Testosterone administration increases the size of womens' peripersonal space: An embodied index of social dominance

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COMPULSORY DECLARATION

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Abstract

Peripersonal space (PPS) is the space immediately surrounding the body, encoded by a specific frontoparietal network of multimodal neurons. Stimuli in PPS are represented in a body-part centred manner in terms of possibilities for action, and PPS representations function to facilitate defensive and/or approaching responses to stimuli. The size of PPS differs between individuals and contexts, with physical and psychological factors having a determining role on the size of PPS. For these reasons, PPS has been conceptualised as 'the space of the bodily self'. In this study we investigated whether the dominance enhancing effects of testosterone may reflect in changes of the representation of PPS. We conducted a double-blind placebo-controlled within-subjects testosterone administration study in women (N=19) where participants performed a multisensory-integration task (a commonly used measure of PPS) while facing an unknown confederate. Results indicated that in comparison to placebo, the administration of testosterone caused a significant enlargement of participants' PPS, suggesting that testosterone caused participants to reflexively appropriate a larger space as their own. This effect was particularly pronounced in participants with higher trait anxiety, converging with other research which has shown that the dominance enhancing effects of testosterone administration can be particularly effective in anxious individuals. Results also indicated a multisensory-facilitation effect around the confederate, which was constant across testosterone and placebo conditions – confirming that the effect of testosterone was *self*-specific. The PPS boundary gradient was unchanged by testosterone. These findings suggest that an enlarged PPS may provide an embodied index of social dominance. Further, because PPS representations function to support approaching and/or defensive responses to the environment, an enlarged PPS due to raised testosterone may support the enhanced approach behaviour and vigilance to threat known to be conferred by testosterone.

Keywords: peripersonal space, testosterone, embodied cognition, multisensory integration, social dominance

Testosterone administration increases the size of womens' peripersonal space: An embodied index of social dominance

Peripersonal space (PPS) is the space immediately surrounding the body. PPS is encoded by a frontoparietal neuronal network, and it has been conceptualised as a sensory-motor interface between body and environment (Làdavas, di Pellegrino, Farnè, & Zeloni, 1998). Because our environmental interactions are more immediate and potentially threatening in PPS, the mapping of PPS primes the rapid execution of approach and defence behaviours within this space (Avenanti, Annela, & Serino, 2012; Brozzoli, Cardinali, Pavani, & Farnè, 2010; di Pellegrino & Làdavas, 2015; Graziano & Cooke, 2006). Recently PPS has become a subject of great interest within the broader framework of embodied cognition (Ambrosini, Scorolli, Borghi, & Costantini, 2012; Gallese & Sinigaglia, 2011). This framework holds that mental processes are situated in the experiences of the body, providing a novel means with which to explore and understand mental phenomena. In this view, cognitive representations are immersed in the sensorimotor functions and experiences of the body and these bodily experiences therefore ground and facilitate prediction, judgement, behaviour and all 'higher order' cognition (Barsalou, 2008; Gallagher & Aguda, 2015; Wilson, 2002). Supporting this view, PPS has been described as the 'space of the bodily self' (Noel, Pfeiffer, Blanke, & Serino, 2015; Serino, 2019) as stimuli in PPS are perceived in a body-part centred reference frame and the dimensions of this space are critically determined by motor abilities or constraints (Canzoneri, Marzolla, Amoresano, Verni, & Serino, 2013) and psychological traits (Iachini, Ruggiero, Ruotolo, di Cola, & Senese, 2015; Sambo & Iannetti, 2013).

Following in the footsteps of others who have linked PPS representations to a range of higher order mental processes (Iachini et al., 2015; Pellencin, Paladino, Herbelin, & Serino, 2018; Teneggi, Canzoneri, di Pellegrino, & Serino, 2013), we sought to explore whether the dominance-enhancing effects of testosterone would reflect at the level of

multisensory information processing in PPS. At the neurochemical level, dominance, which is understood as behaviour motivated by the pursuit and maintenance of social status and control, is closely linked to the activity of the steroid hormone testosterone (Eisenegger, Haushofer, & Fehr, 2011). Testosterone is known to enhance dominance related behaviour by increasing motivational social approach and threat vigilance and by reducing fear (Terburg & van Honk, 2013). Given that both testosterone and PPS support approach behaviour and vigilance to threat, in this study we investigated whether the dominance enhancing effects of testosterone would reflect in changes in the representation of PPS – conferring a larger 'self space' in which to rapidly act. An unconscious enlargement of PPS may provide an embodied index of dominance as well as give further insight into the mechanisms by which testosterone facilitates social dominance.

Testosterone and dominance motivated social approach

Testosterone plays an important role in regulating social-motivational behaviour. A growing body of research has demonstrated a wide range of behavioural outcomes associated with testosterone, both pro- and anti- social in nature, that have been appraised as part of a general repertoire of motivated dominance behaviour (Eisenegger et al., 2011) -- that is, behaviour in the service of gaining or maintaining social status[1]. Indeed, in both sexes throughout mammalian species, testosterone has been linked to the pursuit and defence of territory, social dominance and social status (Eisenegger et al., 2011; Mazur & Booth, 1998; van der Westhuizen & Solms, 2015).

Terburg and van Honk (2013) refer to the dominance motivated behaviour associated with testosterone in mammals as *approach* behaviour, where approach/avoidance is equated with dominance/submission. In this framework, which we will draw on terminologically, avoidance is linked to submission and is seen in threat avoidance and punishment sensitivity,

[1] For a comprehensive multi-level review of how testosterone promotes dominance and high social status, see Terburg and van Honk (2013).

whereas approach refers to appetitive motivation, or taking action in the pursuit of something desirable (Terburg & van Honk, 2013). Although dominance motivated approach behaviour often manifests in social aggression (Montoya, Terburg, Bos, & Honk, 2012), in humans aggression is not always the appropriate route to maintain or achieve status, and thus testosterone can also promote prosocial behaviour, depending on the social context (Dreher et al., 2016; van Honk, Montoya, Bos, van Vugt, & Terburg, 2012). In this way, testosterone promotes social approach behaviours *adaptively* in ways contextually suited to facilitating or defending dominance. Indeed, while many studies have linked basal testosterone levels to a range of dominance indices (suggesting 'trait' findings) (Grant & France, 2001; Sherman et al., 2016; Vermeersch, T'sjoen, Kaufman, Vincke, & Van Houtte, 2010), others have linked context-specific testosterone levels to dominance-enhancing outcomes (i.e., 'state' findings) (Carré & Archer, 2018; Casto & Edwards, 2016b; Geniole & Carré, 2018; Stanton & Schultheiss, 2009). The latter suggest that baseline testosterone levels alone may not explain behavioural phenotypes, but that the effects of testosterone are sometimes only observed in certain eliciting contexts – namely, those where the individual needs to safeguard their position in the social hierarchy. This understanding accords with the social challenge hypothesis which proposes that when confronted with a situation that is threatening to social status, testosterone levels temporarily increase in order to facilitate dominance motivated social approach[2] (Archer, 2006; Mazur & Booth, 1998).

In the service of an approach orientation, testosterone confers high motivational drive, increases vigilance to threat and reduces fear (Eisenegger et al., 2011). Both animal and human testosterone administration studies[3] have shown that testosterone modulates the dopamine system, in particular the striatum, affording increased motivational drive and

[2] For instance, testosterone levels have been found to rise in anticipation of sporting competition (Bateup, Booth, Shirtcliff, & Granger, 2002; Casto & Edwards, 2016b; Salvador, Suay, Martinez–Sanchis, Simon, & Brain, 1999; Suay et al., 1999) and remain higher in competition winners in comparison to competition losers (Carré & Archer, 2018; Mazur & Booth, 1998). See Archer (Archer, 2006) for a review of the evidence supporting the challenge hypothesis in animals and humans.

[3] All testosterone administration studies reviewed in this paper are single-dose administration studies.

reward-processing (Aarts & van Honk, 2009; Hermans et al., 2010). Accordingly, hypogonadal human patients have been found to be apathetic and low in motivational drive (Bhasin et al., 2010).

In addition to increased motivational drive, attending to rather than avoiding threatening stimuli is crucial for approach-preparatory responses. Testosterone administration has been shown to increase amygdala activity in response to approaching angry faces (Radke et al., 2015) and both men and women high in basal testosterone have been found to selectively attend to angry faces – where angry facial expressions represent an important threat signal in competitive dyadic encounters (van Honk et al., 1999; Wirth & Schultheiss, 2007). Moreover, van Honk and colleagues (2001) found that testosterone administration increased cardiac accelerative responses to angry facial expressions in healthy women, suggesting potential proneness to aggression and preparation for fight. Corroborating this, Enter, Spinhoven, and Roelofs (2014) showed that testosterone administration to healthy women reduced avoidance responses to angry faces in comparison to placebo, producing a relative increase in approach to a threatening stimulus. Likewise, Wagels and colleagues (Wagels, Radke, Goerlich, Habel, & Votinov, 2017) found that testosterone administration caused a significant reduction in the amount of personal distance from aggressive individuals that healthy male participants preferred, implying enhanced social aggression and diminished fear in the face of threat.

Indeed, the approach orientation conferred by testosterone is facilitated by testosterone's profound fear-reduction effect. Testosterone is known to down-regulate the hypothalamic-pituitary-adrenal axis, which is strongly involved in stress and fear (Terburg & van Honk, 2013). After exogenous administration, testosterone was found to reduce fear-potentiated startle, but not baseline startle (Hermans, Putman, Baas, Koppeschaar, & van Honk, 2006) and to reduce unconscious fear in healthy women (van Honk, Peper, & Schutter, 2005). In the latter study, only unconscious fear was reduced by testosterone administration

and not consciously experienced anxiety. This is consistent with the understanding that the influence of testosterone on social behavior is unconscious and automatic (Terburg & van Honk, 2013) and points to the utility of an embodied approach for understanding some of the mechanisms supporting social dominance.

Pointing to the context-specificity of the effects of testosterone, Enter and colleagues' (Enter, Terburg, Harrewijn, Spinhoven, & Roelofs, 2016) testosterone administration study on gaze avoidance in healthy women and women with Social Anxiety Disorder (SAD) revealed that the dominance enhancing effects of testosterone administration can be particularly pronounced in socially anxious individuals. Using eye-tracking to monitor spontaneous gaze behaviour toward angry, happy and neutral facial expressions, these authors found that testosterone enhanced fixations to the eye-region of confederates more effectively in participants with SAD than in healthy controls. This finding was further supported by Terburg and colleagues (Terburg et al., 2016) who found that socially anxious womens' gaze aversion to subliminal angry faces was completely abolished after a single administration of testosterone. Gaze avoidance (as well as its partner, gaze aversion – see Terburg, Aarts, and van Honk (2012)) is a key and persistent characteristic of SAD, impairing adequate social interactions and signaling social submissiveness (Enter et al., 2016; Terburg et al., 2016). Unsurprisingly, anxious individuals often have reduced testosterone levels (Giltay et al., 2012).

In summary, there is a wealth of evidence demonstrating that testosterone increases dominance-motivated social approach by reducing fear, enhancing motivation and bolstering vigilance to threats to social status. However, research in this field has only recently started to examine the ways in which sensory-motor processes support these mechanisms (Moeini-Jazani, Knoeferle, de Molière, Gatti, & Warlop, 2017; Obhi, Swiderski, & Brubacher, 2012). For instance, a recent study by our group (van der Westhuizen, Moore, Solms, & van Honk, 2017) found that the administration of a single dose of testosterone increased the implicit

feeling of motor control over goal-directed actions – a phenomenon termed the sense of agency. This finding was taken to suggest that feelings of control and power may manifest firstly in the body, providing an embodied grounding to higher order phenomenology. In support of this proposal, other research has shown that simply making a fist caused male participants to perceive themselves as more assertive and esteemed (Schubert & Koole, 2009), and that competition winners who posed in expansive 'high-power' postures had a rise (albeit small) in testosterone in comparison to competition winners who posed in neutral or constricted 'low-power' poses (Smith & Apicella, 2017). Cook and Beaven (2013) have suggested that variations in testosterone may index motivation and readiness to perform in elite competitive athletes. Together, these studies suggest a strong link between bodily processes that prime the individual for action and enhanced appraisals of social power. Thus, in keeping with the embodied cognition framework, these studies suggest that higher order experiences related to social dominance are influenced by bodily processes that facilitate the ability to take action. What remains unanswered is whether the known increase in dominance-motivated social approach associated with testosterone would reflect in representational changes of the actionable space immediately surrounding the body, that is, in representations of peripersonal space.

