $p = .492$ .

Table J4

*Descriptive Statistics for each of the Experimental Groups each trial of the VPA (N = 50)*

Measure	Stress Group Responders		Control Group	
	Males ( $n = 11$ )	Females ( $n = 9$ )	Males ( $n = 15$ )	Females ( $n = 15$ )
VPA recall trial 1	7.67 (2.87)	6.89 (4.01)	6.13 (2.85)	6.53 (3.50)
VPA recall trial 2	11.00 (2.52)	10.33 (4.18)	9.93 (2.94)	11.27 (2.71)
VPA delayed recall trial	8.08 (2.11)	9.00 (3.46)	7.53 (2.36)	8.80 (3.30)
Percentage retained	73.30 (8.10)	90.00 (14.74)	76.85 (15.48)	76.68 (17.21)

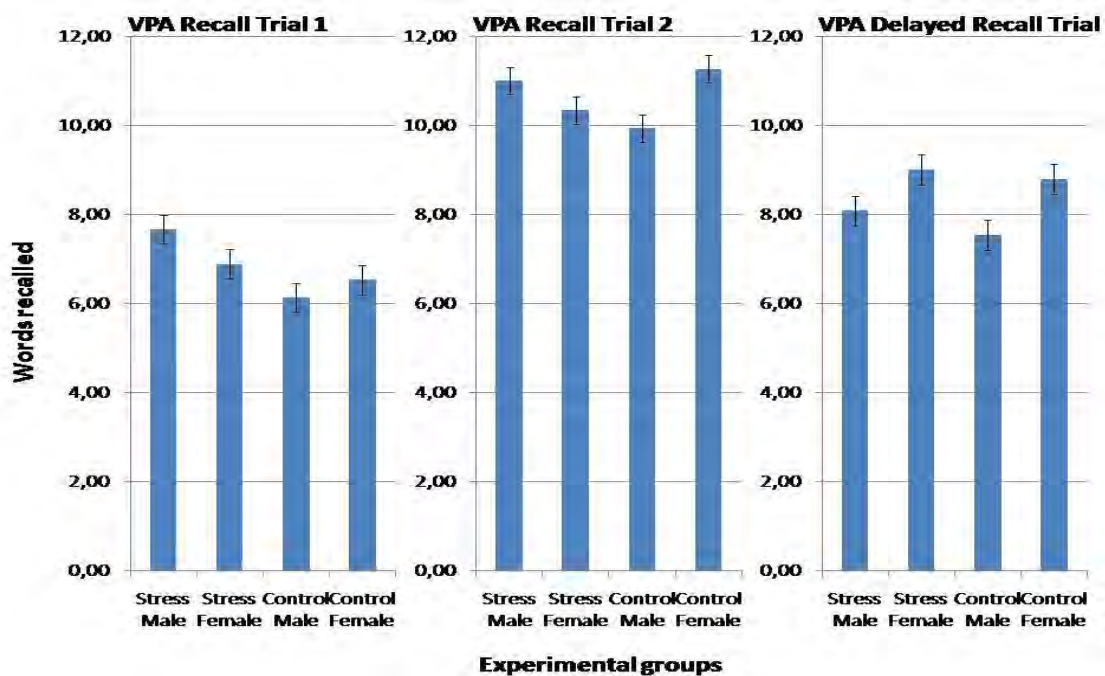


Figure J6. Mean number of words recalled on each trial of the Verbal Paired Associate Test (VPA). Error bars indicate standard error of means.

Comparisons across the first two trials showed that all participants, regardless of experimental group, recalled significantly more words on the second recall trial (see Table J4). This result indicates that the second presentation of the word list benefitted all participants' encoding of the word pairs.

A second set of analyses were conducted in order to determine whether between-group differences were apparent after each recall trial. Analysis of the first recall trial did not

show significant main effects of Experimental Condition,  $p = .319$ , or Sex,  $p = .814$ . There was no significant interaction effect between Experimental Condition and Sex,  $p = .533$ .

Analysis of the second recall trial showed a similar pattern to that which was seen with the first recall trial. That is, an absence of significant main effects of Experimental Condition,  $p = .939$ , or Sex,  $p = .703$ , as well as a non-significant interaction effect between Experimental Condition and Sex,  $p = .256$ .

