THE PERSISTENCE OF THE EFFECTS OF CERTAIN ASPECTS OF INFANTILE EXPERIENCE ON THE BEHAVIOUR OF ADULT RATS

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by

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B. Results of t tests of mean difference between undisturbed and mother-removed groups (none significant).

	Group I (50 days)	Group II (100 days)		Group III (220 days)
	Males	Males	Females	Females
Weight increase	1.9	0.8	1.2	0.5
Preliminary				
Rears	0.5	0.5	0.0	1.0
Crossings	1.1	0.0	0.3	1.2
Latency	0.7	0.8	0.1	0.8
Grooms	0.1	0.0	not normal	0.1
Avoidance				
Trials	1.5	0.4	0.5	1.4
Latency	1.4	0.1	0.1	2.0
Extinction				
Trials	0.7	0.4	1.4	1.8
Latency	0.8	0.2	0.1	0.0
Elevated maze				
Time	0.6	0.4	0.1	0.0
Consumption	0.0	0.4	0.2	0.2
Errors	not normal	0.4	0.1	0.1

C. DISCUSSION AND CONCLUSIONS

Cage size

The only test which reveals significant interaction between cage size and handling is grooming in the preliminary trials. Similarly, it is grooming in the preliminary trials which reveals a fairly consistent effect of cage size. The fact that cage size has had so little measurable effect on behaviour in the series of tests conducted probably accounts for the fact that interaction levels are so low.

The consistency of the interaction in grooming makes us hesitant about entirely rejecting the hypothesis that there is an interaction between cage size and handling.

Besides grooming, the only other test performance affected by cage size is latency in the preliminary runs without shock for group III only. The level of confidence is only 5% though, and the distinction occurs only in group III. This is not sufficient evidence for accepting that cage size affects latency.

At first sight the finding that housing in large cages has no effect on performance in the elevated maze appears to contradict the findings of Forgays and Forgays (1952) and Forgus (1954) who found that experience of a larger and freer environment was significant in performance. But it should be recalled that by the time the rats began their testing on the elevated maze they had already been handled in other tests for twelve days and had entered the new environment of the testing apparatus. Furthermore, the animals from the small cages, though their proprioceptive or muscular experiences was limited, were able to look out through the wire mesh fronts of their cages. The restricted animals in the experiment of Forgays and Forgays were housed in cages with solid walls, and

in the experiment of Forgus they were placed in a solid black box with a mesh roof. In neither of these groups was it possible for the animals to form prominent visual reaction sets. The intention in the present experiment was not to demonstrate the effects of such severe restriction; but perhaps those are the conditions which are necessary for significant interaction scores.

The cages of animals in Levine's experiments also had solid metal walls and vision was extremely limited.

Removal of mother

The hypothesis that removal of the mother is a variable of importance is not supported, at least when removal is for the period of fifteen minutes a day. Longer periods might produce effects on behaviour.

Handling

In the series of trials reported in this thesis, several measures were significantly affected by handling, especially in the preliminary runs in the Miller box without shock.

In all three groups a significant difference was found in the number of rears. Handled and undisturbed subjects differed in crossing the barrier from one half of the box to the other and in latency to first crossing in group II males and in group III females only. Rears, crossing of the barrier, and latency are taken as measures of activity, possibly associated with reduced emotionality. In these measures of activity the handled group proved superior, though differences were not statistically significant in all cases. This finding is in agreement with the findings of Weininger (1953, 1954, 1956) and Levine (1955, 1956).

As in the work of Ader (1959), defecation was found to be atypical in the preliminary trials. The only measure of emotional behaviour in which a difference was found as a result of handling was grooming. Two groups, I and III, of handled animals groomed less than the undisturbed animal. There is not entire consistency, since group II showed no distinction, but the coincidence of two groups revealing significant differences at the 5% level in the same direction makes us hesitate about rejecting the effect.

Of the twelve preliminary trials eight reveal significant differences in the expected direction - six of these at less than one per cent - and the non-significant differences are in the same direction. It appears, therefore, that clear differences exist in the activity of handled and undisturbed animals.

In the avoidance trials there is also some evidence in support of the findings of Levine and others (1955)and Levine (1956). In group III the handled animals spend less time in the shock compartment than the undisturbed controls. It is puzzling that there is no difference between handled and undisturbed animals in groups I and II, since the distinction in group III is at the 1% level of confidence. The handled animals require fewer trials to learn the avoidance response in groups I and III.

In the extinction trials only one difference appeared, at the 5% level, between the handled animals and the undisturbed animals in group III. The level of confidence is too low and the result is too isolated to be accepted as indicating any difference. This finding is in agreement with the results of Levine (1956).

Time to the first consumption of water on the elevated maze was not different for handled and non-handled animals. Therefore, we cannot offer any support to the

finding of Levine (1957b) that early handling accelerates consummation after deprivation. But though no support can be offered, these findings do not contradict his, since the conditions were different. The animals had been handled during preliminary, avoidance and extinction trials before being put on the maze. Ader (1957) has shown that handling of three minutes duration is sufficient to produce behavioural differences. The handling in testing is, therefore, quite sufficient to account for the complete absence of differences between handled and undisturbed animals on later tests.

Persistence of effects

It is clear from the results that differences between the handled and the undisturbed animals in measures of activity, grooming and avoidance learning persist until the age of at least 220 days. It is also clear that there is no decrease in the differences until the age of 220 days. What is not too clear is whether there is a tendency to increase the difference. Scores of activity (rears, crossings, and latency to first crossing) show a clear upward tendency with age, (Appendix 9-11) but scores of grooming and number of trials to learn the avoidance response show a dip at 100 days which may or may not be a genuine trend or an artefact of this experiment. Unrecognised variations, such as the fact that the 100-day group was reared in the summer while the other groups were reared in the winter, might affect the trend. Another possibility is that age-related factors might overshadow the effects of handling at this specific age. In order to check on this, graphs have been drawn up showing the mean scores for grooming and trials to learn avoidance. (Appendix 7-8) Inspection of these shows that there is no sharp rise or fall at this age, so that it does not appear that the drop in difference is directly related to level of performance. The idea that there may be ages at

which various activities share a general rise or decrease irrespective of life history is not supported.

Further evidence is required to discover whether the decrease in difference between handled and undisturbed groups in grooming and avoidance trials is a genuine trend or not.

It can also be seen from the graphs of the F (Appendix 9-15) values that the differences between handled and undisturbed groups in avoidance latency and extinction trials are not significant until the age of 220 days. This is another trend which may be an artefact or not.

Therefore, we may safely say that the effects do persist, and we may tentatively say that there appear to be two patterns of persistence. The first, in measures of activity, is an almost rectilinear function, while the second pattern, which holds for grooms and avoidance learning, may be a U-type of curve. Another finding is that activity measures are highly correlated with one another, and that grooming and avoidance trials are highly correlated with each other.

In an attempt to find out if the handling received during testing was responsible for the obliteration of differences in later tests, bar diagrammes of the difference in performance in each trial of the preliminary runs have been drawn up. (Appendix 1-3) If handling in testing was obliterating the differences between the handled and the undisturbed group, the bar diagrammes of differences should show a steady decline from trial 1 to trial 3. Inspection of the diagrammes shows that there is no pattern common to all the groups. In fact, there are usually three different patterns.

The question, therefore, remains undecided.

The finding that there are no differences in the rate of increase in weight as a function of handling agrees with the finding of Ader (1959), though it disagrees with

the finding of Weininger (1955). No explanation can be offered of the contradictions.

Theoretical aspects

When we review the theoretical contributions to the understanding of the effects of handling, we become aware of contradictions and difficulties of interpretation. This is not surprising, since even the experimental findings are often contradictory.

It is not certain whether the differences in reaction to testing are the result merely of taming or whether they can be explained as far-reaching changes in reaction-threshold to emotion-provoking novelty. On the one hand we have the evidence that handled rats are more resistant to stress which has been offered by Weininger (1954, 1955, 1956) and Levine (1957a) and Levine, Alpert and Lewis (1958). On the other hand there is the contradictory and thorough study of Ader (1959). Evidence of far-reaching homeostatic changes is found in Ruegamer, Bernstein and Benjamin's (1954) report on more efficient food utilisation by handled animals and Levine's (1960) report of the more rapid adjustment of adrenalin level among handled animals.

Bovard (1954) has postulated that handled animals have reduced sympathetic nervous activity, and Griswold and Gray (cited in Ader, 1959) have found that repeated autonomic activity results in a gradual reduction of sympathetic activity. Therefore, if we assume that handling acts as a stress and produces repeated autonomic activity, such a gradual reduction in sympathetic activity will occur.

Those who have handled previously unhandled animals will agree that it is a very exciting occasion. The squealing, urination and defecation indicate that the handling is a stress, using the word in the general sense assigned to it by Selye.

Selye's work is, therefore, important in making clearer to us the effects of stress, but the explanation of the mechanism of heightened threshold is not yet clear. The rôle of the ascending reticular activating formation may turn out to be important, but suggestions are tentative at this stage. Bruner's (1961) suggestion is that the more varied the experience of the animal, the more likely it is to develop centrifugal control of the sensory system; and the work of Riesen (1961) shows that such centrifugal control, enabling the animal to monitor sensory input may be important in controlling emotional response. Helson's (1948) and McClelland's (1953) concept of an adaptation level is, I believe, important in understanding the reaction of an animal to novel stimulation. Though unsupported by a great deal of evidence as yet, the proposal by McClelland that the hedonic effect is a joint rational function of three constants in receptor functioning - lower threshold, upper threshold, and the Weber fraction - may be extended to cover broader patterns of experience.