Peripersonal space

It is now widely accepted that the brain has a specific neuronal system dedicated to representing the space immediately surrounding the body, termed peripersonal space (PPS). PPS was first discovered in monkeys when electrophysiological studies detailed a network of neurons that respond to multiple sensory modalities and which are dedicated to representing PPS in the ventral intraparietal area, the ventral premotor cortex, dorsal parietal cortex (area 7) and the putamen (Fogassi et al., 1992; Graziano & Gross, 1993; Graziano & Yap, 1994; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997). Typically the neurons in this network have a body-part centred tactile receptive field which overlaps spatially with a visual and/or auditory

receptive field, the depth of which extends between 5 and 100cm from the body (Serino, Noel, et al., 2015). PPS representations thus occur through an integration of somatosensory information with auditory and/or visual information occurring near the body, creating a body-part centred, self-referential representation of the space immediately surrounding the body (di Pellegrino & Làdavas, 2015).

Studies confirmed the existence of PPS mapping in humans by showing that the perception of a tactile stimulus is more strongly modulated by auditory or visual inputs when these are presented close to the body (Serino, Noel, et al., 2015). In fact, the point at which visual or auditory stimuli significantly speed up reaction times to tactile stimuli has been operationalised as a proxy for the PPS boundary (Canzoneri, Magosso, Serino, & Williams, 2012). In experimental laboratory settings, an individual's PPS therefore refers to the space extending from the body surface to the furthest position at which multisensory integration facilitates significantly faster reaction times to tactile stimuli than in extrapersonal space. The PPS boundary can be described both as a distance value and in terms of "the spatial extent over which the interactions between touch and the major exteroceptive senses (i.e., vision and audition) transitions from being absent to being complete" (Noel, Cascio, Wallace, & Park, 2017: p. 9) – in other words, the gradient of the PPS boundary can be described in terms of the steepness or shallowness of the transition from extrapersonal to PPS (Noel, Cascio, Wallace, & Park, 2017; Pellencin et al., 2018; Spaccasassi, Romano, & Maravita, 2019). Neuroimaging in humans has paired this multisensory integration effect to processing in fronto-parietal regions homologous to those representing PPS in monkeys (di Pellegrino & Làdavas, 2015; Serino, Noel, et al., 2015). In a meta-analysis of PPS neuroimaging studies, Grivaz, Blanke and Serino (2017) found that there were seven consistently activated clusters in the processing of uni- and multi-sensory events in PPS in humans. Three clusters were found in the left and right dorsal parietal cortex, two in the left and right temporo-parietal

cortex and two in the left and right ventral premotor cortex (Grivaz, Blanke, & Serino, 2017).[4]

Functional significance of peripersonal space

Studies describing the functional significance of the PPS brain network provide several insights into why it may be linked to social dominance behaviour. Because stimuli in PPS are within reach and are also more directly threatening to the integrity of the body, the mapping of PPS does not serve only a sensory function, but is also crucial for the sensory guidance and preparation of action (di Pellegrino & Làdavas, 2015). PPS neurons have been found to directly project to the motor system – allowing more rapid responses to external objects (Avenanti et al., 2012). For example, presenting visual (Makin, Holmes, Brozzoli, Rossetti, & Farnè, 2009) or auditory (Serino, Annella, & Avenanti, 2009) stimuli either within or outside of human participants' PPS differentially impacts the excitability of the representation of the hand in the motor cortex. Serino and colleagues (2009) showed that the distance from the body at which an auditory stimulus is presented results in time-specific differences in motor system excitability, such that when an auditory stimulus is presented within an individual's peri-hand space, it modulates the excitability of the hand corticospinal motor representation in a very short time window. On the other hand, if an auditory stimulus is presented in extrapersonal space, motor system excitability is enhanced in a later time window (Serino et al., 2009). Thus, the early facilitation of the motor cortex for near, but not far, stimuli allows for the preparation of an immediate motor response for stimuli occurring within PPS. As a result, the mapping of PPS is defined as ultimately having a motor function (Brozzoli et al., 2010; Bufacchi & Iannetti, 2018) and PPS representations are specifically egocentric in nature as they represent near space in a body-part centred reference frame in terms of possibilities for action (Costantini, Ambrosini, Tieri, Sinigaglia, & Committeri,

[4] For more detailed information on the neural bases of PPS in humans see Cléry, Guipponi, Wardak, and Ben Hamed (2015) and di Pellegrino and Làdavas (2015).

2010; Holmes & Spence, 2004; ter Horst, Lier, & Steenbergen, 2011). The fact that the PPS network integrates percepts in near-space with representations of the body has led to PPS being conceptualised as 'the space of the bodily self'[5] (Noel, Pfeiffer, et al., 2015; Serino, 2016, 2019) – where the bodily self is grounded in the congruent integration of multisensory information within the spatiotemporal dimensions of the body (Noel, Pfeiffer, et al., 2015), and where the space of the bodily self is that in which percepts are integrated with and constrained by representations of the body (Holmes & Spence, 2004).

Indeed, PPS representations are not static nor fixed and are known to be determined by contextual action demands and egocentric constraints – both physical and psychological. For instance, alterations of proprioceptive information by wearing wrist weights caused a contraction of PPS (Lourenco & Longo, 2009) and amputees have shown an expansion of their PPS when wearing a prosthetic limb in comparison to when it is removed (Canzoneri, Marzolla, et al., 2013). Moreover, PPS representations have been found to dynamically project toward the end goal of actions such as walking (Noel, Grivaz, et al., 2015) or reaching (Brozzoli et al., 2010), or to the end point of a tool being wielded, but, in keeping with the centrality of the motor function of PPS, this effect is only seen when a tool is being used functionally (Bonifazi, Farnè, Rinaldesi, & Làdavas, 2007; Canzoneri, Ubaldi, et al., 2013). These studies show that PPS may be thought of as an action space, and that this action space is shaped both by egocentric possibilities for action, as well as the action demands of different contexts. Of particular relevance to social dominance, a critical context in which immediate action is required is when defending the body from spatiotemporally immediate threats. In this regard, PPS is well known for its defensive function. Several studies have shown that electrical stimulation of bimodal neurons representing PPS in the monkey ventral premotor cortex (Graziano, Taylor, & Moore, 2002) and ventral intraparietal area (VIP)

[5] See Serino (2019) for an extensive review of the theory behind and evidence for the conceptualization of PPS as the 'space of the self'.

(Cooke, Taylor, Moore, & Graziano, 2003) results in defensive motor behaviours such as ducking and deflecting potential threats. This indicates that in PPS networks sensory representations of space and motor representations of action *overlap* – i.e. the same areas that integrate multisensory information in the space immediately surrounding specific body parts are also responsible for the defensive motor responses of those body parts in the monkey brain (Serino et al., 2009). Indeed, it is now widely accepted that the PPS network forms part of the brain's core system of defence and it is associated with amygdala activation (Kennedy, Gläscher, Tyszka, & Adolphs, 2009; Wabnegger, Leutgeb, & Schienle, 2016). Together these properties have led to PPS being conceptualised as the sensory-motor interface between body and environment with a dual function: facilitating both approach and defence behaviours (de Vignemont & Iannetti, 2015).

With this functionality in mind, we hypothesised that the increase in social approach and vigilance to threat facilitated by testosterone may reflect in the modulation of PPS representations. Importantly, like individual differences in trait dominance and positions in status hierarchies, PPS representations differ both inter-individually in ways that are not directly related to body size (Longo & Lourenco, 2007) and intra-individually across contexts. A growing body of research has shown that social contexts have a determining influence on PPS representations and the PPS boundary has been found to be shaped by both threatening stimuli and the motivation to interact with others.

Peripersonal space and social threat

In terms of the impact of threatening stimuli on PPS, Bisio and colleagues (2017) showed that the motion of a threatening stimulus modulated PPS, such that an approaching (and therefore more threatening) stimulus resulted in an expanded PPS boundary in comparison to a receding stimulus. Moreover, in keeping with research within the angry-face threat paradigm, showing that testosterone biases toward threat, Ruggiero and colleagues (2017) found PPS boundaries to be larger when participants viewed angry approaching

virtual reality (VR) confederates than happy approaching confederates. These authors (2017: p. 1237) thus concluded that "the need of maintaining a feeling of safety and controlling the motor approach is particularly cogent when the angry person who invades our space is perceived as potentially harmful."

Furthermore, by comparing PPS boundaries in the face of approaching sounds of different emotional valences, Ferri and colleagues (Ferri, Tajadura-Jiménez, Väljamäe, Vastano, & Costantini, 2015) demonstrated that larger PPS boundaries were elicited by sounds where the physical properties of the sound had a negative, as opposed to a neutral emotional valence. In a second experiment, these authors used ecological sounds where the content elicited emotional responses of either neutral (brushing teeth), positive (baby laughing) or negative (woman screaming) valence. In agreement with their first experiment, they found PPS boundaries to be larger in relation to negatively-valenced emotional sonic experiences than positive or neutral experiences.

On the individual level, subjects with phobias (Taffou & Viaud-Delmon, 2014) and those high in anxiety (Iachini et al., 2015; Sambo & Iannetti, 2013) and claustrophobic fear (Lourenco, Longo, & Pathman, 2011) have larger PPS boundaries than healthy controls. These findings have been interpreted as consistent with the defensive function of PPS and, in keeping with the embodied cognition framework, it has been suggested that the oversizing of PPS in these patient populations may play a causal role in the development of anxiety disorders (Lourenco et al., 2011).

Together these studies suggest that PPS may expand to meet the emotional needs of the acting individual, and more specifically, that the perception of threat appears to function as a particularly potent modulator of PPS in this regard. Given the important motor and defensive function of PPS -- that is, given that PPS representations allow for a rapid execution of sensory-guided action – an increase in defensive PPS would be highly adaptive for maintaining the safety, and by extension, the social status, of the individual. For instance,

Rossetti and colleagues (Rossetti, Romano, Bolognini, & Maravita, 2015) showed that expanding PPS through tool use led participants to respond sooner to potential threats. This functionality of PPS suggests that the well-established increase in threat-vigilance produced by testosterone might reflect in changes in PPS mapping in the social context – specifically, we hypothesised, in an expanded defensive, threat-vigilant space with a sharper self-other boundary.

Peripersonal space and motivated action

In addition to defensive monitoring, studies have shown PPS boundaries to modulate according to goal-directed actions or the motivation for approach action. In fact, after a review of the literature, de Vignemont and Iannetti (2015) concluded that PPS should be understood using a dual model, based on the functional distinction between bodily protection and motivated goal-directed action. For example, a recent study by Spaccasassi and colleagues (Spaccasassi et al., 2019) found that PPS expanded when participants viewed positively-valenced (for example, money, chocolate) and negatively-valenced (knife, broken glass) images but did not expand when neutral images were shown. Accordingly, depending on the context, an increased PPS boundary can signify a larger defensive space or the motivation for goal-directed approach behaviours (Patané, Farnè, & Frassinetti, 2017). With respect to the latter, Teneggi and colleagues (2013) found that after a confederate behaved cooperatively with participants in an economic game, participants' PPS boundaries extended to include the confederate, such that there was no longer a detectable PPS boundary between participant and confederate. This only occurred when the confederate behaved cooperatively – when they behaved uncooperatively no extension of PPS was seen. The expanded PPS boundary was interpreted by the authors as a social extension of PPS in accordance with a feeling of communion with the confederate. More recently, this finding has been construed as "an effect compatible with the appetitive function of the working space interface" (Patane, et al., 2017: p. 21; also see Ferri, et al., 2015). This perspective is supported by a recent study

by Pellencin and colleagues (2018) who demonstrated that the perception of virtual confederates as 'moral' elicited larger PPS boundaries than those perceived as 'immoral'. Importantly, they found that the expansion of the PPS boundary towards the moral confederate correlated significantly with the behavioural intention to interact with her.