Thus, consistent with the whole-group analysis, analysis of the first two acquisition trials showed that all participants, regardless of experiential group, benefitted from the second presentation of the word list, as all groups recalled a greater number of words after the second trial. There were, however, no other within- or between-group differences seen on either recall trial, indicating that no group showed a distinct advantage or disadvantage in recalling words from the list.

**Day 2: Delayed recall trial.** Repeated measures analysis showed a significant main effect of Trial,  $F(1, 47) = 91.50$ ,  $p < .001$ ,  $\eta_p^2 = .66$ , in the absence of significant main effects of Experimental Condition,  $p = .785$ , and Sex,  $p = .381$ . There were no significant interaction effects between Trial x Experimental Condition,  $p = .521$ , Trial and Sex,  $p = .118$ , Experimental Condition x Sex,  $p = .469$ , or Trial x Experimental Condition x Sex,  $p = .090$ .

Comparisons across the final two recall trials showed a significant effect of Trial, indicating that all participants, regardless of experimental group or sex, recalled significantly less words on the final recall trial. Analysis showed that the 24-hour delay in recall of the word list resulted in all participants recalling fewer words in comparison to Trial 2.

The second set of analyses were conducted in order to determine whether between-group differences were apparent on Trial 3. Analysis did not show significant main effects of Experimental Condition,  $p = .645$ , or Sex,  $p = .183$ , nor was there a significant interaction effect between Experimental Condition and Sex,  $p = .830$ .

Thus, analysis of Trial 3 revealed that all groups showed a decrease in the number of words recalled compared to Trial 2. This result indicates that the 24-hour delay in recall had a detrimental effect on all groups' recall memory of the word list, regardless of experimental condition or Sex. No other within- or between-group differences were seen across the final two trials, and no between-group differences were seen on Trial 3.

*Percentage retained.* Descriptive data for percentage of words retained can be seen in Table J4, while Figure J7 displays these data graphically.

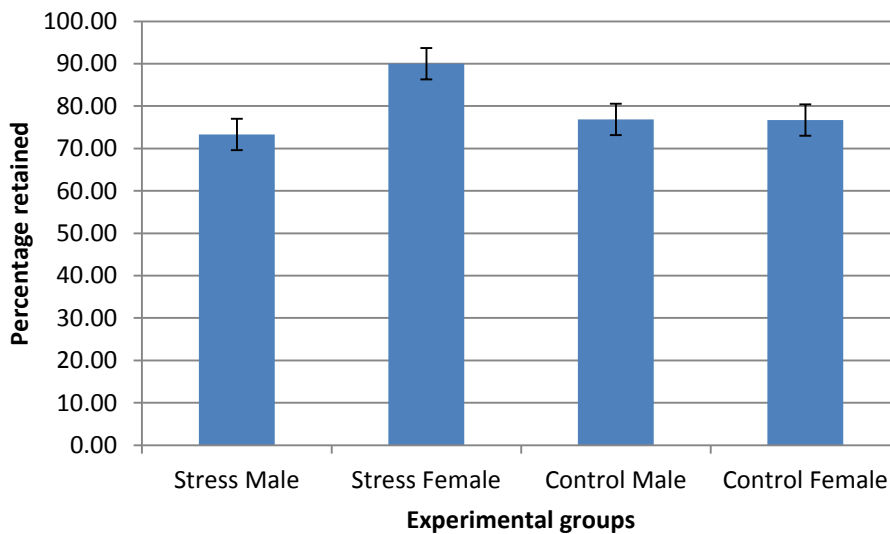


Figure J7. Mean percentage retained scores for Trial 3 of Verbal Paired Associate Test (VPA). Error bars indicate standard error of means.

Analysis showed a significant interaction effect between Experimental Condition and Sex,  $F(1, 47) = 4.09$ ,  $p = .049$ ,  $\eta_p^2 = .08$ , in the absence of a significant main effect of Sex,  $p = .053$ ,  $\eta_p^2 = .07$ , or Experimental Condition,  $p = .247$ . Thus, comparison of percentage retained scores only showed a significant interaction effect between Experimental Condition and Sex. As can be seen in Table J4, the Stress Female groups showed the highest percentage of retained scores and the Stress Male group showed the lowest. The results of Bonferroni post hoc comparisons failed to show the same pattern as was seen in the whole-group analysis, as there was no significant difference between the Stress Female group and the Stress Male group,  $p = .075$ . There was also no significant differences between the Stress Female group and the Control Male group,  $p = .225$ , or between the Stress Female and the Control Female group,  $p = .221$ . It must also be noted that no significant difference was seen between the Control Female and Stress Male groups, or between the Stress Male and Control Male groups, both  $p$ 's = 1.000.