According to this view, the experience of handling in the test situation presents a smaller discrepancy from expectation for the handled animals than for the undisturbed. McClelland, discussing the effect of different levels of expectation, proposes that fulfilment of low expectancy produces fear, of moderate expectancy produces satisfaction, and of high expectancy produces boredom. Since the expectancy of the undisturbed animals is at a lower level than the expectancy of the handled animals, the discrepancy of the handling experience from the constant pattern of their lives is much greater and produces a higher level of fear.

There are two important questions for theory to solve here. Firstly, is there a definite trend in the differences between handled and undisturbed animals as they grow older? Secondly, how can an adaptation-level theory,

explain this trend?

As to the first point, it can be said with assurance that differences do not decrease with age up to 220 days. There is also some evidence that they increase in measures of activity, if not in other measures.

The adaptation-level theory may be used to explain this trend in two ways.

The first way is to assume that the major differences between the handled and undisturbed animals are caused by their adaptation to handling. Those that have been trained prior to testing show up more favourably in testing. The tendency for differences to increase might be ascribed to the fact that older animals are generally more difficult to tame than younger animals. The evidence against this view, that handled animals resist stress better and show better endocrine economy, has been mentioned. A distinction may have to be made between those parameters which are affected mainly by the tameness of the animals and those which reveal stress-adaptation.

The second way of using an adaptation-level theory to explain the major differences between handled and undisturbed animals is to emphasise the ability of the animal to adapt to the testing situation as a whole. The argument here could be that handling permanently raises the threshold of emotional response in the rat, but that the later it occurs, the less effective it is. Such a view would hold that handling is only one of many forms of stress which could be used to demonstrate such a general rise in the adaptation-level of the animal. This view rests on the slender evidence of the experiment of Levine, Chevalier and Korchin (1956) which found that handling and shock both raised the performance level of animals in avoidance learning. The fallacy is that the shocked animals were also handled. Another finding by Levine and Lewis (1959) that shaking animals

in their cages without touching them raises their resistance to cold, provides firmer evidence for at least one effect of early stimulation which does not depend on familiarity with the experimenter, but does not dispose of the possibility that it is the most important factor in our results. The work of Ader (1959) leads us to question the scope of the effects of stimulation other than handling on performance in the open field and in learning situations.

A great deal more refinement of technique is required to discover what the scope of the effects of various forms of early stimulation is. Perhaps lumping too many variations together as 'early stimulation' and expecting them all to affect the same aspects of behaviour is fallacious.

Conclusions

The hypothesis that interaction between stimulation by handling and conditions of housing reduces differences between handled and undisturbed rats in scores of activity, emotional behaviour, and learning when the rats are housed in large cages and increases them when the rats are housed in small cages was not borne out, except in the case of grooming behaviour. Inter-action of effect on grooming behaviour was significant and the differences in the small cages (group I :F=2.2; group III :F=3.2) were larger than differences in the large cases (group I :F=0.4; group III :F=0.8).

Interpretation of this limited effect is not attempted. The rationale of the hypothesis, that stimulation by housing in a large cage might compensate for the lack of stimulation by handling among undisturbed animals, cannot be supported conclusively enough for development by this isolated result.

The hypothesis that removal of the mother during the nursing period is an important variable to control in experiments on the effects of handling before weaning must be rejected.

The rationale of this hypothesis, that the agitated mother might stimulate the pups by her behaviour when returned to them, is not supported.

The hypothesis that the effects of early stimulation on growth, activity, emotional behaviour and learning persist into maturity is borne out with the qualification that no effects on growth, defecation and urination, or maze learning are observed at any age.

All the effects observed at 50 days (on rears, grooms, trials to learn avoidance) are present at 220 days; and some of the effects observed at 220 days (crossings, latency to crossing, latency to avoidance response, and trials required to extinguish avoidance) are not present at 50 days.

It appears from these results that the effects of handling on measures of activity and avoidance learning increase with age at which testing is commenced.

Handling increases activity and speed of learning the avoidance response at all ages.

It is also concluded that the data of this experiment do not enable us to decide whether the effects of handling are the result of early taming of the handled animals and an increasing inability of the undisturbed animals to adjust to handling in the testing situation as they grow older, or whether the effects of handling are the result of profound changes in the development of the handled animals.

More work with different kinds of stimulation, in which the effects of handling are eliminated or controlled, is needed to settle which of these two explanations, if either, can be accepted.

D. SUMMARY

Hypotheses

This experiment was designed to test the following hypotheses :

(i) That the interaction between stimulation by handling and conditions of housing reduces differences between handled and undisturbed rats in scores of activity, emotional behaviour, and learning when the animals are housed in large cages and increases them when the animals are housed in small cages.

(ii) that the removal of the mother during the nursing period is an important variable to control in experiments dealing with the effects of handling before weaning; and

(iii) that handling in infancy produces effects on growth, emotional behaviour, activity and learning which persist into maturity.

Subjects

A total of 126 subjects representing 5 types of treatment was divided into three groups, each group to be tested at a different age. This made a total of 15 sub-groups. The ages at which the three groups were tested were: Group I, consisting of 40 male subjects was tested at 50 days; group II, consisting of 20 male subjects and 32 female subjects was tested at 100 days; group III, consisting of 34 female subjects commenced testing at 220 days.

Treatment

Each group contained all five types of treatment : handled and housed in small cages; handled and housed in large cages; undisturbed and housed in small cages; undisturbed and housed in large cages; and mother removed and

housed in small cages.

The animals were weaned at 25 days and housed 4 per cage undisturbed till the day of testing.

Testing

Testing was identical for all three groups.

Firstly, animals were weighed at weaning and on the day of testing to determine ratio of increase of weight.

Secondly, all animals were given 3 runs of 3 minutes each in the avoidance training apparatus without shock. Rears, crossing-the-barrier, latency to first crossing in each trial, grooms, defecation and urination scores were recorded.

Thirdly, all animals were trained to avoid shock by crossing the barrier and this response was then extinguished.

Fourthly, all animals learnt an elevated T-maze for a water reward.

Results

Growth was not affected by handling, removal of the mother, or cage size.

Activity differences between handled and non-handled animals, as measured by rears, latency to 1st crossing of the barrier, and number of crossings of the barrier from one compartment to the next, increased with age. Activity was not affected by removal of the mother or by cage size.

A U-shaped curve was found for F values of differences between handled and non-handled animals in grooming and avoidance learning trials; latency to response in avoidance trials and trials to extinction of the avoidance response were found to distinguish between handled and non-handled animals at 220 days only, supporting the finding that there are more differences between handled and non-handled animals at 220 days than at either 50 days or 100 days.

The hypothesis that interaction between cage size and handling would significantly affect scores was supported only by the scores for grooming at 50 and 220 days, when interaction was significant at the 5% level.

The hypothesis that removal of the mother is a significant variable to control in experiments on the effects of handling before weaning is rejected. In no case did removal of the mother significantly affect performance.

The hypothesis that the effects of handling on growth, activity, emotional behaviour, avoidance learning and maze learning persist into adult life was supported in the case of activity, grooming, and avoidance learning. All differences found at 50 days were also found at 220 days.

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APPENDIX

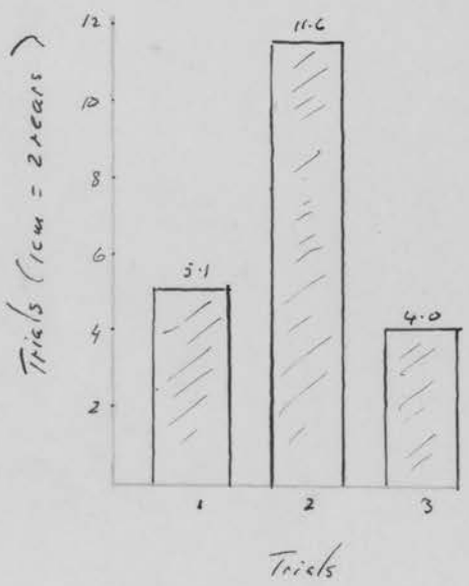
CONTENTS

A. Graphs I - 15.

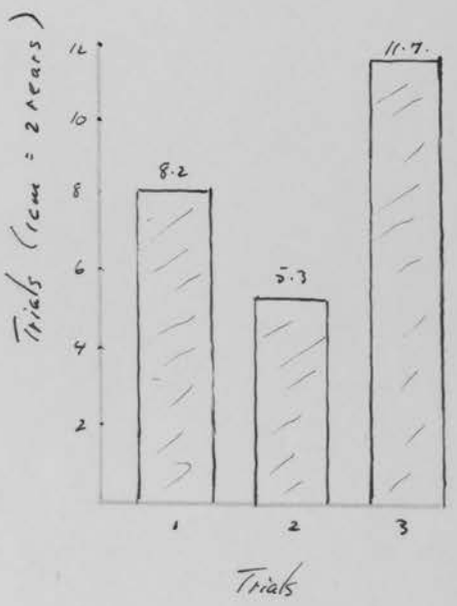
B. Tables 8 - 42.

A. 1. Bar diagramme of average difference, in number of years, between handled and undisturbed subjects in three preliminary trials.