Not all social contexts, however, call for communal interaction. In ambiguous or more hostile settings, the mapping of action-space may instead be compromised by the presence of a competitor. Two studies have demonstrated participants' PPS to be smaller in the face of a neutral passive stranger than a non-living object (Pellencin et al., 2018; Teneggi et al., 2013). This has been interpreted as the *accommodation* of the neutral stranger – i.e. giving the neutral stranger their space (Teneggi et al., 2013). In accordance with this finding, Heed and colleagues (Heed, Habets, Sebanz, & Knoblich, 2010) found that when performing a visual-tactile integration task while facing a stranger in near space who concurrently performed the same task, the PPS effect measured by the task was reduced. The authors suggested that because the confederate was acting on the same visual stimuli in the PPS task as the participants, in a top-down modulation these stimuli might have been perceived as less likely threats or action-targets. Alternatively, this finding might be interpreted as an implicit demonstration of submissive avoidance behaviour, where the shrinking of PPS reflects a compromise of one's own space and of action-preparation in the face of another. Of relevance to the current study, these findings suggest that PPS mapping can be modulated by the presence of others even when their presence is not explicitly inviting or threatening. Moreover, they provide additional opportunity for exploring how social dominance motivation might register in PPS mapping – in the case of testosterone-driven dominance motivation, the diminishing of own space to accommodate another's action space may be reduced.

Peripersonal space around the other

The social modulation of PPS is not only reflected in the expansion or contraction of the PPS boundary around the self. Recent research has demonstrated that the near-space of others may be *remapped* onto individuals PPS representations (Maister, Cardini, Zamariola, Serino, & Tsakiris, 2015). In monkeys, single cell recordings have shown that some parietal visuotactile neurons forming part of the PPS network respond to visual stimuli presented near a monkey's own body as well as to visual stimuli presented near the same body part of the experimenter who was facing the monkey (Ishida, Nakajima, Inase, & Murata, 2010). Neuroimaging in humans demonstrated the same outcome in neural populations in the premotor cortex that were found to encode the space immediately around participants' own hands and another person's hand (Brozzoli, Gentile, Bergouignan, & Ehrsson, 2013). These studies therefore identify subpopulations of PPS neurons with mirror properties (Brozzoli et al., 2013). Mirror neurons populate areas adjacent to the PPS network -- for instance, area F5 in the premotor cortex, where mirror neurons were first discovered in the monkey brain (Rizzolatti, Fadiga, Gallese, & Fogassi, 1996). They are cells that respond both when monkeys execute a particular action, and when they observe the same action being executed by someone else (Holmes & Spence, 2004). By recruiting the same neurons used to perform actions in the observation of others' actions, the action of mirror neurons is believed to subserve an embodied self-referential understanding of the actions of others, and has been linked to empathising and social cognition (Ferrari & Coudé, 2018; Rizzolatti & Sinigaglia, 2010). Accordingly, PPS neurons with mirror properties may provide a common reference frame and assist with understanding or anticipating the actions and/or tactile perceptions of others (Brozzoli et al., 2013; Teramoto, 2018).

Behaviourally, two studies have demonstrated a multisensory facilitation effect in the space surrounding confederates. Maister and colleagues (2015) found that after performing an interpersonal multisensory stimulation task, where participants experienced synchronous

interpersonal stimulation shared with a confederate, their reaction times to tactile stimuli were significantly faster both when an auditory stimulus was perceived as close to their own body and when it was perceived as close to the confederate's body – indicating facilitated audio-tactile integration not only in the expected location around their own body, but also in the confederates near-space. Importantly, as these authors pointed out, this effect is indicative of a different mechanism from the *expansion* of the PPS boundary discussed in previous sections, because it does not attempt to incorporate the PPS of the other into the PPS of the self. However, in Maister and colleagues' study (2015) the PPS effect around the other (referred to by the authors, as well as Teramoto, 2018, as the 'remapping effect') was only seen after the induction of a body ownership illusion. The multisensory stimulation task used in the study to induce the illusion involved participants being touched by a cotton bud on their left check every two seconds while watching the confederate's face being touched in the same manner, either synchronously or asynchronously.

Because our bodily selves are grounded in the congruent integration of multisensory information within the spatiotemporal dimensions of the body (Noel, Pfeiffer, et al., 2015; Serino, 2019), altering multisensory stimulation can cause neurologically healthy people to include extracorporeal body parts (Botvinick & Cohen, 1998) or even whole bodies (Blanke & Metzinger, 2009; Petkova et al., 2011) into their own body schema[6]. Spatiotemporally aligned multisensory integration is crucial for these body ownership illusions and indeed, in Maister and colleagues' study (2015) the remapping effect was only seen after synchronous interpersonal stimulation with the confederate, and was not elicited after *asynchronous* stimulation, leading the authors to conclude that the increased saliency of the confederate in relation to the self enhanced the ability to remap events approaching the confederate into participants' own PPS representations. This idea is in keeping with experiments that have

[6] See Blanke (2012) and Serino et al. (2013) for reviews of body ownership illusions.

shown that PPS – as the space of the bodily self – shifts to the perceived location of the self after body ownership illusions (Noel, Pfeiffer, et al., 2015).

However, in a more recent series of experiments, Teramoto (2018) demonstrated the remapping effect without the induction of a body ownership illusion – meaning that the space around the other did not relate to an alteration in perceived self-location, but that this additional multisensorially mapped space might have a different function. In his study when visual stimuli approached the space close to either participants', or the confederate's hand, participants responded to tactile stimuli more rapidly. In addition to showing that a body ownership illusion is not necessary for the remapping effect, his findings indicated that participants do not need to be acquainted with the other in order for the remapping effect to occur and that the remapping effect does not have to be body-part specific. In other words, even when visual stimuli were presented to different body parts between the participant and confederate, the same PPS remapping effect was seen (Teramoto, 2018). In trying to understand this only recently observed phenomenon, Teramoto (2018) suggested that the mapping of PPS around others may aid in understanding their actions and perceptions and could potentially contribute to optimising one's behaviour to protect another person, or oneself, from threats.

Importantly, in both behavioural studies (Maister et al., 2015; Teramoto, 2018), the PPS effect around the self was more pronounced than the PPS effect around the other, indicated by faster multisensory integration reaction times in the PPS around the self than that of the other. Maister and colleagues (2015: p. 459) therefore assert that the multisensory integration effect close to the body of the other does not reflect a remapping of the other's PPS as one's own PPS as "responses to events within the participant's own PPS representation were still distinguishable from those to events in the other's PPS, suggesting that a distinction between self- and other-PPS was partially maintained." This new research allowed us to further measure the effects of testosterone on PPS to provide insight into

whether the dominance enhancing effects of testosterone are exclusively indexed by sensory-motor changes pertaining to the self, or whether changes are seen in the perception of the space of the other, or both.

The gradient between self and non-self space

Although infrequently described in the literature, distinctions between the space of the self and the space of the other may also be indexed by the PPS boundary gradient. This is a measure of the transition from extrapersonal to peripersonal space and can be steeper or shallower. For instance, by defining the PPS boundary in social contexts as a boundary between self and other, Noel and colleagues (2017) propose that autism may be accounted for in part by an abnormally steep self-other boundary. On the other hand, these authors contend that the weakened distinction between self and other seen in schizophrenia may reflect in overly porous PPS representations (Noel et al., 2017). In this framework, the steepness of the PPS gradient may relate to the ease or difficulty with which individuals disembody their bodily self during body ownership manipulations. In other words, those individuals who are more amenable to disembodiment during body ownership illusions may also have shallower self-other boundaries. Importantly, individuals differ in the extent to which they are amenable to such illusions (Kállai et al., 2015). For instance, in a study using the rubber hand illusion (see Botvinick & Cohen, 1998, for a description of this illusion), autistic children who displayed lower empathy were the least likely to experience the illusion (Cascio, Foss-Feig, Burnette, Heacock, & Cosby, 2012). Moreover, amenability to body ownership illusions has been found to be determined by various factors including conformity behaviour (Paladino, Mazzurega, Pavani, & Schubert, 2010).

Considering that testosterone has been found to reduce empathy (Erno Jan Hermans, Putman, & van Honk, 2006; Knickmeyer, Baron-Cohen, Raggatt, Taylor, & Hackett, 2006; van Honk et al., 2011), conformity (van Honk & Schutter, 2007) and social collaboration (Wright et al., 2012), we hypothesised that raised testosterone would be associated with

diminished blurring between the self and other, which in our study may be elicited as a stronger distinction between self-other space (i.e. a steeper PPS boundary gradient). More specifically, we hypothesised that the salience of the *self* and protection of one's own status that is associated with the dominance-enhancing effects of testosterone would reflect in a steeper self-other boundary.

Summary

The studies reviewed here have shown that PPS is conceptualised as the space of the bodily self and the mapping of this space has a dual function – facilitating self defence and approach behaviour. PPS differs both inter and intra individually and is highly responsive to the social environment. Consistent with its dual function, PPS has been found to expand both in the face of threatening and inviting social contexts which accords with the possibility of taking action, either to protect oneself from harm or to interact with the outside world. Moreover, a 'remapping' effect has recently been documented, whereby a PPS effect is seen not only in the near-space of one's own body, but also around the body of another. Given that testosterone facilitates heightened threat vigilance and approach behaviour, and that these effects of testosterone are understood as occurring to enhance the social status of the *individual*, we hypothesised that the effects of raised testosterone (achieved via single-dose exogenous administration) would reflect in a larger motor-preparatory space around the *self* in the face of a stranger. We also predicted that the boundary of this space will be steeper after raising testosterone, maintaining a clear division between the territory of the self and that of the other. Moreover, because testosterone is known to enhance egocentrism, and reduce empathy (van Honk et al., 2011; Zilioli, Ponzi, Henry, Maestripieri, & Physiology, 2015) and collaboration (Wright et al., 2012), we hypothesised that the effects of testosterone will be primary to self-space and will not reflect in changes in the remapping of the other's PPS.

Aims and hypotheses

Currently no research has been conducted exploring the relationship between testosterone and PPS and we therefore aimed to determine, as a starting point, the effects of testosterone on PPS in the face of an ambiguous stranger. We noted that it was possible that the effect of testosterone on PPS might only be seen in the face of an explicitly threatening stranger; however, because the PPS boundary has been found to be smaller in the face of a neutral stranger in comparison to a non-human object in order to accommodate the stranger (Teneggi et al., 2013), we hypothesised that the dominance enhancing effects of testosterone might be elicited in a seemingly 'neutral' situation by preventing the accommodation of the other in order to maintain a larger actionable space.

We tested our hypotheses using a within-subjects testosterone administration design so that we could establish the *causal* effects of testosterone by comparing to the placebo condition.

Hypotheses

In the presence of a stranger, compared to placebo, elevated testosterone will result in:

1) Primary hypothesis: A larger PPS boundary around the *self*.

Sub hypothesis: Following studies that have shown that testosterone administration can be highly effective at diminishing submissive behaviour and promoting dominant approach behaviour in individuals with social anxiety (Enter et al., 2014; Enter et al., 2016; Terburg et al., 2016) – for instance, Enter and colleagues (2016) showed that the approach enhancing effects of testosterone administration can be *particularly* marked in individuals with social anxiety – we hypothesized that the increase in the PPS boundary after testosterone administration will likewise be particularly pronounced in participants higher in trait anxiety.