However, further contrast analysis revealed a significant difference between the Stress Female group and the other three groups,  $t(47) = 2.69$ ,  $p = .010$ ,  $d = 0.78$ , in the absence of significant difference between the Stress Male group and the other three groups,  $p = .110$ ,  $d = 0.48$ . In addition, contrast analysis showed a significant difference between the Stress Female and Control Female groups,  $t(47) = 2.17$ ,  $p = .035$ ,  $d = 0.63$ , in the absence of a significant difference between the Stress Male and Control Female groups,  $p = .532$ .

Therefore, analysis of the percentage-retained scores failed to show the significant sex difference that was seen in the whole-group analysis. However, the significant difference that was seen between the Stress Male and Stress Female groups seemed to have strengthened (signified by a slightly greater effect size;  $d = 0.78$ ) in comparison to the whole-group analysis ( $d = 0.72$ ). This increased difference seems to be driven by the higher percentage retained scores of the Stress Female group in the responder analysis. In addition, the Stress Female group recalled significantly more words in comparison to the other three groups and in comparison to the Control Female group. This result provides further evidence that stress, and importantly increased cortisol response, may have had a positive effect on the recall of word pairs for participants in the Stress Female group.

**APPENDIX K:  
Informed Consent Form for Study 2**

*Informed Consent to Participate in Research and  
Authorization for Collection, Use, and Disclosure  
of Cognitive Performance and Other Personal Data*

You are being asked to take part in a research study. This form provides you with information about the study and seeks your authorization for the collection, use and disclosure of your cognitive performance data, as well as other information necessary for the study. The Principal Investigator (the person in charge of this research) or a representative of the Principal Investigator will also describe this study to you and answer all of your questions. Your participation is entirely voluntary. Before you decide whether or not to take part, read the information below and ask questions about anything you do not understand. By participating in this study you will not be penalized or lose any benefits to which you would otherwise be entitled.

**50. Name of Participant ("Study Subject")**

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**51. Title of Research Study**

The effects of stress on visual-spatial cognition

**52. Principal Investigator and Telephone Number(s)**

Kevin G. F. Thomas, Ph.D.  
Senior Lecturer  
Department of Psychology  
University of Cape Town  
021-650-4608

Christopher du Plooy (Ph.D. candidate)  
Department of Psychology  
University of Cape Town  
082-594-9939

**53. What is the purpose of this research study?**

The purpose of this research is to collect information about how people find their way around different kinds of environments under different conditions of arousal and stress.

**54. What will be done if you take part in this research study?**

This study will require you to participate in two sessions on two consecutive days. On your first session, you will be administered a series of cognitive tests. These tests measure certain aspects of memory and spatial abilities, as well as general cognitive functioning. You will also be asked to complete some short questionnaires.

On your second session, you will randomly be assigned to either the experimental group or the control group but neither you nor the researcher attending to you will know your status. You will consequently either receive 25 mg of oral cortisone (Prednisone) or a placebo (sugar tablet). You will then be administered a series of cognitive tests and we will take two saliva samples to acquire hormonal measures. The dose of cortisone used in this study is considered a safe, low dose. A once-off intake of oral cortisone is not known to have any negative long-term effects and will wash out of your system within 18 hours of administration. However, you may experience slight dizziness, tiredness or headache as a temporary side effect of the dose.

After the experimental session is over, you will be informed in detail about the design of the study and the research questions we hope to answer with this study. You will also have the opportunity to ask questions and to thus learn more about psychological research.

If you have any questions now or at any time during the study, you may contact the Principal Investigator listed in #3 of this form.

This study has been approved by the Research Ethics Committee of the Faculty of Health Sciences of the University of Cape Town and you should feel free to contact Professor Marc Blockman, chairperson of the committee (021 4066496), if you have any concerns about your rights and welfare as a research participant.