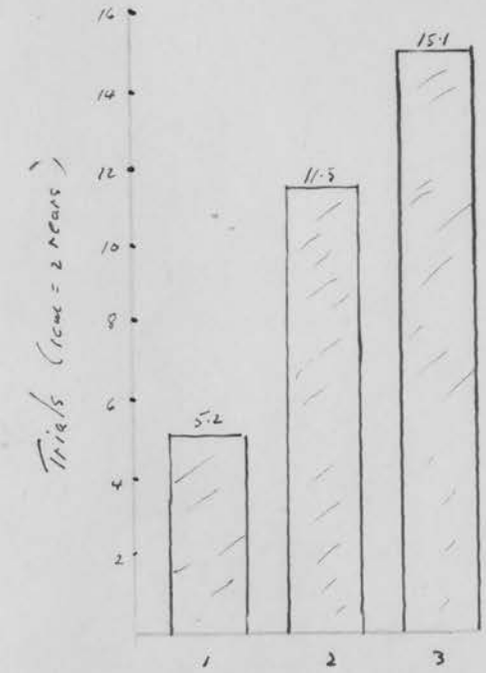
Group I (50 DAYS)



Group II



Group III



Scores

Group I (N20)

	Trials 1	2	3
handled	210	260	262
undisturbed	159	144	222

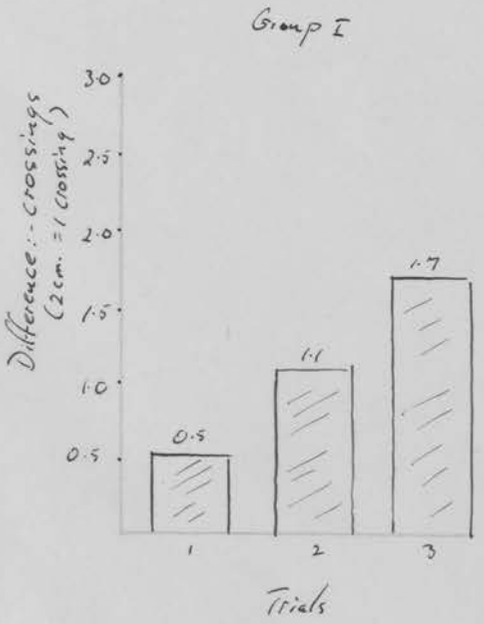
Group II (N24)

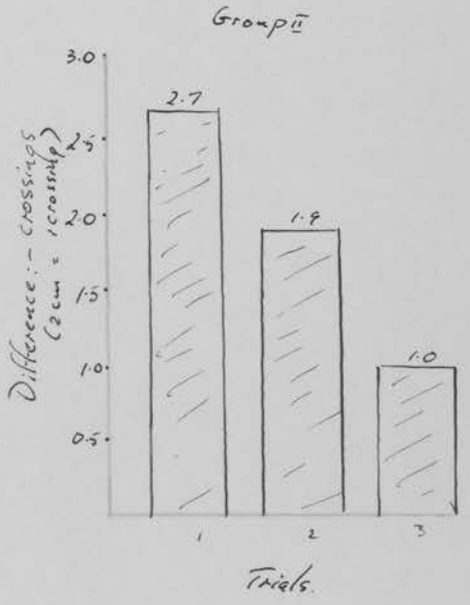
	Trials 1	2	3
handled	269	331	402
undisturbed	190	268	262

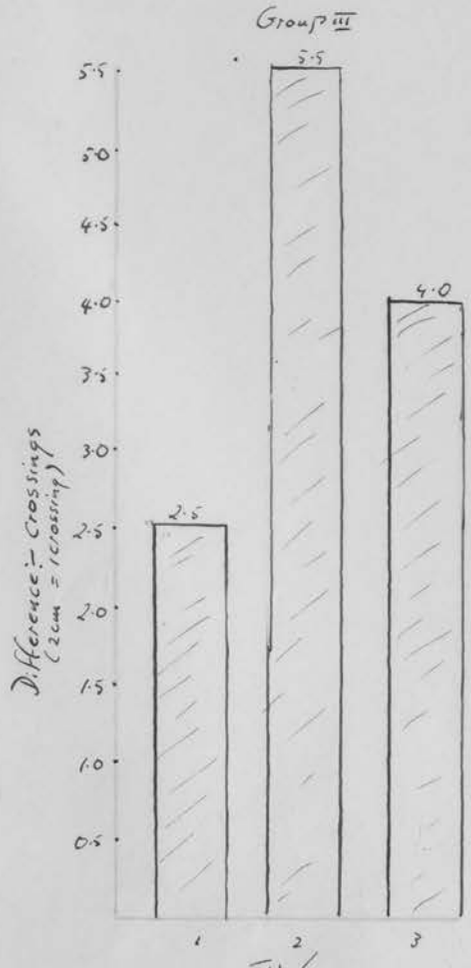
Group III (N16)

	Trials 1	2	3
handled	214	250	260
undisturbed	173	158	139

A 2. Bar diagramme of average difference, in number of crossings between handled and undisturbed subjects in three preliminary trials







Scores

Group I (N20)

Trials	1	2	3
handled	5	18	24
undisturbed	0	7	17

Group II (N24)

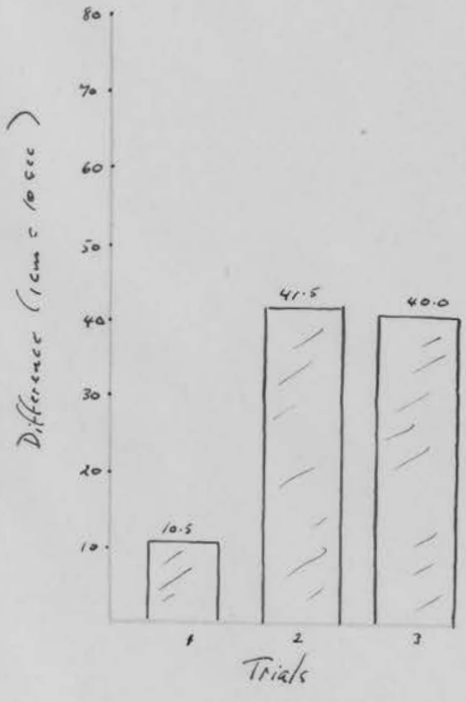
Trials	1	2	3
handled	36	69	73
undisturbed	7	45	61

Group III (N16)

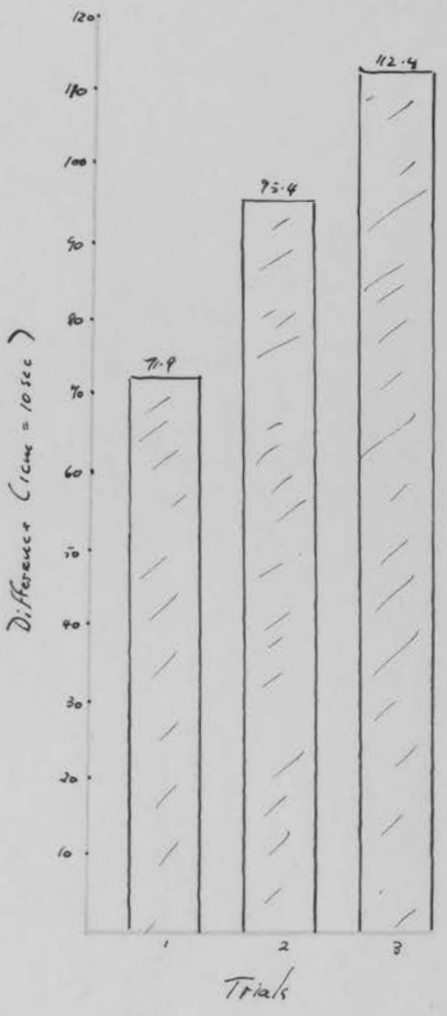
Trials	1	2	3
handled	22	50	46
undisturbed	2	6	14

A. 3. Bar diagrammes of average difference, in latency to crossing, between handled and undisturbed subjects in three preliminary trials.

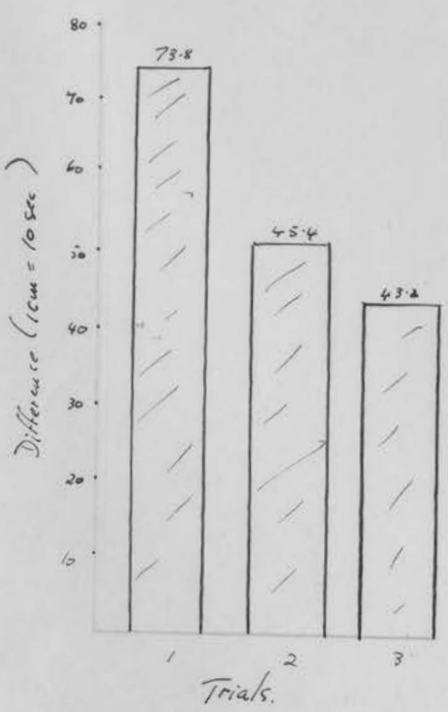
Group I



Group II



Group III



Scores

Group I (N20)

Trials

	1	2	3
handled	1695 sec	1180	830
undisturbed	1800 "	1595	1230

Group II (N24)