2) Second hypothesis: A sharper boundary gradient.

3) Third hypothesis: No specific changes to the mapping of PPS around the other.

Methods

Ethical considerations and safety

This study has ethics approval from the UCT Psychology Department and the UCT Health Sciences Human Research Ethics Committee (HREC 868/2014). Safety has been established at the dosage of testosterone being used – in over 25 studies (Tuiten et al., 2000; van der Westhuizen et al., 2017; van Honk et al., 2005; van Honk et al., 2011; van Honk & Tuiten, 2001) no aversive effects, with the exception of headaches in very rare cases have been reported.

Design

This hormone administration study used a within-subjects design that was randomly assigned, placebo controlled and double-blind.

Independent variable 1. Treatment - two levels: testosterone and placebo. All participants receive testosterone on one day of testing and placebo on another day of testing, in randomized order, with a 2 day latency between sessions.

Independent variable 2. PPS Distance – 5 levels: The size of the PPS boundary is measured at distance levels from the participant's body. The distance levels are 20cm apart, labelled D1-D5, where D1 is 20cm from the participant's body, and D5 is 100cm from the participant.

Dependent variable. Reaction time (RT) – The amount of time it takes the participant to respond to the vibro-tactile stimulus (see experimental task for details).

Setting. A private laboratory in J2 Psychiatry at Groote Schuur Hospital, Cape Town.

Participants

Sample size and recruitment. We recruited 19 participants, but our final sample size was 18 as the data for one participant had to be discarded due to an excessive amount of outliers in her data set, suggesting that the participant did not understand the task.

Participants were recruited using convenience sampling via the University of Cape Town's Student Research Invitation Initiative.

Group allocation. A randomization engine was used (GraphPad) to allocate participants to two groups – one which receives placebo on the first day of testing, and the other which receives testosterone on the first day of testing. Each group will then receive the alternative substance (testosterone or placebo) on the second day of testing.

Inclusion and exclusion criteria. We recruited right-handed women aged 18-25, during the first 10 days following their last menstruation (the most stable period in a woman's cycle). These parameters replicate those of previous studies that have reliably established the time-course effects of a single dose of 0.5mg of testosterone in women (see Tuiten et al., 2000). Moreover, women have significantly lower circulating testosterone levels than men and thus exogenous testosterone administration will have a larger effect on women than man (Tuiten et al., 2000). Participants with a history of psychiatric disorders were excluded to prevent potential significant subject differences in the study outcomes (for example, see Noel and colleagues, 2017, on Schizophrenia and PPS). Participants on hormonal or psychiatric medication were excluded to prevent potential confounding interactions with testosterone administration. Subjects with visual impairments were excluded as the experiment contains an important visual component.

Tasks, materials and resources

PPS measurement task. A well-established measure of PPS, a visuo-tactile integration task (Serino, Canzoneri, Marzolla, di Pellegrino, & Magosso, 2015; Serino, Noel, et al., 2015), was used to measure the size and gradient of the PPS boundary. In this task, participants were asked to respond as quickly as possible to a tactile stimulus administered on a part of their body, while task-irrelevant approaching visual stimuli are presented. Because visual stimuli will significantly speed up the reaction to tactile stimuli in PPS, the aim of the task is to determine the furthest distance from the body at which a visual stimulus

significantly affects tactile processing. That is, the distance at which visuo-tactile RTs are significantly faster than RTs to unimodal tactile stimulation – a proxy for the PPS boundary (Serino, Noel, et al., 2015; Serino et al., 2018).

In our task, participants were fitted with vibrotactile devices, attached to their cheek, and we used a programme run using a virtual reality (VR) head mounted display (HMD, an Oculus Rift), which superimposed a programmed approaching visual stimulus, travelling from far to near, on the participant's external world (perceived via cameras attached to the VR HMD) – thus creating a 'mixed-reality' setup (Serino et al., 2018). The approaching visual stimulus is a tridimensional virtual ball looming towards the face of the participant. On most trials of the task, the vibrotactile device briefly vibrated and the participant was instructed to respond as quickly as possible to the vibration, by pressing a key on a computer keyboard, placed comfortably on a desk next to the participant. Each trial in the task was 2660ms long and on each trial, tactile stimulation (a vibration) was administered at one of five different temporal delays from the onset of a trial (after 2165, 1732, 1299, 866, and 433 ms) and thus was perceived when the virtual ball was at 5 different distance points from the participant (D1 – D5). Specifically, when the tactile stimulation was perceived after 2165ms since the start of the trial, the virtual ball was perceived at the closest distance to the participant (D1, 20cm), while conversely, when the tactile stimulation was administered at 433ms it corresponded to the virtual ball being at the furthest distance from the participant (D5, 100cm). Otherwise stated, a longer delay corresponds to a closer distance.

The experimental programme included three types of trials presented in a randomised order – tactile-only trials, visuo-tactile trials, and catch trials. 60.60% of the trials were experimental bimodal visuo-tactile trials, in which the tactile stimulus was delivered in combination with the approaching visual stimulus. 30.30% of trials were unimodal tactile-only trials, in which the tactile stimulus was delivered in the absence of the visual stimulus. These trials are considered baseline trials and are used to show the bimodal facilitation effect

on RTs to tactile stimuli (see Analysis). Tactile-only trials are important in that they can be used to control for individual differences in RTs to tactile stimuli (see Analysis). In both the unimodal and bimodal trials, the tactile stimulus was delivered at one of the five distance points (D1-D5) in a randomised order, to prevent entrainment or expectancy effects. Lastly, 9.09% of trials were catch trials in which the approaching visual stimulus was presented and no tactile stimulus was delivered. Catch trials necessitate withholding a response and thus ensure that participants are attentive to the task; they also further prevent the entrainment of an automatic motor response (Serino, Noel, et al., 2015).

In total the experiment consisted of 165 trials: 20 bimodal trials per distance (100) + 10 unimodal trials per distance (50) + 15 catch trials. The task was rendered by means of specialised software - ExpyVR, designed at the Swiss Federal Institute of Technology (Ecole Polytechnique Fédérale de Lausanne, EPFL).

Confederate. Our experiment involved the measurement of the PPS boundary in the face of a stranger unknown to the participants, and thus student confederates were hired to perform this role. Our aim was not to measure PPS in a particularly threatening or enticing social environment, but rather to assess whether testosterone affects a larger social PPS baseline in a relatively neutral social context. We thus matched participants and confederates on ethnicity and gender, to prevent potential confounding effects of a confederate from a different ethnic or gender group. For example, male confederates have been found to elicit a larger defensive PPS boundary than female confederates, especially in female participants (Iachini et al., 2016). In addition, only confederates who fell in a height range of 149 – 169cm (10cm below to 10 cm above the average South African female height) were hired to ensure that height didn't impact on perception of the confederate. Moreover, to prevent a familiarity effect on the second day of testing (which itself could influence the PPS boundary), a different confederate was used on each day of testing. To induce a degree of uniformity, confederates dressed in the same way. Finally, confederates were instructed to

stand in front of the participant (at a designated point approximately 1.5 meters from the participant) and face her while maintaining a neutral expression. Confederates did not interact in any way with participants.

Physiological Materials – Testosterone and placebo solution. A single dose of 0.5mg of testosterone, with a hydroxypropyl-β-cyclodextrin liquid carrier, was administered sublingually. Following administration at this dosage, testosterone level is known to peak between 3 and 4.5hrs after being injested (Tuiten et al., 2000). The placebo solution used is identical in appearance and taste as the testosterone. Vials were filled and coded 'X' and 'Y' by an external researcher to maintain blind-administration.

The State-Trait-Anxiety-Inventory for Adults (STAI). The STAI (Spielberger, Gorsuch, & Lushene, 1970) is the most commonly used questionnaire to measure anxiety. It is split into two self-report questionnaires – the STAI-Trait (see Appendix A) and STAI-State to measure trait anxiety and current anxiety, respectively. This measure has been used in both the testosterone and PPS literature. For example, PPS boundaries have been found to be larger in participants with high trait anxiety (Sambo & Iannetti, 2013). Testosterone has been found to have anxiolytic effects (Terburg et al., 2016; Terburg & van Honk, 2013; van Honk et al., 2005) and, importantly, to show a marked reduction of avoidance tendencies in socially anxious research participants (Enter et al., 2014; Enter et al., 2016). We therefore included the STAI-Trait measure to allow for analyses of whether the anxiolytic approach-enhancing effects of testosterone may be particularly efficacious in changes of the PPS boundary in socially anxious individuals.

Procedure

Pilot study. A pilot study was run with a sample of eight participants. The pilot was conducted to provide training in the use of the VR equipment and software, and to validate the PPS-mapping task.

Initial procedures. The study was advertised to students via the Student Research Invitation Initiative. Subjects who responded to the recruitment invitation were invited to register for the study online by filling out a registration form, including details pertaining to the sample inclusion and exclusion criteria. Suitable candidates were then provided with time slot options and signed up for four session slots – two per day (testosterone/placebo administration session and experimental session four hours later), on two separate days, two days apart. Participants were seen at the same time of day for each administration and experimental session, respectively, as testosterone fluctuations are known to occur according to the time of day (Wirth & Schultheiss, 2007). Only one participant was seen at the lab at a time for all four sessions.

Data collection

Day 1. ***Session 1 (substance administration).*** Participants arrived at the lab and were briefed with information on what will occur during the session and the second session later in the day. They were given a consent form (see Appendix B) to read and sign, and the opportunity to ask questions if they had any uncertainties. Thereafter, participants were given the testosterone or placebo solution (administered blind). They were asked to hold the solution under their tongue for one minute (timed by the administrator) and then swallow. Before leaving, participants were reminded about the guidelines for the period between substance administration and returning to the lab. These instructions were to limit nicotine and caffeine consumption, to avoid eating in the hour prior to the second session and to refrain from strenuous activity. Participants were previously informed of these instructions via email.

Session 2 (data collection). Participants arrived at the lab and were provided with an overview of what will occur during the session. They were then seated comfortably at a desk and dressed with the experiment equipment: first a vibro-tactile device was attached to their cheek using a plaster. Second, they were fitted with the Occulus Rift virtual-reality headset.

They were shown where the computer keyboard was and how to access it comfortably for responses during the task. Participants were informed that they will feel a vibration on their cheek, see a virtual ball approaching them and that a person unknown to them will enter the room and stand in front of them. They were told that the virtual ball is task irrelevant, and asked to respond as quickly as possible to the tactile vibration. They were also instructed to look in the direction of the confederate for the duration of the task, but not to interact with her. At this point, the confederate entered the room and stood in front of the participant, at a designated point approximately 1.5 meters from the participant. The experimental task was run and there was a pause half-way through the task where the participant was given the option of a short break if they felt they needed it. The duration of the task is 11 minutes and no participants opted for the break. After completion of the task, the VR headset and vibrators were removed, the participant was ushered into a waiting room, thanked and reminded of the time of their next session.

Day 2. ***Session 3 and 4.*** Sessions 3 and 4 were identical to Sessions 1 and 2, respectively, with the exception of the substance administered in Session 3 (participants who received testosterone on day 1 received placebo on day 2 and the inverse for those who received placebo on day 1). After completing session 4, participants were provided with a debriefing form (Appendix C) and received financial remuneration (R350) for their participation.

Data management. The reaction times from the PPS task were captured on Microsoft Excel. They were then copied and coded on IBM SPSS and MatLAB for statistical analysis.