If you have questions about this trial you should first discuss them with your doctor or the ethics committee (contact details as provided on this form). After you have consulted your doctor or the ethics committee and if they have not provided you with answers to your satisfaction, you should write to the South African Medicines Control Council (MCC) at:

The Registrar  
SA Medicines Control Council  
Department of Health  
Private Bag X828  
PRETORIA  
0001  
Fax: (012) 312 3105  
e-mail: labusa@health.goc.za

**55. If you choose to participate in this study, how long will you be expected to participate in the research?**

The experiment consists of two sessions, which should not last longer than 180 minutes in total. If at any time during the experiment you find any of the procedures uncomfortable, you are free to discontinue your participation without penalty. Please note that you will not receive SRPP credits if you do not attend the second session.

**56. How many people are expected to participate in the research?**

**57. What are the possible discomforts and risks?**

There are only low or minimal risks associated with your participation in this study. One possible discomfort you may experience is with the graphic content of the pictures you will see during testing. In order not to cause you too much distress, we will show you a sample of the type of pictures you will encounter in the testing session and you will have the choice to continue with the study. If after the study you still feel distressed, we will talk with you and give a referral for care if necessary.

Another possible discomfort you may encounter is slight fatigue. If you become tired during any of the paper-and-pencil or computer-based tests or questionnaires, you can take a break. You will be allowed to take breaks whenever you want to. A further possible source of discomfort is that you may find out that some of your thinking and memory abilities are worse than you expected, and this may cause some sadness or distress. Again, if this happens, we will talk with you and give a referral for care if necessary.

If you wish to discuss the information above or any discomforts you may experience, you may ask questions now or call the Principal Investigator listed on the front of this form.

**58. What are the possible benefits to you?**

You may or may not personally benefit from participating in this study. Participation in this study may, however, improve your mental test performance due to training and practice.

**59. What are the possible benefits to others?**

One major benefit of this study is that scientists, and society in general, will have better understanding of the effects of stress on cognitive functioning. This knowledge can then be applied to many different individuals and situations, including students who are taking exams, business managers who have to present to their boards, and so on.

The information from this study may also help improve our understanding of spatial abilities and other cognitive processing in adults under conditions of stress. Additionally, this research will allow us to gather information about the performance of healthy adults on the administered tests. This research can then be applied to people who have experienced a neurological injury or other change in brain functioning, in that it may help (a) identify people who may have problems with memory and spatial processing, and (b) improve treatment of people who have experienced such injuries or changes in functioning.

**60. If you choose to take part in this research study, will it cost you anything?**

Participating in this study will not cost you anything.

**61. Will you receive compensation for taking part in this research study?**

You will receive no compensation for taking part in this study. Information already collected may be used.

**62. Once personal and performance information is collected, how will it be kept secret (confidential) in order to protect your privacy?**

Information collected will be stored in locked filing cabinets or in computers with security passwords. Only certain people have the right to review these research records. These people include the researchers for this study and certain University of Cape Town officials. Your research records will not be released without your permission unless required by law or a court order.

**63. What information about you may be collected, used and shared with others?**

This information gathered from you will be demographic information, records of your performance on cognitive tests. If you agree to be in this research study, it is possible that some of the information collected might be copied into a “limited data set” to be used for other research purposes. If so, the limited data set may only include information that does not directly identify you. For example, the limited data set cannot include your name, address, telephone number, ID number, or any other photographs, numbers, codes, or so forth that link you to the information in the limited data set.

**64. How will the researcher(s) benefit from your being in the study?**

In general, presenting research results helps the career of a scientist. Therefore, the Principal Investigator and others attached to this research project may benefit if the results of this study are presented at scientific meetings or in scientific journals. This study is being undertaken for the Principal Investigator’s Doctorial degree.

**65. Signatures**

As a representative of this study, I have explained to the participant the purpose, the procedures, the possible benefits, and the risks of this research study;; and how the participant’s performance and other data will be collected, used, and shared with others:

\_\_\_\_\_  
Signature of Person Obtaining Consent and Authorization

\_\_\_\_\_  
Date

You have been informed about this study’s purpose, procedures, possible benefits, and risks; and how your performance and other data will be collected, used and shared with others. You have received a copy of this form. You have been given the opportunity to ask questions before you sign, and you have been told that you can ask other questions at any time.

You voluntarily agree to participate in this study. You hereby authorize the collection, use and sharing of your performance and other data. By signing this form, you are not waiving any of your legal rights.

\_\_\_\_\_  
Signature of Person Consenting and Authorizing

\_\_\_\_\_  
Date

Method of contact:

Phone number: \_\_\_\_\_

E-mail address: \_\_\_\_\_