Trials

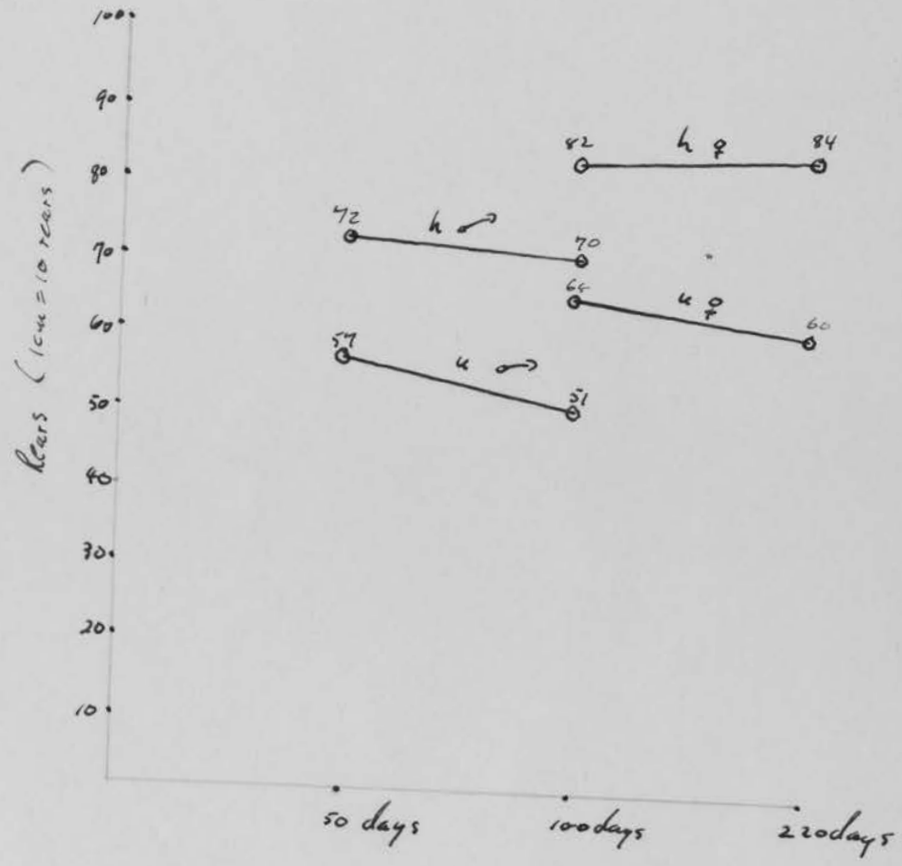
	1	2	3
handled	1170 sec	635	396
undisturbed	2055 "	1180	914

Group III (N16)

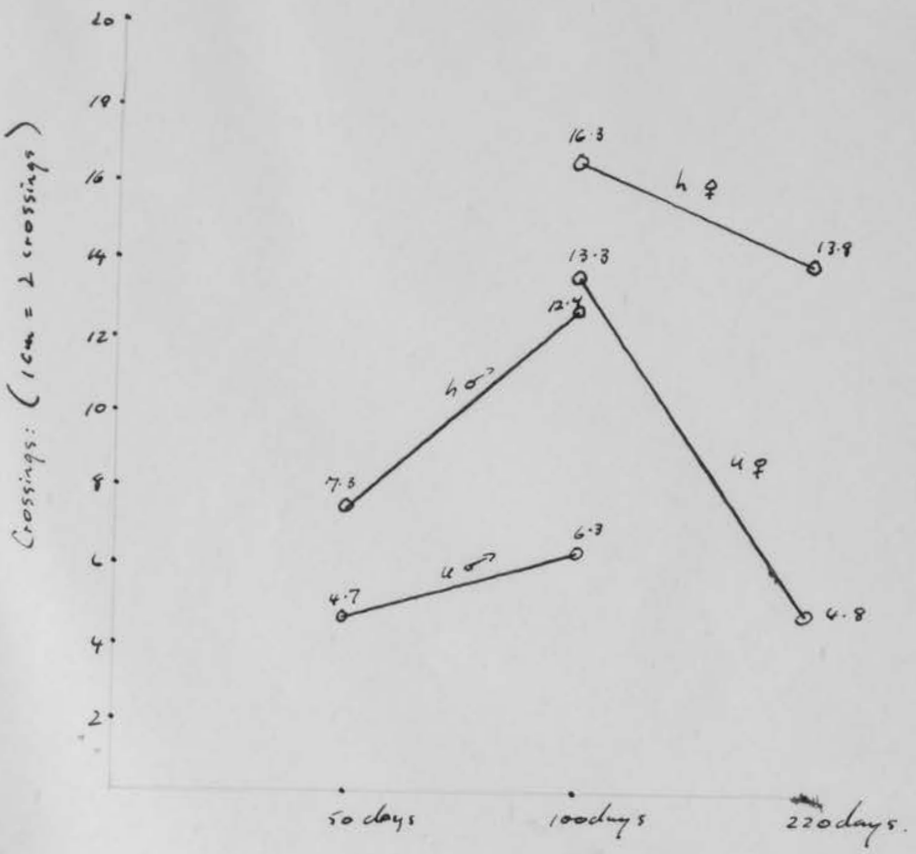
Trials

	1	2	3
handled	485 sec	367	172
undisturbed	1360 "	1130	1071

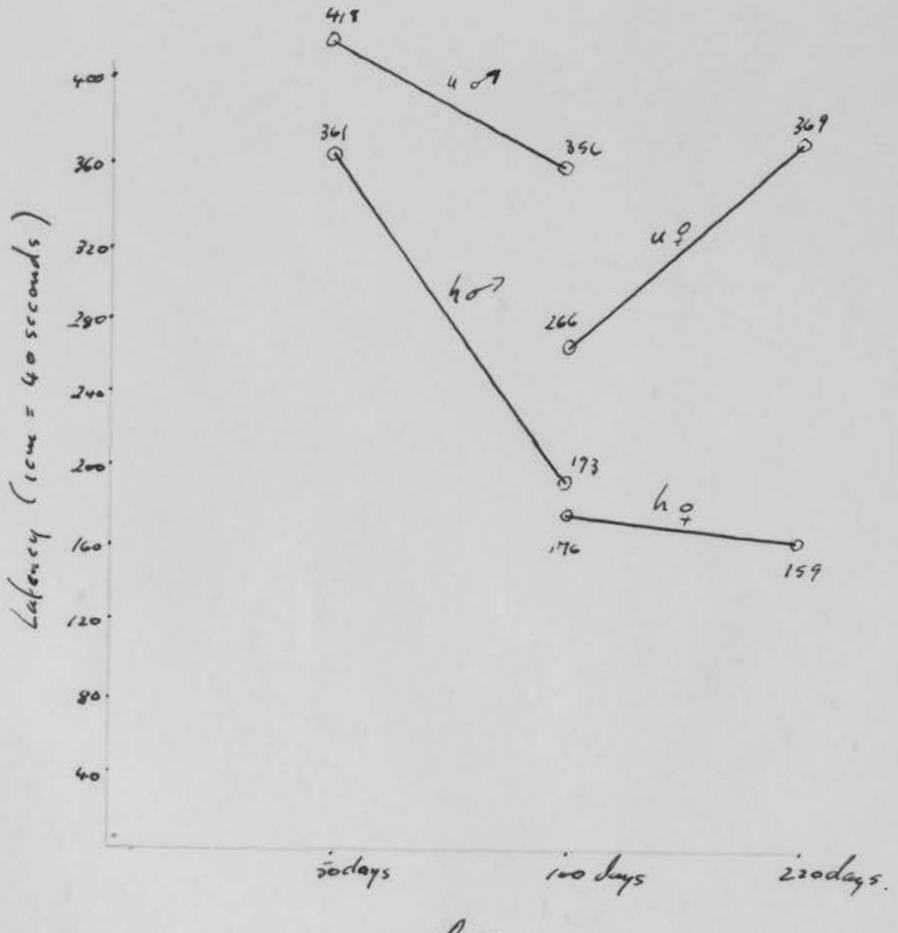
A. & Rears:- Means of handled (h) and undisturbed (u) subjects at three ages.



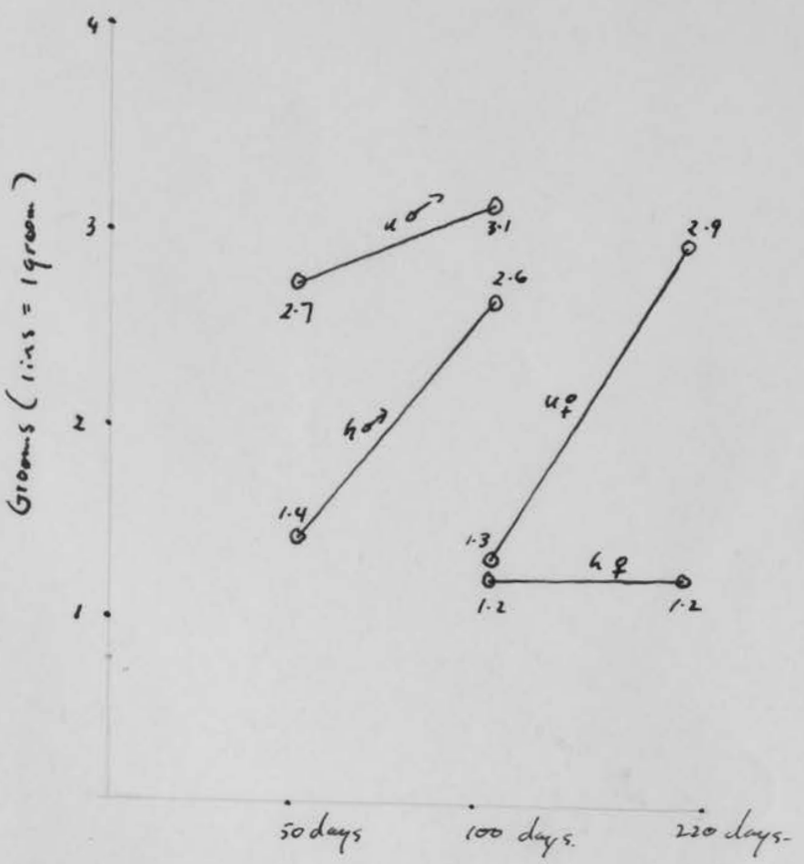
A. 5. Crossings:- Means of handled (h) and undisturbed (u) animals at three ages