Analyses

Peripersonal space

Reaction times (RTs) to visuo-tactile (VT) and tactile-alone (T) stimulation were recorded as the temporal duration between vibrotactile stimuli onset and button press. For each

subject individually we binned RTs as a function of the distance between the visual stimuli and the observer (D1 through D5), and as a function of sensory stimulation (VT vs. T) and testosterone condition (testosterone vs. placebo). Then, mean tactile RTs for each sensory stimulation and testosterone condition were subtracted from the analogous VT condition in order to compute 'baseline-corrected' RTs (Pfeiffer, Noel, Serino, & Blanke, 2018; Serino et al., 2018). In other words, for each individual participant, the average tactile-only RT per distance is subtracted from each visuotactile RT at the corresponding distance. This baseline correction is employed to offset temporal expectancy effects (Kandula, Van der Stoep, Hofman, & Dijkerman, 2017) and determine whether any putative modulation in RTs as a function of distance is truly a multisensory PPS effect (i.e., visuo-tactile RT < tactile RT). The baseline correction also controls for between-subjects variance in RT to tactile stimuli, allowing for more robust PPS comparisons between subjects. Baseline-corrected VT RTs are therefore used for all of the below analyses. All significant outliers (those that had studentised residuals with an absolute value greater than 3) were corrected for.

After correcting multisensory RTs in the pre-processing step described above, we submitted these RTs to a two-factor repeated measures ANOVA to ascertain if a PPS effect was engendered in our mixed-reality setup (i.e. a significant main effect of *Distance*) and, importantly, if there was a significant interaction between the factors *Distance* and *Testosterone* – suggesting that testosterone influences PPS representations. After finding a significant effect of *Distance* and a significant interaction between *Distance* and *Testosterone* (as detailed below) we explored this interaction by establishing at which distances were VT RTs significantly faster in each testosterone group separately. To do so we conducted repeated measures ANOVAS on each *Testosterone* condition separately to determine if there were main effects of *Distance* in each condition. Bonferroni-corrected post-hoc pairwise comparisons from the two groups ANOVA analyses were then effectuated in order to establish at which distance points (D1-D5) a PPS effect was observed (Pellencin et al., 2018; Teneggi et al., 2013). As detailed below, this

analysis suggested a quickening of RTs when visual stimuli were presented both near the participants (i.e., self) and the confederate (i.e., other; see Teramoto, 2018, for a similar effect) and revealed an enlarged PPS boundary around the self in the testosterone condition. Thus, in order to further study these findings, we aimed at estimating the size and gradient of the PPS representation both around the self and the other.

Estimation of the size and gradient of PPS was accomplished via function fitting, which permitted for fine-grain estimates (vs. solely indicating at which discrete distances RT were significantly faster) and served as a data-reduction technique. The shape of the PPS boundary is not linear, and is known to take the form of a sigmoid (Serino et al., 2018). As a result, data extraction after fitting to a sigmoidal function is a commonly used form of PPS boundary analysis in the literature (Ferri, Costantini, et al., 2015; Serino, 2016; Serino et al., 2018). Visuo-tactile RTs were fit to a sigmoidal function (Eq. 1),

$$y(x) = \frac{y_{min} + y_{max} \times e^{(x-x_c)/b}}{1 + e^{(x-x_c)/b}} \qquad (Eq. 1)$$

where x represents the distance between visual and tactile stimuli and y(x) is the RT to tactile stimulation at a given visual distance x. y_{min} and y_{max} are saturation points of the sigmoidal, and are fixed to the slowest and fastest average RT in the VT trials. x_c and b respectively represent the central point and the slope of the sigmoidal at x_c and are free to vary in order to maximize goodness of fit. The central point of this function is taken as a proxy for the size of PPS; the location of the PPS boundary, while the slope of the function (inversely proportional to *b*), represents the steepness with which the near (peri-personal) and far (extra-personal) space are divided (Noel, Blanke, Magosso, & Serino, 2018; Noel, Park, et al., 2018; Pfeiffer et al., 2018). To limit impact of the confederate on self-PPS estimates, distances D1 through D4 were utilized in the self condition. Similarly, distances D2 through D5 were utilized in the other-PPS estimates, and these were inverted (from D5 to D2) before fitting. In this manner

central point estimates for self and other were on the same scale (i.e., low values for the central point indicate a small PPS, while large values indicate a large PPS).

After obtaining the central point and slope around the self and other for each participant in each testosterone condition, two separate repeated-measures ANOVAs were conducted with factors *Testosterone* (testosterone vs placebo) and *Self vs Other* (self vs other PPS), the first with the central point as the dependent variable, the second with the slope as the dependent variable. Within-subjects t-tests were used to clarify the significant effects of the ANOVAs.

Trait anxiety. Having ascertained that testosterone enlarged PPS representations around the self, in a final step we explored whether this change was pronounced in anxious individuals. To do so, we conducted Pearson correlations on the change in PPS size (i.e. the central point) due to testosterone administration (i.e. testosterone – placebo) with participants' STAI-Trait scores.

Results

Peripersonal space

See Table 1 for the mean RT at each distance level for each testosterone condition (i.e. testosterone, placebo).

Table 1.

Descriptive Statistics for RT at each Distance Level

		M	*SD*	*N*
Placebo	D1	-.03	.06	360
	D2	.01	.07	360
	D3	.02	.05	360
	D4	.01	.05	360
	D5	-.01	.05	360
Testosterone	D1	-.02	.06	360
	D2	-.001	.05	360
	D3	.01	.05	360
	D4	.01	.06	360
	D5	-.01	.04	360

For the two-factor repeated measures ANOVA, Mauchley's test for the assumption of sphericity indicated that this assumption was violated for *Distance* ($\chi_2(9) = 35.06$, $p < .001$) as well as for the interaction between *Distance and Testosterone* ($\chi_2(9) = 31.80$, $p < .001$). In both cases epsilon was greater than .75 ($\varepsilon = .97$), and so the Huynh-Feldt correction was used. Applying the Huynh-Feldt correction, the two-factor repeated measures ANOVA revealed a significant main effect of *Distance,* $F(3.86, 1386.09) = 69.87$, $p < .001$, $\eta^2_p = .16$), demonstrating that we successfully elicited a PPS effect in our mixed-reality setup. There was no significant main effect of *Testosterone,* $F(1, 359) = 3.25$, $p = .072$, indicating that reaction times were not uniformly modulated by testosterone. Crucially, there was a significant interaction between *Distance* and *Testosterone*, $F(3.88, 1391.83) = 3.98$, $p = .004$, $\eta^2_p = .01$, suggesting that testosterone influenced the PPS boundary representation at certain distance points.

In order to explore the source of the significant two-way interaction, we conducted repeated measures ANOVAS on each of the testosterone conditions separately to determine the effects of *Distance* in each group. Mauchly's test indicated that the assumption of sphericity was violated for the factor *Distance* $\chi_2(9) = 26.71$, $p = .002$, and epsilon was larger than .75 ($\varepsilon = .98$), so the Huynh-Feldt correction was applied. Both conditions showed significant main effects of *Distance*, revealing the presence of a PPS effect in each condition (Placebo group: $F(3.90, 1400.68) = 51.51$, $p < .001$, $\eta^2_p = .13$); Testosterone group: $F(3.89, 1396.88) = 28.32$, $p < .001$, $\eta^2_p = .07$). Bonferroni-corrected pairwise comparisons between the sequential distances (D1-D5) in each condition (see Table 2) revealed significant differences in the placebo condition between D1 ($M = -.03$, $SD = .06$) and D2 ($M = .01$, $SD = .07$), $p < .001$, and between D4 ($M = .01$, $SD = .05$) and D5 ($M = -.01$, $SD = .05$), $p < .001$. In the testosterone condition, significant differences were found between D1 ($M = -.02$, $SD = .06$) and D2 ($M = -.001$, $SD = .05$), $p < .001$; D2 ($M = -.001$, $SD = .05$) and D3 ($M = .01$, $SD = .05$), $p = .007$; and D4 ($M = .01$, $SD = .06$) and D5 ($M = -.01$, $SD = .04$), $p < .001$. These

results indicate that multisensory reaction times were significantly faster in the space from the body up to D2 in the placebo condition, and up to D3 in the testosterone condition – revealing an expanded PPS around the self in the testosterone condition. In both conditions multisensory reaction times were also significantly faster in the space surrounding the confederate, suggesting that a PPS effect was also engendered close to the confederate, at D5.

Table 2.

Pairwise Comparisons in the Distance Factor for Placebo and Testosterone Conditions

		Placebo		Testosterone	
Distance 1	Distance 2	Distance 1-2	*p*	Distance 1-2	*p*
D1	D2	-.04	<.001*	-.02	<.001*
D2	D3	-.01	1.00	-.01	.007*
D3	D4	.01	.493	.01	1.00
D4	D5	.02	<.001*	.02	<.001*

* Significant at $\alpha = .05$

Having established that a multisensory PPS representation was successfully indexed (Bernasconi et al., 2018) around the self and the other and that testosterone significantly expanded the self-PPS, in order to allow for more fine grained analyses of these findings we subsequently fit individual subject data and extracted estimates of the location (central point) and gradient (slope) of PPS representation around the self and other, and as a function of testosterone or placebo administration (see Analyses for detail). Goodness-of-fit was variable (see Serino et al., 2017), with 4 participants showing poor fits (average $R^2 < 0.2$), and thus, following the procedure of previous studies (Pellencin et al., 2018; Teneggi et al., 2013), the data for these participants was discarded for the rest of analyses. The average R^2 of the remaining participants was 0.55.

Regarding the central point, as illustrated in Figure 1, a 2 (testosterone vs. placebo) x 2 (self vs. other) repeated-measures ANOVA revealed a significant main effect of testosterone administration ($F(1,13) = 8.9$, $p = 0.010$, $\eta^2_p = 0.40$), a significant main effect of self vs. other ($F(1, 13) = 19.3$, $p < 0.001$, $\eta^2_p = 0.59$), and most importantly a significant interaction between

these variables ($F(1, 13) = 6.29$, $p = 0.026$, $\eta^2_p = 0.32$). The interaction was driven by the fact that self-PPS enlarged after administration of testosterone (placebo: 1.80 ± 0.16; testosterone: 2.42 ± 0.35; $t(13) = 6.07$, $p < 0.001$), while other-PPS remained unaltered (placebo: 2.57 ± 0.51; testosterone: 2.60 ± 0.49; $t(13) = 0.162$, $p = 0.87$). These results suggest that testosterone administration increased the PPS boundary around the self, but did not affect the PPS boundary around the confederate.

In terms of the gradient of PPS, a 2 (testosterone vs. placebo) x 2 (self vs. other) repeated-measures ANOVA demonstrated a main effect of self vs. other ($F(1, 13) = 46.22$, $p < 0.001$, $\eta^2_p = 0.78$), yet no main effect of testosterone administration ($F(1, 13) = 3.41$, $p = 0.08$), nor an interaction between these variables ($F(1, 13) = 0.030$, $p = 0.86$). The main effect was driven by a steeper slope around the self (b-parameter value: 0.43 ± 0.42) than around the other (2.0±0.98).

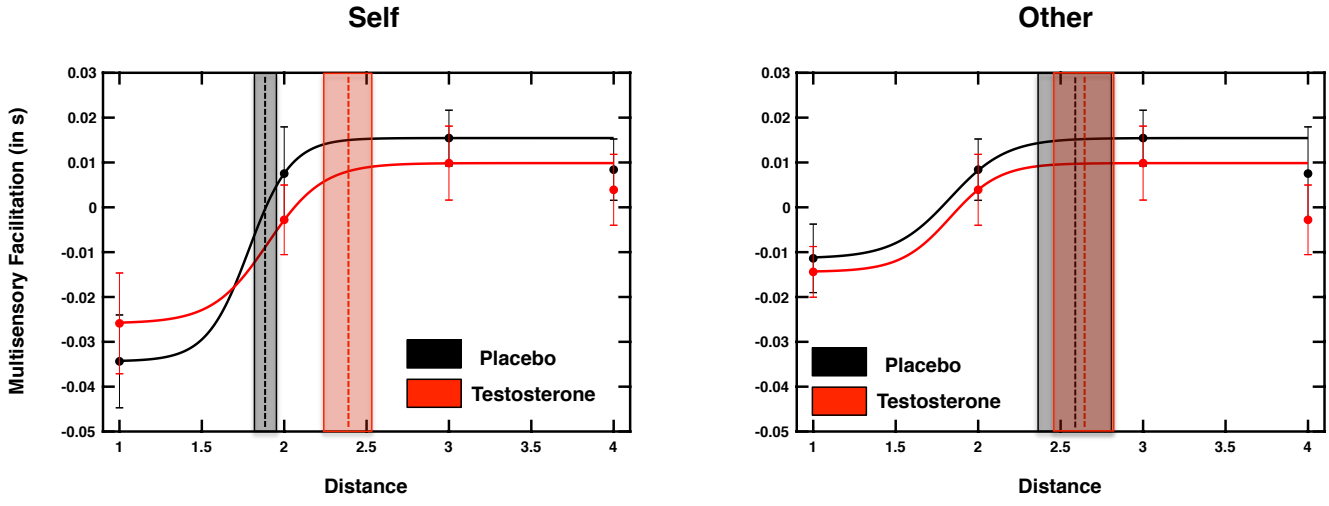

Figure 1. Effect of testosterone on PPS representation of the self and other. Left panel: multisensory facilitation in seconds (visuo-tactile reaction times corrected for tactile reaction times; negative values indicating multisensory facilitation) as a function of distance (near to far; Distance 1-4) from the self, and administration of either placebo (black) or testosterone

(red). Dots are mean reaction time and error bars represent +/- 1 standard error of the mean (SEM). Dashed vertical lines represent the average central point (size) of PPS for the given condition, and shaded area around the dashed lines is SEMs. Note sigmoidal functions are fit for the average reaction time, while the vertical dashed lines are average central points of individually fitted sigmoidals. Right panel: multisensory facilitation as a function of distance from the other (confederate), and administration of either placebo or testosterone. Conventions follow as for the left panel.

Interplay between trait anxiety and change in peripersonal space due to testosterone

Seemingly testosterone administration enlarged the PPS representation around the self, and thus we queried whether this remapping was related to trait anxiety (see Noel et al., 2018, for a similar approach). In order to limit the possibility for Type I errors (i.e., false positives), correlational analyses were restricted to the change in PPS size (i.e., central point) due to administration of testosterone (i.e., testosterone – placebo). No correlational analysis is conducted on the slope of PPS – as this variable did not change due to testosterone – and no correlational analysis is conducted on central point values during placebo or testosterone (only on the difference of these). As illustrated in Figure 2, this analysis suggested that participants with higher trait anxiety were particularly prone to enlargements of PPS due to administration of testosterone (Pearson correlation; $r = 0.55$, $p = 0.04$).

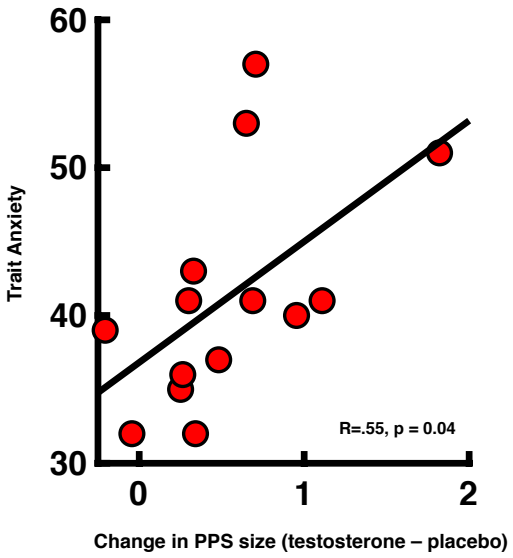

Figure 2. Correlation between trait anxiety score and change in self-PPS due to testosterone. Trait anxiety score (y-axis) as a function of change in PPS size (testosterone – placebo). Each dot represents a participant.

Discussion

Research on PPS has taught us that our ability to coordinate interactions with the world around us is facilitated by a neuronal network dedicated to representing the space immediately surrounding our body (Serino, 2019). This network has a motor function, allowing us to plan defensive or approaching motor responses to stimuli in our immediate environment (Graziano & Cooke, 2006; Serino et al., 2009). In recent years, there has been great interest in the ways in which individual and environmental factors shape our PPS (e.g. Iachini et al., 2015; Pellencin et al., 2018; Teneggi et al., 2013). Differences in the size of the PPS boundary have been linked to a range of 'higher order' phenomena, from mental disorders such as anxiety and autism (Noel et al., 2017; Sambo & Iannetti, 2013), to the feelings elicited by stimuli – such as enticement or fear (Ferri, Tajadura-Jiménez, et al., 2015; Pellencin et al., 2018; Spaccasassi et al., 2019; Valdés-Conroy, Román, Hinojosa, & Shorkey,

2012). In this study, we continued along this line of inquiry, and sought to explore whether PPS representations may support dominance behaviour. Specifically, we hypothesised that dominance may register in the mapping of a larger self-space and that such a change in PPS might support the known mechanisms by which testosterone enhances dominance; for instance, by increasing approach behaviour and threat vigilance.

Testosterone-induced expansion of the PPS boundary around the self

Our major hypothesis was that in the face of a stranger with unknown intentions, testosterone administration would confer a larger PPS boundary around the self in comparison to a placebo condition. This hypothesis was confirmed by the repeated measures ANOVA test that revealed a significant interaction effect between the factors *Testosterone* and *Distance* with post-hoc testing revealing that on placebo participants had significantly faster multisensory reaction times around the self at D1 (indicating a PPS boundary between D1 and D2), while on testosterone, significantly faster multisensory reaction times around the self were not only seen at D1 but also at D2 (indicating a PPS boundary between D2 and D3). In other words, this analysis showed an expansion of PPS on testosterone of up to 20cm around the self. While this form of statistical analysis is useful in indicating the major outcomes of the experiment, it can only tell us the discrete distance points where significant changes in reaction times are seen (i.e. that changes are occurring between two distance points, such as between D1 and D2). We therefore included a second step in our analyses, whereby individual's multisensory reaction times were fitted to a sigmoidal curve, allowing us to extract fine-grain estimates of each individuals' PPS boundary (the central point of the sigmoid). This allowed us to compute a more detailed estimate of the increase in PPS size around the self, and also served as a means of triangulating our results. This analysis confirmed a significant increase in the central point values on testosterone – rising from an average central point value of 1.80 (equivalent to a PPS boundary at 36cm from the body) on placebo to 2.42 (PPS boundary at 48.4cm from the body) on testosterone – translating to an

increase of 12.4cm in the PPS boundary size around the self. Because the average goodness of fit for the sigmoid function fitting was only moderate (average $R^2 = 0.55$) we are aware of the limitation of this analysis. However, it is reassuring that this analysis reproduced the findings of the previous analysis – not only in trend, but also in the size of the PPS boundary. Specifically, the post-hoc pairwise comparisons revealed that on placebo PPS around the self fell between D1 and D2 which is commensurate with the central point value of 1.80 and on testosterone it fell between D2 and D3, again commensurate with the central point value of 2.42.

The significant increase in the PPS boundary around the self after the administration of testosterone implies a causal role of testosterone in facilitating a larger 'self-space'. In other words, after raising participants' testosterone levels, our participants unconsciously appropriated a larger space into their bodily domain, allowing them a greater actionable space in the face of an unknown person. While this finding alone may reflect an implicit embodied index of enhanced social dominance, its implications in terms of the functions of PPS offer insight into the established dominance-related behavioural patterns described in the testosterone literature. For instance, the expansion of participants action space is consistent with the view that testosterone increases social approach (Radke et al., 2015; Terburg & van Honk, 2013). Representations of PPS ultimately have a motor function and thus this space is conceptualised as the space in which to plan motor responses to stimuli in the immediate environment (Serino et al., 2009). Having an expanded PPS is akin then to having an expanded action space, which has been demonstrated in other studies when a tool, for example, utilised in far space increases PPS to the end point of the action (Canzoneri, Ubaldi, et al., 2013), or where the intention to act or approach another individual has been shown to expand the PPS boundary (Pellencin et al., 2018). It follows that the increase in the motivation for social approach conferred by testosterone, which is coupled with reduced fear (Terburg & van Honk, 2013), is associated with a larger self-referential action space in the

face of an unknown other which may serve as an implicit, embodied indicator of action-readiness. Lending behavioural evidence to this idea, Enter and colleagues' (2014) showed that testosterone administration induced a direct behavioural shift from social avoidance to social approach toward angry faces in healthy women and in patients with Social Anxiety Disorder (Enter, Spinhoven, et al., 2016). Applying the results of our study, it is possible that such a behavioural change may be facilitated in part by an enlargement of participants' action space. It is noteworthy that in both studies (Enter et al., 2014; Enter, Spinhoven, et al., 2016) there was no significant increase in approach action to neutral or happy faces, which led the authors to align their findings with the challenge hypothesis – which holds that the effects of testosterone occur in a 'state' rather than 'trait' manner, where testosterone is seen to rise in the face of a socially challenging or threatening encounter in order to initiate approach motivation and reduce fear (Carré & Archer, 2018). For instance, previous research in healthy women demonstrated that testosterone administration increased cardiac accelerative responses to angry facial expressions, which was interpreted as a physiological indicator of readiness to fight (van Honk & Tuiten, 2001). With this in mind, our finding that raised testosterone caused an increased PPS around the self in the face of an ambiguous - and therefore potentially threatening - confederate may also relate to the enhanced threat vigilance conferred by testosterone. Indeed, the PPS network is defined as having a key defensive function (Graziano & Cooke, 2006; Sambo, Liang, Cruccu, & Iannetti, 2012) and is also known to expand in the face of threatening stimuli, providing a larger defensive space. For instance, PPS has been shown to be larger in the face of angry confederates than happy ones (Ruggiero et al., 2017), larger in the face of men than women (Iachini et al., 2016), and larger in response to threatening sounds than neutral sounds (de Haan, Smit, Van der Stigchel, & Dijkerman, 2016; Ferri, Tajadura-Jiménez, et al., 2015; Taffou & Viaud-Delmon, 2014). The expansion of the PPS boundary in the face of threat is thought to be highly adaptive, as it provides a larger action space in which to anticipate others' actions and protect oneself (di

Pellegrino & Làdavas, 2015; Rossetti et al., 2015). An expansion of participants' PPS, as seen in our study in the presence of the ambiguous confederate, may therefore support the enhanced vigilance to threat conferred by testosterone (Goetz et al., 2014; Terburg & van Honk, 2013; Wirth & Schultheiss, 2007).

Indeed, while we aimed to have ambiguous confederates who maintained neutral facial expressions and did not interact with our participants, we may have underestimated the potential threat of our confederates. Being faced by a stranger with unknown intentions who was *standing* (and therefore at an advantage for taking action) while our participants were seated could have elicited the perception of potential threat, producing a challenge-preparatory response in the testosterone condition. The design of the task may have emphasised this further, as the virtual ball was perceived to approach participants from where the confederate was standing – possibly creating the impression of being actively thrown by the confederate.

This is an important caveat when interpreting our findings, as we had initially set out to ascertain, as a starting point, whether raised testosterone would result in a larger PPS in a relatively neutral social situation. We took this route because of the novelty of our research, and with the aim of shedding light on whether the dominance enhancing effects of testosterone could be seen in a relatively neutral social environment, as opposed to being activated exclusively in contexts that directly threaten social status, like several studies have suggested (Carré & Archer, 2018). Retrospectively, we believe that our confederates may have been perceived as subtly threatening and, if so, we cannot unequivocally conclude that the enlarged PPS conferred by testosterone would equally occur in a completely neutral social situation.