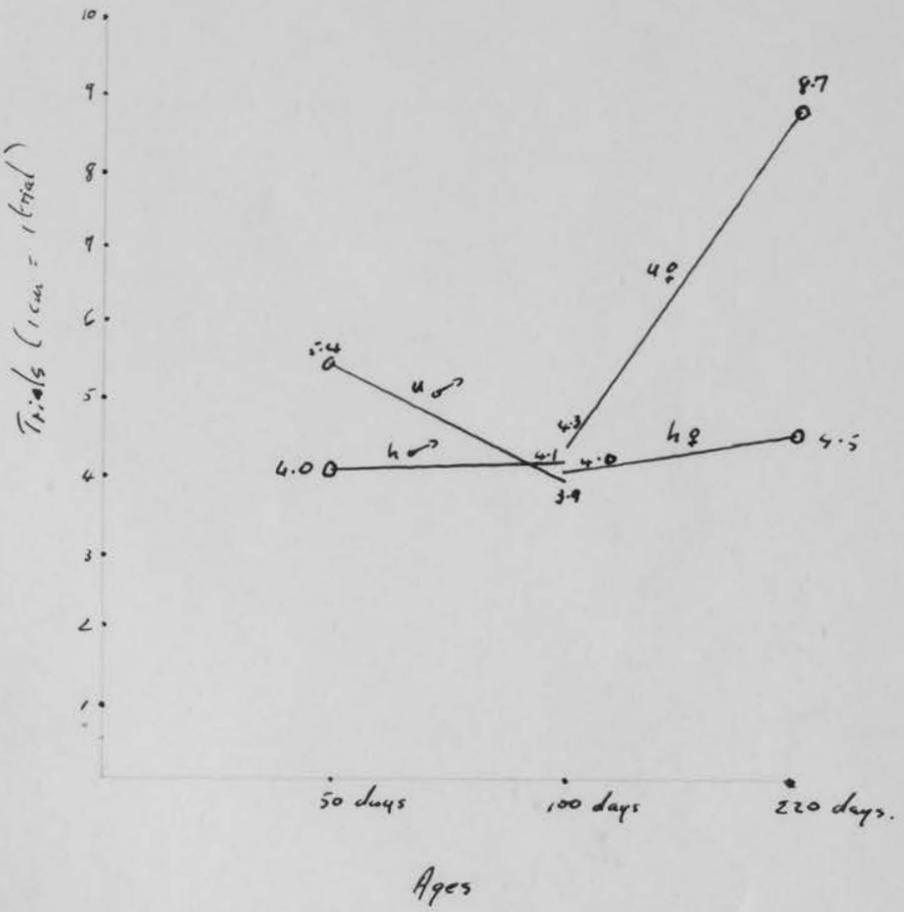
A. 6. Latency:- Means of handled (h) and undisturbed (u) animals at three ages.



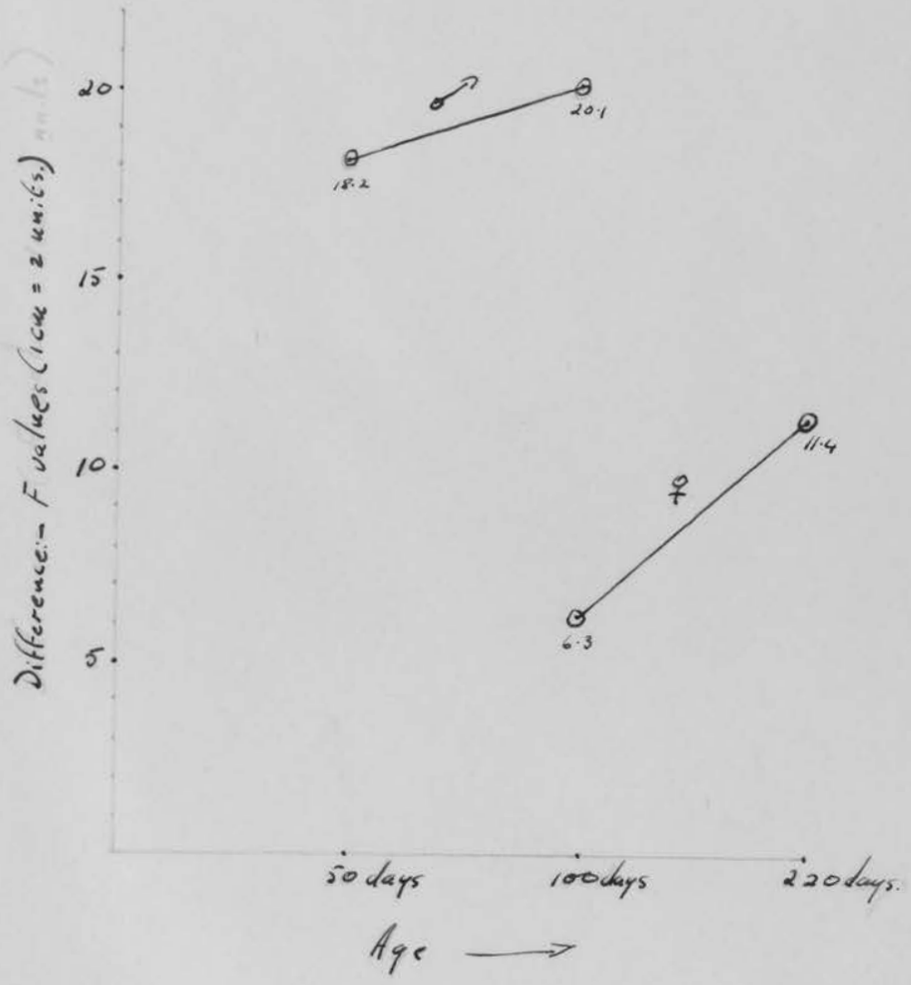
A. 7. Grooms:- Means of handled (h) and undisturbed (u) subjects at three ages.



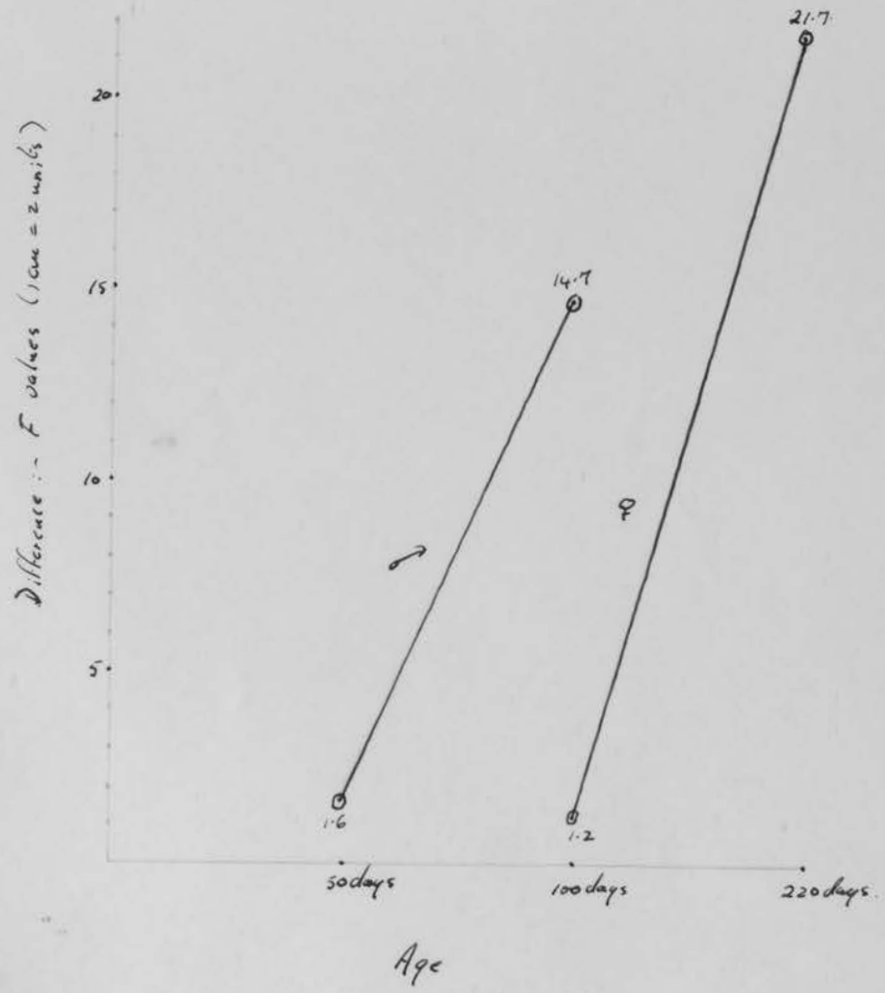
A. 8 Avoidance Trials:- Means of handled (h) and undisturbed (u) subjects at three ages.