Nevertheless, whether the confederate was perceived as a threat or not, the expansion of our participants' PPS indicates that raised testosterone caused participants to unconsciously map a larger space as their own, which may serve as an implicit measure of

dominance. Moreover, this change in the representation of PPS would confer our participants heightened action-readiness, which is fitting with the known enhancement of social approach associated with testosterone. What remains uncertain, because of the ambiguity of our confederates, is whether the enlargement of self-space signals a trait-dominance effect, or if this response was more explicitly tied to the perception of a threat (i.e. a 'state' effect).

This raises the need for future research to determine whether the same effect would be elicited by more neutral and/or positively valenced confederates, and, likewise, it would be useful to reproduce this study with explicitly threatening stimuli (see Future Directions).

Testosterone induced enlargements of the PPS boundary and social anxiety

Having found an enlargement of the PPS boundary around the self after testosterone administration, in a further step in our analyses we tested whether this enlargement may relate to participants' trait anxiety level – as social anxiety is strongly related to threat avoidance and submission (Terburg et al., 2012; Weeks, Heimberg, & Heuer, 2011) and therefore changes in PPS in response to testosterone may be particularly marked in this group. To do so we performed a correlative analysis on participants' scores on the STAI-Trait Inventory and the increase in their PPS boundary size due to testosterone administration. This analysis was significant, showing that participants with higher trait anxiety were particularly prone to enlargements of PPS due to the administration of testosterone.

Given that anxiety is associated with avoidance behaviour and lower levels of testosterone (Giltay et al., 2012), it may be that anxious individuals are particularly amenable to the dominance-enhancing effects brought about by raising testosterone levels exogenously. Indeed, as has already been mentioned, testosterone is well known for its anxiolytic effects and these effects are believed to be initiated in order to support approach behaviour.

Our finding that the expansion of the PPS boundary around the self was particularly pronounced in participants with higher levels of anxiety is congruent with research that has shown that testosterone administration increased approach tendencies to threatening stimuli

in participants with Social Anxiety Disorder (SAD) (Enter, Spinhoven, et al., 2016), that it completely abolishes gaze aversion to subliminal angry eye contact in anxious women (van Honk et al., 2012), and that it alleviates gaze avoidance in participants with SAD, where the same effect was not seen in healthy participants (Enter, Terburg, et al., 2016). Enter and colleagues' (Enter, Terburg, et al., 2016) finding that testosterone administration reduced gaze avoidance tendencies, but only in participants with SAD who displayed higher baseline gaze avoidance behaviour, is in keeping with literature that suggests that both individual differences and social context affect the manner in which testosterone influences social dominance behaviour (Carré & Archer, 2018). For instance, testosterone administration has been found to decrease interpersonal trust, but only in participants who trusted easily (Bos et al., 2010) – showing an adaptive increase in social vigilance only in, to use the authors' term, "naïve" individuals. Considering that anxiety is associated with avoidant behaviour, and that an enlarged PPS may confer an enlarged action-space, it follows that in the current scenario the approach-enhancing effects of testosterone were particularly pronounced in participants higher in trait anxiety.

What may present as an issue of conflict here is that anxious individuals have been found to have larger PPS boundaries in general (Sambo & Iannetti, 2013). This has been interpreted as an embodied indicator of threat sensitivity and vigilance (Lourenco et al., 2011; Sambo & Iannetti, 2013). While an expanded PPS in the face of a threat is highly adaptive for maintaining the safety of the individual, as is the case with many evolutionarily built-in adaptive mechanisms, maladaptive iterations are seen in psychopathology – in the case of trait anxiety, a larger defensive PPS may be pathologically elicited. The finding that anxious individuals have larger PPS boundaries may seem at odds with our interpretation that the dominance enhancing effects of testosterone manifested in a larger PPS boundary in the face of a stranger. However, these points are reconciled by a key similarity between anxious-avoidance and dominant-approach, namely, heightened threat vigilance. It is likely that

because the PPS network has a key defensive function and contributes to threat vigilance, an enlarged PPS may be seen in both anxious and dominant individuals, even though, as Terburg and van Honk explain:

> Anxious and aggressive personalities typically dissociate in their basic reaction to social threat. *Both respond vigilantly* [emphasis added], but the first will subsequently avoid it, whereas the second will approach and confront it in search of a rewarding outcome. (Terburg & van Honk, p. 298)

With this difference in the response to threat in mind, as well as the known approach-enhancing effects of testosterone in anxious individuals (Enter et al., 2014; Enter, Spinhoven, et al., 2016), our finding that testosterone was especially effective at increasing the PPS boundary in our more anxious participants corroborates our interpretation that the enlarged PPS after the administration of testosterone may support the enhanced social approach conferred by testosterone.

Peripersonal space boundary gradient around the self

The second hypothesis in our exploration of the effects of testosterone on PPS was that raised testosterone would confer a steeper PPS boundary gradient around the self. PPS boundaries represent the distance point furthest from the body where multisensory facilitation significantly boosts reaction times to tactile stimuli. While almost all research in this field reports on this discrete distance point when looking at PPS boundaries, in practice the differentiation between extrapersonal and peripersonal space is not represented by a stark, absolute distinction, but rather by more or less gradual changes in reaction times which take the form of a gradient (Spaccasassi et al., 2019). Unfortunately very few authors comment on the gradient of the PPS boundary they have measured, leaving a gap in the field and difficulty to form *a priori* hypotheses about contextually specific gradient differences.

With the aim of providing a contribution in this regard, and to better appreciate the effects of testosterone on PPS, we included a gradient analysis in our investigations. We

extracted the slope value from the sigmoid function for each individual in each testosterone condition separately, and separately for the boundary around the self and that around the other. This analysis was conducted separately for the 'self-PPS' condition and the 'other-PPS' condition in order to obtain more accurate estimates from the sigmoid (that is, estimates that were less skewed by the presence of another PPS effect in far space or the inverse in near-space). The slope values were submitted to a repeated-measures ANOVA which demonstrated no main effect of testosterone, thus nullifying our hypothesis. In fact, the trend of the data indicated the opposite effect of what we had anticipated – a marginally steeper slope around the self in the placebo condition. This seems to be explained by a general quickening of multisensory reaction times across all spatial points after the administration of testosterone. Findings here thus did not support the proposal that testosterone sharpens the PPS gradient. Based on this finding, and from the theoretical stand point that PPS gradients may reflect grounded distinctions between self and other (Noel et al., 2017), it appears that testosterone does not exert a major influence on sharpening self-other boundaries. However, this analysis may have been confounded by the presence of the multisensory facilitation effect around the confederate, which would have altered the gradient between self and other in both testosterone and placebo conditions. For further clarity, it would be useful to compare the PPS boundary gradient between placebo and testosterone conditions in either a non-social scenario, or where the confederate is at a further distance from the participant – in order to diminish the possibility of a multisensory facilitation effect occurring in the near space of the confederate.

Peripersonal space around the 'other'

In addition to a PPS effect around our confederates, our results are consistent with what has been termed the 'remapping effect' (Teramoto, 2018)– that is, a multisensory facilitation effect around the confederate, suggesting that we successfully elicited a compelling social environment in our mixed reality setup. Analysing the remapping effect

allowed us to better appreciate the effects of testosterone on PPS by confirming our expectation that testosterone administration would cause no changes to the representation of the space around the other. This was demonstrated in the initial analyses (RM Anova and post-hoc testing) as well as in the sigmoid analysis – where no significant difference was found in the size or gradient of the PPS boundary between testosterone and placebo conditions.

Given that testosterone is known to reduce empathy (Van Honk et al., 2011; Zilioli et al., 2015) and minimise collaboration (Wright et al., 2012), it follows that the effect of testosterone on the PPS boundary would be seen in the expansion of the action space around the *self* rather than that around the other – where authors have suggested such a satellite multisensory effect may aid in interactive spatial attention (Brozzoli et al., 2013), understanding the actions and perceptions of others, and may even possibly aid in the defence of the other (Teramoto, 2018). In this way our result seems not only consonant with testosterone research, but also to reinforce the current interpretations of the function of the remapping effect. For instance, Brozzoli and colleagues (2013) suggested that shared representations of PPS could allow for a common reference frame, in which individuals can anticipate each other's motor behaviours and interactively deploy spatial attention, thus facilitating cooperative performance (Brozzoli et al., 2013). Yet, the anticipation of a potentially threatening confederate's actions could equally be understood as an important component of threat vigilance and in this sense, one might expect the remapping effect to be enhanced in the testosterone condition. However, of relevance here is behavioural and electrophysiological (event-related potential) research that has demonstrated that individuals vary in the extent to which they form shared representations of action when performing tasks with another individual. Importantly, De Bruijn and colleagues (2008) showed that participants who incorporate a co-actor's actions into their own action plan perform less successfully (slower and with less accuracy) in a competitive task than participants who do

not form shared representations. The authors concluded that although flexibly adapting one's own behaviour to accommodate others in cooperative settings may be beneficial, in competitive encounters shared action space representations may hinder one's ability to carry out one's own intended actions (de Bruijn, Miedl, & Bekkering, 2008). In this sense, because testosterone is known to enhance competitive behaviour (Casto & Edwards, 2016a), we would not expect raised testosterone to facilitate a shared action space. Considering all of these points, on balance it seems apt that the remapping effect elicited in our study was constant and consistent in size and gradient across testosterone and placebo conditions – allowing participants with raised testosterone to still anticipate the actions of the other, while focusing on oneself. Moreover, this finding indicates that the dominance enhancing effects of testosterone are elicited in perceptions of the space participants unconsciously appropriate for themselves, rather than in alterations in the perception of others' self-spaces.

To our knowledge, our study is the third behavioural study to demonstrate the remapping effect and provides a few new key insights into this effect. Consonant with the results from Teramoto's (2018) study, our findings confirm that neither the induction of a body ownership illusion, nor prior acquaintance with a confederate, are necessary conditions for producing the remapping effect. Our study also reproduced the finding of faster multisensory reaction times near participants in comparison to near confederates – suggesting a stronger PPS effect around the self than the other. In this vein, the gradient analysis in our study provided an interesting new insight into the difference between the PPS around the self and the other by showing that the gradient of the PPS boundary around the self was significantly sharper than that around the other – reinforcing the important distinction between mapping of the space of the bodily self and the mapping of another person's PPS in a manner that has hitherto not been reported. An important caveat here though, is that in our experimental setup the virtual ball only approaches the self and recedes from the other, which may contribute to a steeper gradient around the self than the other. The difference in our

experimental design also provides an important new insight into the remapping effect. In Maister and colleagues' (2015) study, a remapping effect was *only* elicited after the induction of a body ownership illusion and in Teramoto's (2018) study the remapping effect was elicited in an experimental paradigm in which moving visual stimuli were task-*relevant* and where the other was a co-actor who also responded to the same stimuli, which may have increased the saliency of the other's action space. In our experiment, the approaching virtual ball (the visual stimulus) was task-*irrelevant* and the confederate a passive presence. This difference suggests that a remapping effect may be present when the moving visual stimulus is close to another individual, even when the other individual does not interact with this stimulus. Rather, in our experiment a remapping phenomenon was elicited merely by an *implied* interaction with the visual stimulus on the part of the other (the implication of an approaching ball from the direction of the confederate is that the confederate threw the ball). In this way our study shows that a remapping effect is less contingent on specific contextual and embodiment criteria than previously thought, suggesting that such an effect may be more common than previously anticipated and more akin to a mirror neuron effect of another's actions than the projection of self-space onto another social agent. It would be interesting in future studies to ascertain whether the presence of a passive stranger may elicit the remapping effect in a paradigm where no interaction from the other is implied – for instance, by using an *audio*-tactile as opposed to a visuo-tactile interaction task, where the audio is not conceptually or ecologically related to the confederate in any way, and to include a receding condition with the audio stimulus.

Limitations

In addition to those already discussed above, our study has the following limitations. Firstly, the sample size of the study: having a larger sample size than 19 participants would have boosted the statistical power of the analysis. However, the study used a within-subjects design, which increased the power provided by our sample and this sample size is very

common in studies that have been published in the within-subjects testosterone and PPS literature. Moreover, results concerning the central hypothesis were validated by statistical triangulation, lending validity to the findings. Secondly, we had no data on participants' PPS in a non-social context. This would have been helpful in order to ascertain whether participants' PPS boundaries *expanded* or *contracted* in the social context in comparison to a non-social 'baseline' PPS – and how these changes relate to testosterone administration. Moreover, under such conditions, a gradient effect may be more likely to arise without the confounding of re-mapping. However, we chose not to include this additional step due to concern of practice and anticipation effects if performing the PPS task multiple times.

Thirdly, while we collected saliva samples at every experimental session – i.e. on both days before testosterone/placebo administration, and 4 hours after testosterone/placebo administration just before completing the PPS task, due to financial and logistical constraints we were not able to get these samples analysed. This analysis would have been valuable both to empirically show that the testosterone administration had raised salivary testosterone levels and also to allow for additional analyses based on differences in individuals' baseline testosterone levels. For example, using the placebo data it would have been interesting to see if participants with higher baseline testosterone had larger PPS boundaries in the face of the ambiguous stranger in comparison to participants with lower baseline levels.

Finally, as already discussed, the ambiguity of our confederates is another limitation of this study. More overtly threatening or neutral confederates would have allowed for more confidence in interpreting our results.

Future directions

To address the final limitation mentioned, it would be useful in future studies to examine the effects of testosterone administration on the PPS boundary separately in an overtly threatening or competitive context and in an overtly neutral context in order to provide more clarity on the meaning of our result. Specifically, would an explicitly

threatening social scenario elicit a larger PPS boundary size after testosterone administration and would the same occur in the face of a truly neutral confederate, or would the lack of a direct threat to social status attenuate a testosterone induced effect? Moreover, it would also lend evidence to understanding whether testosterone influences PPS in a 'trait' manner – for example, conferring individual baseline differences in the mapping of self-space, or, following the challenge hypothesis, if the effects of testosterone on PPS are only seen in an encounter posing a challenge to social status (as may have been elicited by our ambiguous confederates). This produces a challenge experimentally, however, as eliciting or constructing a truly neutral social experience is difficult per se. For example, might any other person, particularly a stranger, always present a subtle threat to social dominance? Moreover, as the effects of testosterone are generally studied in social contexts, eliminating a social component to the experiment in an attempt to resolve this experimental challenge (for example, by measuring participants' PPS in the face of an inanimate object) would potentially flaw *a priori* hypotheses.

In order to further our understanding of the results observed in our study, and in keeping with the embodied cognition framework that understands bodily processes as providing a foundation for cognition and emotion (Gallese & Sinigaglia, 2011), it would be useful to ascertain whether the unconscious enlargement of the 'space of the bodily self' elicited by raised testosterone translates to any consciously felt affective or psychological changes – for instance, did our participants consciously *feel* more powerful, more capable, or more in control after their PPS had expanded? Likewise, did they feel a heightened intention or desire to interact with or approach the confederate? This could be measured using questionnaires and semi-structured interviews after each experimental session, or by presenting participants with options for a course of action following the PPS task (e.g. the option to engage individually with a mind-game or interact competitively with a confederate). Moreover, this could be studied further and in a potentially more ecologically valid way by

measuring the PPS boundary of individuals high in confidence and other indices of trait dominance.

Conclusion

In this study PPS and testosterone, two well established fields of enquiry in the neurosciences, were brought together in the laboratory for the first time. Given the importance of PPS in planning approaching and defensive responses (de Vignemont & Iannetti, 2015), and the reputation of testosterone as a hormone which promotes social approach and vigilance to threats to social status (Terburg & van Honk, 2013), we hypothesised that the dominance enhancing effects of testosterone might reflect at the bodily level in changes in the mapping of PPS. Indeed, we found that raised testosterone changed the mapping of PPS such that a larger area around the body was incorporated into the representation of PPS, thought of as the 'space of the bodily self' (Noel, Pfeiffer, et al., 2015; Serino, 2019). This finding provides two key takeaway messages. Firstly, raised testosterone (and therefore, putatively raised dominance motivation) unconsciously and reflexively caused participants to appropriate a larger space as their own – in other words, it caused participants to represent a larger space specifically in relation to their bodily representations, potentially allowing them a greater space in which to 'take charge' by rapidly executing responses to stimuli. In this way, at the level of the body, we have shown that a larger PPS may provide an index of social dominance. Thus, measures of PPS might prove useful in other research domains where reliance on introspective methods for ascertaining dominance motivation has proven unreliable. Secondly, the functional significance of PPS – that it is the body's *actionable* space, the mapping of which allows for rapid approaching or defensive responses to stimuli within this space – suggests that an enlargement of PPS may support the already well described increase in social approach behaviour and vigilance to threat associated with testosterone (Eisenegger et al., 2011; Terburg & van Honk, 2013).

Further, our results indicated that testosterone did not have a significant effect on the

gradient of the PPS boundary, although this analysis may have been confounded by the presence of a multisensory facilitation effect around the confederate. Analysis of the multisensory facilitation effect found around the confederate confirmed that the effects of testosterone on PPS were *self*-specific, as no differences in other-PPS were recorded. Finally, our finding that participants higher in trait anxiety were most prone to PPS enlargement after testosterone administration converge with recent research that has shown that the dominance enhancing effects of testosterone can be particularly effective in anxious individuals where an increase in dominance and approach behaviour may be most needed (Terburg et al., 2016). These findings offer novel support to the notion of the inter-dependence between higher-order cognition and bodily processes, and support the nascent body of literature on how the effects of testosterone on social dominance may be grounded in sensory-motor systems of the body.

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Appendix A

SELF-EVALUATION QUESTIONNAIRE

STAI Form Y-2

Name_____ Date_____

DIRECTIONS

A number of statements which people have used to describe themselves are given below. Read each statement and then circle the appropriate number to the right of the statement to indicate how you *generally* feel. There are no right or wrong answers. Do not spend too much time on any one statement but give the answer which seems to describe how you generally feel.

	ALMOST NEVER	SOMETIMES	OFTEN	ALMOST ALWAYS
21. I feel pleasant	1	2	3	4
22. I feel nervous and restless	1	2	3	4
23. I feel satisfied with myself	1	2	3	4
24. I wish I could be as happy as others seem to be	1	2	3	4
25. I feel like a failure	1	2	3	4
26. I feel rested	1	2	3	4
27. I am "calm, cool, and collected"	1	2	3	4
28. I feel that difficulties are piling up so that I cannot overcome them	1	2	3	4
29. I worry too much over something that really doesn't matter	1	2	3	4
30. I am happy	1	2	3	4
31. I have disturbing thoughts	1	2	3	4
32. I lack self-confidence	1	2	3	4
33. I feel secure	1	2	3	4
34. I make decisions easily	1	2	3	4
35. I feel inadequate	1	2	3	4
36. I am content	1	2	3	4
37. Some unimportant thought runs through my mind and bothers me	1	2	3	4
38. I take disappointments so keenly that I can't put them out of my mind	1	2	3	4
39. I am a steady person	1	2	3	4
40. I get in a state of tension or turmoil as I think over my recent concerns and interests	1	2	3	4

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STAIP-AD Test Form Y
www.mindgarden.com

Appendix B

Are there any benefits to you if you take part in this research?
You will be compensated with R350 for taking part in this study. If you are a psychology student, you will be compensated with course credit (3 SRPP points) for taking part in this study.

What happens if you do not want to take part in this research?
Nothing. It is your right to not take part in the research, or to withdraw at any time during the research with no consequence to you whatsoever. Furthermore, you may request that your data be removed confidentially from the dataset.

What happens at the end of this research?
Debriefing will take place once all data is collected. This will allow you the opportunity to learn more about the aims and objectives of the study.

Having read through all the questions and answers, please comment on whether you understand everything written in it, if not then please comment on what you did not understand, or any concerns that you might have:

_____
_____
_____
_____
_____

Full names and surname (please print):

_____

Signature: _____ Date:_____

What if something goes wrong?

Professor Mark Solms is covered under the no fault clause of the University of Cape Town Insurance.

As per this:
The University of Cape Town (UCT) undertakes that in the event of you suffering any significant deterioration in health or well-being, or from any unexpected sensitivity or toxicity, that is caused by your participation in the study, it will provide immediate medical care. UCT has appropriate insurance cover to provide prompt payment of compensation for any trial-related injury according to the guidelines outlined by the Association of the British Pharmaceutical Industry, ABPI 1991. Broadly-speaking, the ABPI guidelines recommend that the insured company (UCT), without legal commitment, should compensate you without you having to prove that UCT is at fault. An injury is considered trial-related if, and to the extent that, it is caused by study activities. You must notify the study doctor immediately of any side effects and/or injuries during the trial, whether they are research-related or other related complications.

UCT reserves the right not to provide compensation if, and to the extent that, your injury came about because you chose not to follow the instructions that you were given while you were taking part in the study. Your right in law to claim compensation for injury where you prove negligence is not affected. Copies of these guidelines are available on request.

What if you have complaints about the study?

If you want any information regarding your rights as a research participant, or have complaints regarding this research, you may contact Professor Marc Blockman, the **Chairperson of the Research Ethics Committee** at the University of Cape Town.

The contact information for the HREC is as follows:

Human Research Ethics Committee
Faculty of Health Science
E-52-54 Groote Schuur Hospital Old Main Building
Observatory 7925
Tel: (021) 406 6626
Fax: (021) 406 6411
Email: lamees.emjedi@uct.ac.za

If you have consulted your doctor or the ethics committee and they have not provided you with answers to your satisfaction, you should write to:

The Registrar, South African Medicines Control Council (MCC),
Department of Health, Private Bag X 828, PRETORIA 0001.

Appendix C

PARTICIPANT DEBRIEFING INFORMATION SHEET

We thank you for your participation in our study!

Prevention of disclosure of study information

We would like to remind you that all information you provide will be kept strictly confidential and that your identity will remain anonymous throughout the research. The saliva samples will be used to check your baseline testosterone levels and nothing else. They will be stored in a security-controlled laboratory.

Safety reminder

All women have naturally circulating testosterone in their bodies and the dosage that you ingested is less than the total amount produced during one day. It will be out of your system within about six hours from the time of administration and you will not experience any harmful side-effects. No long term harmful effects have been reported with this dosage of testosterone. The placebo solution is a harmless fluid with no active ingredients, made to taste the same as the testosterone.

What if something goes wrong?

Professor Mark Solms is covered under the no fault clause of the University of Cape Town Insurance.

As per this:
The University of Cape Town (UCT) undertakes that in the event of you suffering any significant deterioration in health or well-being, or from any unexpected sensitivity or toxicity, that is caused by your participation in the study, it will provide immediate medical care. UCT has appropriate insurance cover to provide prompt payment of compensation for any trial-related injury according to the guidelines outlined by the Association of the British Pharmaceutical Industry, ABPI 1991. Broadly-speaking, the ABPI guidelines recommend that the insured company (UCT), without legal commitment, should compensate you without you having to prove that UCT is at fault. An injury is considered trial-related if, and to the extent that, it is caused by study activities. You must notify the study doctor immediately of any side effects and/or injuries during the trial, whether they are research-related or other related complications.

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If you have consulted your doctor or the ethics committee and they have not provided you with answers to your satisfaction, you should write to:
The Registrar, South African Medicines Control Council (MCC),
Department of Health, Private Bag X 828, PRETORIA 0001.

Why is this research being done – what is it trying to find out?
This is an exploratory study. This research is being done to investigate how the brain interprets the space around the body. We have used testosterone experimentally to boost feelings of social confidence and explore whether this increases reaction times to sensory input in our immediate space.

If you would like to see the final results of this study, please send us an email. You are also invited to email us with any further questions that you may have.