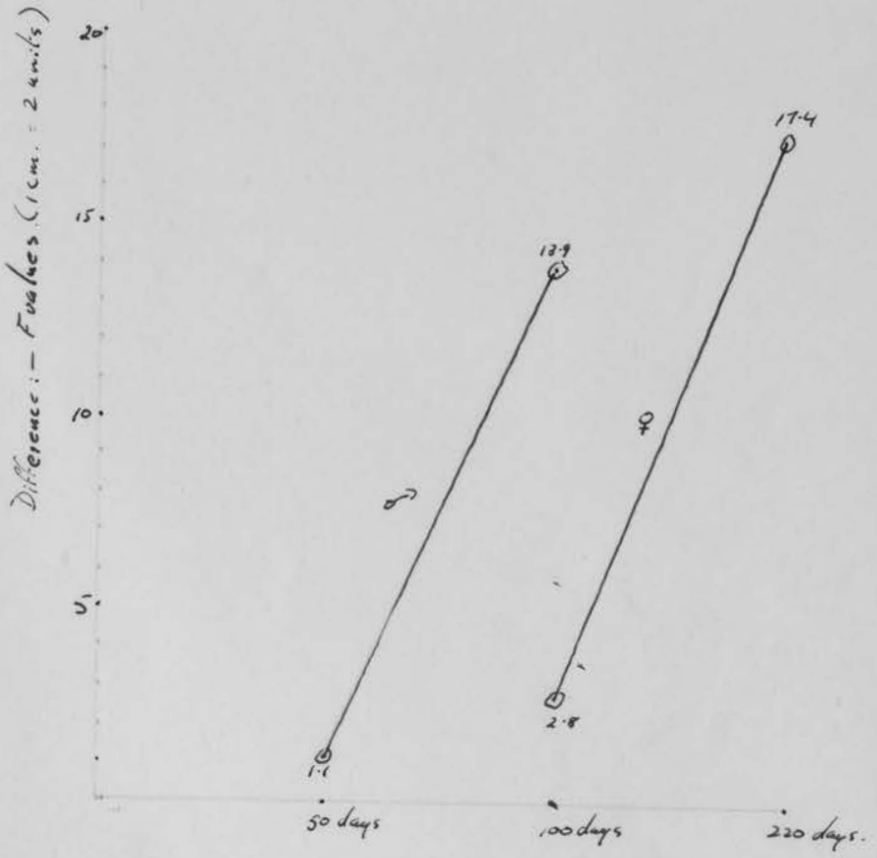
A. 9. Rears:- Persistence of difference between handled and undisturbed animals.



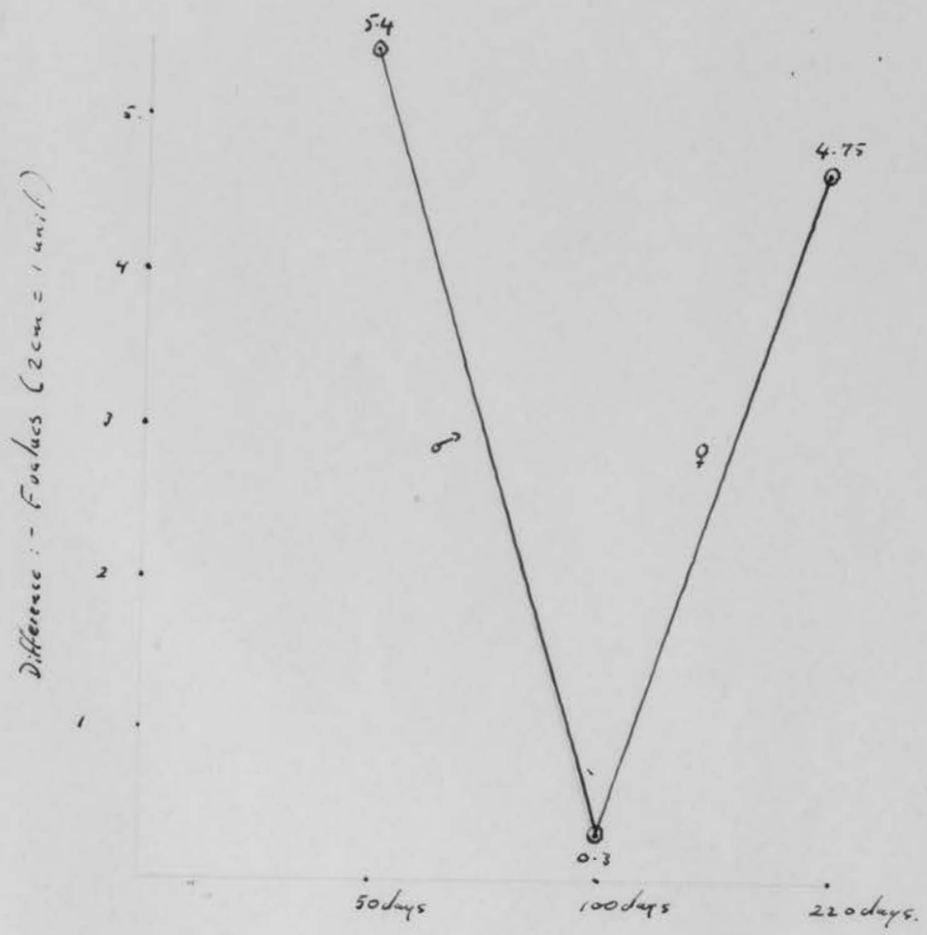
A. 10. Crossings: — Persistence of difference between handled and undisturbed animals.



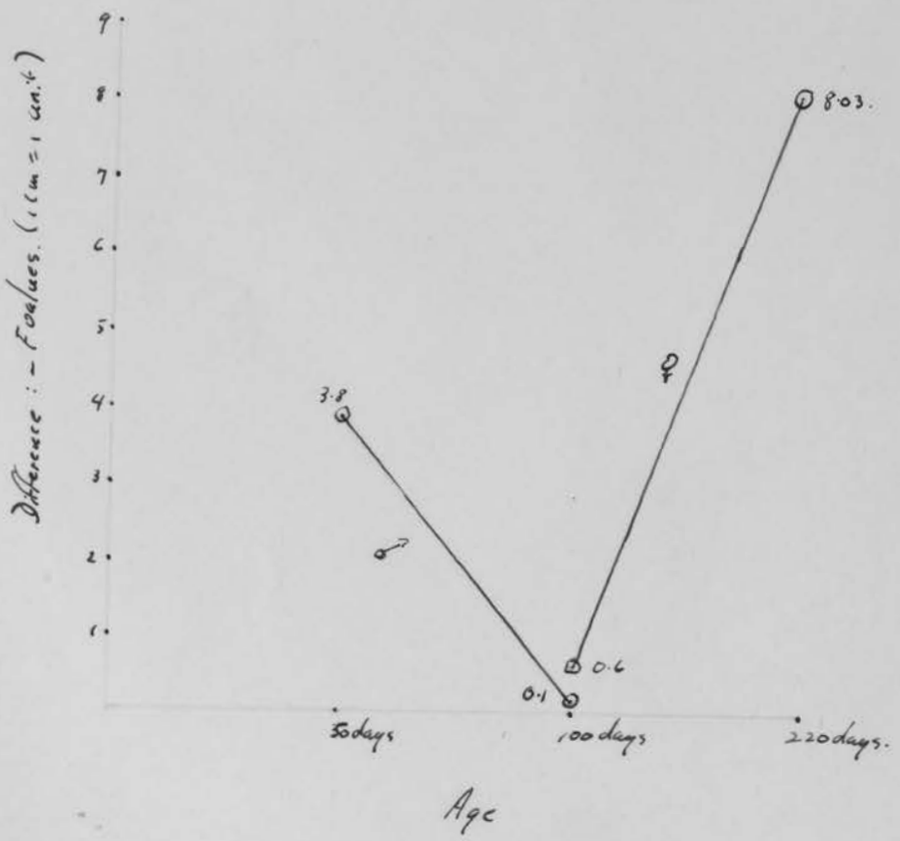
A. II. Latency to 1st crossing in preliminary trials :- Persistence of difference between handled and undisturbed animals.



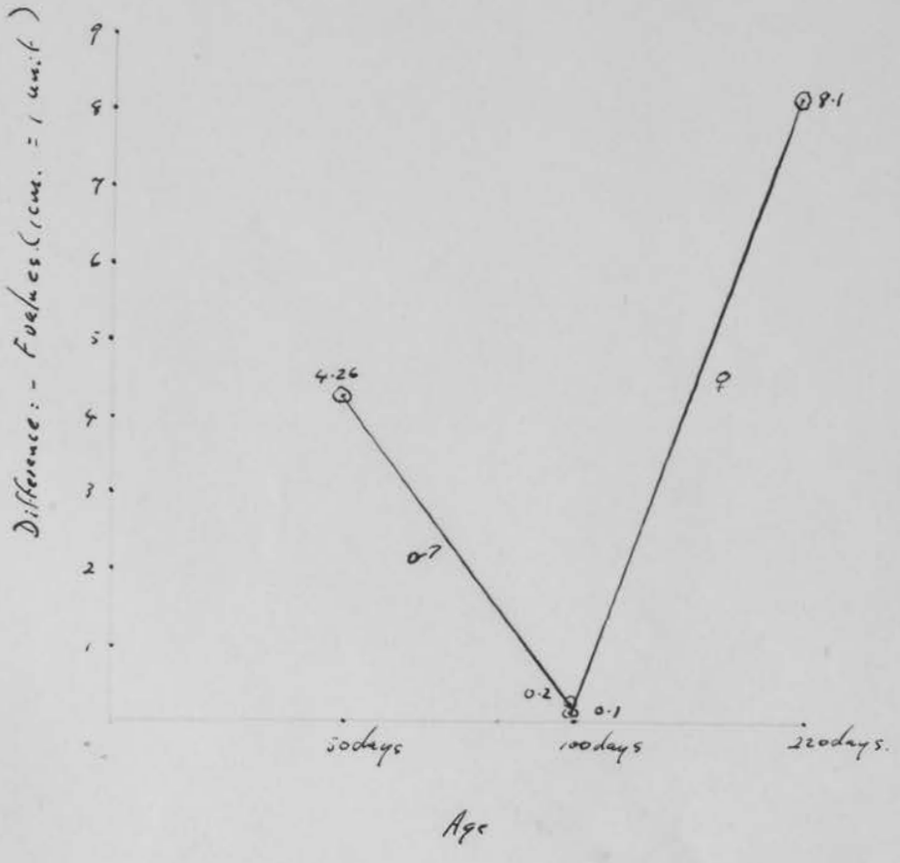
A. 12. Grooms:- Persistence of difference between handled and undisturbed animals.



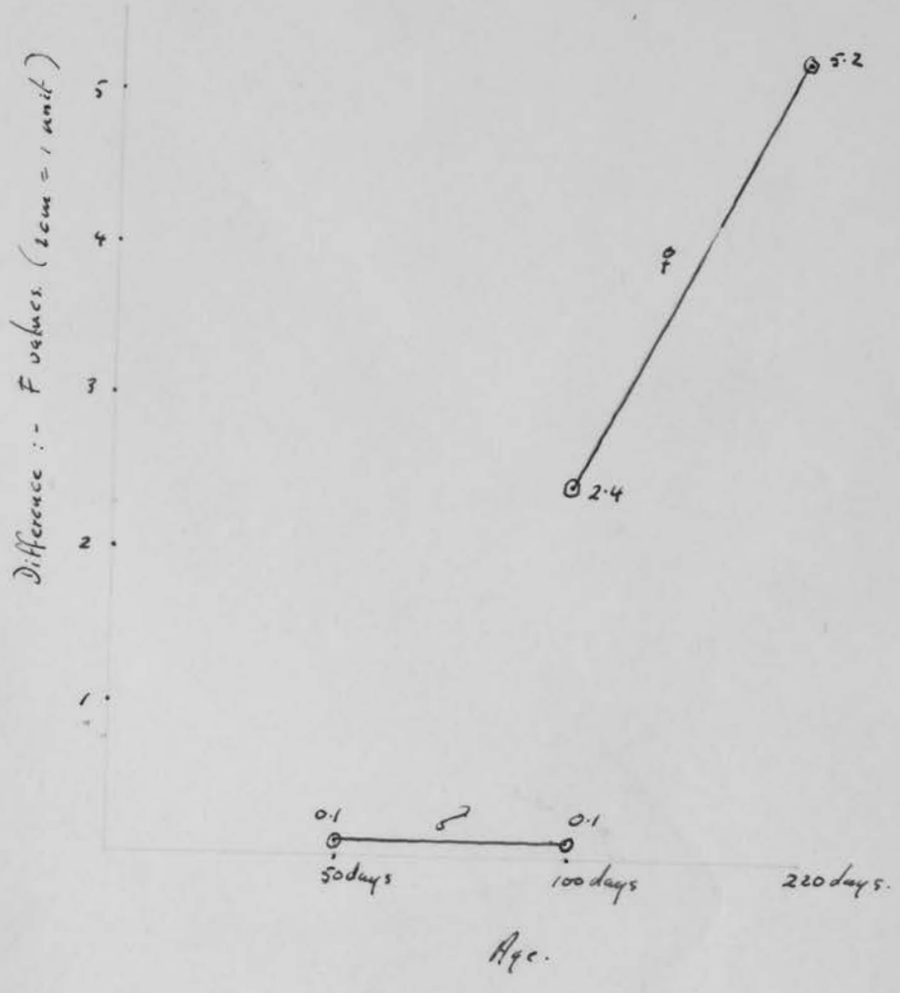
A. 13. Latency to avoidance response:- Persistence of difference between handled and undisturbed animals.



A. 14. Trials to learn avoidence response:- Persistence of difference between handled and undisturbed animals.



A 15. <u>Trials to extinguish avoidance response</u>:- Persistence of difference between handled and undisturbed animals.



Notes on statistical treatment.

1) To determine whether removal of the mother before weaning had any effect on behaviour in the tests used in this experiment, the results of the undisturbed control and the mother-removed group were subjected to the "t" test. No differences were found.

2) The results of the handled and the undisturbed subjects in two sizes of cage were subjected to an analysis of variance. A summary of the results of their analysis is provided at the end of the statistical section. Full presentation of the analysis of variance is made only where differences were significant.

Notes on the Abbreviations.

sh. (handled animals in small cages).

sm. (animals which experienced daily removal of the mother during infancy, housed in small cages).

su. (undisturbed animals in small cages).

lh. (handled animals in large cages).

lu. (undisturbed animals in large cages).

TABLE 8

Weights (males)

The weights in grams of forty subjects at 50 days and 25 days, and the ratio of the weight at 50 days to the weight at 25 days multiplied by ten.

TABLE 8

Group I tested at 50 days:- Weights in grams.

Small Cages. (10 subjects per group)

	Handled			Mother Removed			Undisturbed.		
	50days	25days	Ratio*	50days	25days	Ratio	50days	25days	Ratio
	154 gr	41 gr	38	160 gr	46 gr	35	147 gr	40 gr	37
	118	36	33	129	43	30	107	39	27
	142	38	37	120	36	33	121	38	32
	143	43	33	121	35	35	143	38	38
	118	41	29	126	36	35	85	22	39
	120	37	32	132	38	35	124	36	34
	118	40	30	126	43	29	126	30	42
	128	39	33	131	41	32	88	26	34
	150	42	36	121	31	39	145	40	36
	128	42	30	95	29	33	146	43	34
T	1319gr	399gr	331	1261gr	378gr	336	1232gr	352gr	353
M	131.9gr	39.9gr	33.1	126.1gr	33.8gr	33.6	123.2gr	35.2gr	35.3
SD.	13.4	2.2	2.9	15.1	5.2	2.7	22.2	6.51	3.9

Large Cages. (5 subjects per group)

	handled.			undisturbed.		
	50days	25days	Ratio	50days	25days	Ratio
	127 gr	39 gr	33 gr	115	36	32
	124	38	33	127	33	38
	138	43	32	97	32	30
	133	44	30	121	38	32
	146	38	38	124	36	34
T	668 gr	202 gr	166	584 gr	175 gr	166
M	133.6gr	40.4gr	33.2	116.8gr	35gr	33.2
SD	7.9	2.6	2.6	10.7	2.2	2.7

* Ratio is W50/W25 x 10.

TABLE 9

Preliminary trials (males)

The total number of rears, the total latency in seconds to crossing the barrier, the total number of crossings, and the total number of grooms for each subject in three trials of three minutes each. The subjects belonged to group I, tested at 50 days.

TABLE 9

Group I:- 3 x 3 min preliminary runs in conditioning apparatus without shock.

Small Cages. (10 subjects per group)

Handled.			mother removed.			undisturbed.		
rears	latency *	cross x	rears	latency	cross	rears	latency	cross
77	490 sec.	1	46	540 sec.	0	65	245sec.	10
66	285	11	46	430	3	66	530	2
70	315	13	61	540	0	70	540	0
79	120	14	49	540	0	60	295	13
79	195	13	49	410	4	32	540	0
75	540	0	54	540	0	31	540	0
91	230	10	57	485	1	44	455	2
62	450	2	59	405	5	52	490	1
70	540	0	38	540	0	40	540	0
63	540	0	38	480	1	65	450	3
T 732	3705 sec	64	497	4910 sec.	14	525	4625sec.	31
M 73.2	370.5sec	6.4	49.7	491.0sec	1.4	52.5	462.5sec	3.1
SD 8.4	151.9	1.9	7.7	54.6	1.8	14.0	102.4	1.5

Small Cages (grooms)

H.	MR.	U.
0	4	1
1	3	0
1	0	1
0	1	5
0	3	4
0	2	5
0	2	2
1	3	2
1	4	5
1	4	2
T 5	26	27
M 0.5	2.6	2.7
SD 0.5	1.3	1.8

Large Cages (grooms)

H.	U.
2	2
5	4
4	3
3	2
2	3
T 16	14
M 3.2	2.8
SD. 1.17	0.75

Large Cages. (5 subjects per group)

Handled.			Mother removed.			Undisturbed.		
rears	latency	cross.				rears	latency	cross.
67	220	12	-			63	165	10
86	135	16	-			46	540	0
67	540	0	-			69	95	14
71	400	10	-			60	540	9
64	380	7	-			62	300	7
355	1675 sec	45	-			300	1640 sec	40
71	335 sec	9				60	328 sec	8
7.9	142.5	5.4				7.6	185.2	4.6

* Latency : time to first crossing in each trial.

x Cross : crossing the barrier from one half the box to the other.

TABLE IO

Avoidance Trials (males)

The total number of trials required to learn an avoidance response to a criterion of two successive avoidances and the sum of the latency in seconds for all trials before the correct avoidance response, for each subject in group I tested at 50 days.

TABLE I0

Group I:- Avoidance learning.

Small Cages. (I0 subjects per group)

Handled		Mother removed.		Undisturbed.	
trials	latency sec.	trials	latency sec.	trials	latency. sec.
5	93 sec	6	147 sec	3	54 sec
3	88	3	55	4	127
3	60	5	125	4	116
3	49	3	135	5	182
3	92	5	119	5	87
5	150	3	121	6	109
5	162	5	157	10	205
3	97	6	134	9	435
5	155	5	162	3	81
5	91	3	87	9	450
T 40	1037 sec	44	1242 sec	58	1846 sec
M 4.0	103.7	4.4	124.2	5.8	184.6
SD 1.0	37.1	1.2	30.4	2.5	128.7

Large Cages. (5 subjects per group)

Handled		Undisturbed.	
trials	latency sec.	trials	latency. sec.
4	119 sec	5	89 sec
3	87	6	258
5	165	3	89
3	140	5	109
5	90	4	200
T 20	601 sec	23	745 sec.
M 4	120.2	4.6	149
SD .9	29.7	1.0	68.2

* Trials : trials to criterion of two successive advoidances of shock.

x Latency : total time spent in shock compartment until criterion.

TABLE II

Extinction Trials (males)

Total number of trials required to extinguish the avoidance response to a criterion of two successive no-responses of thirty seconds, and the sum of the latency to the avoidance response in all trials, for each subject in Group I, tested at 50 days.

TABLE II

Group I:- Extinction trials.

Small cages. (10 subjects per group)

	Handled		Mother removed		Undisturbed.	
*	trials	x latency sec.	trials	latency sec.	trials	latency sec.
	5	64 sec	6	70 sec	7	96 sec
	20	113	20	62	11	73
	4	64	4	65	9	89
	7	29	16	133	5	66
	12	134	4	49	5	65
	8	101	12	91	14	83
	20	50	6	72	8	73
	17	141	11	96	7	71
	5	75	5	72	20	151
	8	67	4	66	20	96
T	106	838 sec	88	776 sec	106	863 sec
M	10.6	83.8	8.8	77.6	10.6	86.3
SD	9.76	3.5	5.4	22.5	5.35	24.2

Large Cages. (5 subjects per grpup)

Handled		Mother removed		Undisturbed.	
trials	latency sec.	trials	latency sec.	trials	latency sec.
20	93 sec	-	-	8	82 sec
8	67	-	-	13	139
10	73	-	-	11	150
5	78	-	-	14	95
9	65	-	-	7	87
T 52	376 sec	-	-	53	553 sec
M 10.4	75.2			10.8	110.6
SD 5.08	10.0			2.76	89.2

* Trials ; trials to criterion of two successive no-respours of thirty seconds.each.

x Latency : time in seconds up to but not including two criterion trials.

TABLE I2

Elevated Maze (males)

The total time in seconds and number of errors to reach goal for each subject in Group I, tested at fifty days, in five learning trials on the elevated maze. The time spent of the elevated maze before the first consumption of water occurred is also shown, in seconds, for each subject.

TABLE I2

Group I:- Elevated Maze

Small Cages (I0 subjects per group)

Handled			Mother removed			Undisturbed.		
* Time	x error	± 1st Cons	time	error	1st cons.	time	error	1st cons
143sec	0	100secs	192	0	150secs	132	3	60secs
129	4	110	216	1	170	465	6	440
183	3	130	450	8	405	130	1.	105
174	0	115	180	0	150	I48	o	20
169	1	105	320	3	245	218	3	50
127	1	90	167	2	120	171	1	35
83	1	75	91	1	80	232	1	215
372	9	255	192	1	170	253	3	205
146	3	100	108	1	85	395	8	370
111	0	90	97	0	75	164	0	135
T 1637	22	1170	2013	17	1650	2308	26	1635
M 163.7	2.2	117.0	201.3	1.7	165.0	230.8	2.6	163.5
SD 75.6	2.6	15.2	104.7	2.5	93.8	108.3	2.5	137.2

Large Cages. (5 subjects per group)

Handled.			Undisturbed.		
time	error	1st cons.	time	error	1st cons.
134 sec	2	80	162	0	120
252	1	150	251	1	235
106	2	75	164	3	135
171	2	105	201	3	110
180	4	120	187	3	115
T 843	11	530	965	10	715
M 168.6	2.2	106	193	2.0	143.6
SD 49.5	0.98	27.5	32.5	1.26	46.8

* time : total time in five trials to reach goal.

x errors : total errors in five trials.

± 1st cons. : time before subject first consumes water.

TABLE I3

Weights (males and females)

Weights in grams of twenty male subjects and twenty-four female subjects at Ioo days and 25 days,and the ratio of the weight at I00 days to the weight at 25 days multiplied by ten.

TABLE I3

Group II. :- Weights in grams of males.

Small Cages. (4 subjects per group)

Handled.			Mother removed.			undisturbed.		
1oo days	25days	Ratio *	100days	25days	Ratio	100days	25days	Ratio
240gr	33gr	73	254gr	41gr	62	257gr	37gr	69
291	42	69	224	37	61	214	35	61
242	34	71	248	34	73	222	39	57
240	37	65	240	36	67	252	38	66
T 1013gr	146gr	278	966 gr	148gr	263	945gr	149gr	253
M 253gr	36.5gr	69.5	241.5gr	37gr	66	236gr	37gr	63
SD 21.8	3.5	2.96	11.3	2.5	4.8	18.55	1.5	4.6

Large Cages. (4 subjects per group)

Handled			Undisturbed.		
100days	25 days	Ratio	100 days	25 days	Ratio
266	41gr	65	230gr	37gr	62
250	34	74	247	38	65
246	37	67	248	36	69
245	38	65	250	37	68
1007gr	150gr	271	975gr	148gr	264
252gr	37.5gr	68	244gr	37gr	66
8.4	2.5	3.7	8	0.7	2.7

* Ratio : W 100/W25 x 10.

Group 11. :- Weights in grams of females.

Small Cages. (8 subjects per group)

Handled			Mother removed.			undisturbed.		
100days	25 days,	ratio	100days	25days,	Ratio	100days,	25days,	Ratio
180gr	34gr	53	180	33	55	153gr	34gr	45
159	34	47	160	35	46	170	33	52
170	36	47	159	33	48	155	27	57
184	37	50	160	30	53	153	24	64
177	37	48	172	31	55	180	30	60
175	40	44	174	37	47	168	27	62
169	35	48	168	34	49	171	36	48
170	32	53	175	35	50	160	38	42
1384gr	285gr	390	1348gr	268gr	403	1310gr	249gr	430
173gr	35.6gr	49	168.5	33.5gr	50.4	164gr	31.1gr	54
7.2	2.3	2.9	7.5	2.1	3.3	9.9	4.6	7.7

TABLE I4

Weights (females)

Weights in grams of eight female subjects at I00 days and at 25 days, and the ratio of the weight at I00 days to the weight at 25 days, multiplied by ten, for each subject.

TABLE I4

Group 11.:- Weights in grams of females.

Large Cages.

Handled			Undisturbed.		
100days,	25 days	ratio	100 days	25 days	Ratio.
163gr	34 gr	48	170 gr	35 gr	49
170	36	47	165	35	47
171	37	46	162	37	44
168	33	51	168	36	47
672 gr	140 gr	192	665 gr	143 gr	187
168 gr	35 gr	48	166 gr	36 gr	47
3.1	1.6	1.9	3.1	0.87	1.8

TABLE I5

Preliminary trials (males)

The total number of rears, the total latency in seconds to crossing the barrier, the total number of crossings of the barrier, and the total number of grooms for each subject in three trials of three minutes each, in Group II, tested at I00 days.

TABLE I5

Group 2 :- 3x3 min. peliminary runs in conditioning apparatus without shock.

A Males.

Small Cages. (4 subjects per group)

R : Rears, L* : latency, C x : Crossings, G : grooms.

Handled				Mother removed				Undisturbed.			
R	L	C	G.	R	L	C	G.	R	L	C	G.
78	195sec	14	2	53	400	3	1	52	450	2	1
95	133	18	3	50	360	4	2	45	385	5	4
75	37	21	2	46	320	1	1	47	540	0	1
80	142	12	2	47	480	7	3	48	350	9	1
T 328	507	65	9	196	1560.15		7	192	1725	16	7
M 82	127	16	2.3	49	390	3.8	1.8	48	431	4	1.8
SD 7.7	56.9	3.5	0.4	2.7	59.2	2.2	0.8	2.6	72.3	3.4	1.3

Large Cages. (4 subjects per group)

Handled				Undisturbed.			
Rears	latency sec.	crossings	grooms	rears	latency sec.	cross.	grooms
48	385	5	2	56	250	11	7
75	343	9	3	51	209	7	6
46	132	10	5	57	352	9	3
61	175	10	2	53	314	7	2
T 230	1035	34	12	217	1125	34	18
M 57.5	258.8	8.2	3.0	54	281	8.5	4.5
SD 11.6	107.3	2.1	1.2	2.4	110.9	1.7	2.1

* Latency : time inseconds to first crossing on each trial

x Crossings : crossing the barrier from one half the box to the other.

TABLE I6

Preliminary trials (females)

The total number of rears, the total latency in seconds to crossing the barrier, the total number of crossings of the barrier, and the total number of grooms for each subject in three trials of three minutes each. The subjects belonged to Group II, tested at I00 days.

TABLE I6

Group 2. :- 3x3 minute preliminary runs in conditioning apparatus without shock.

B. Females.

R : Rears, L : latency, C: Crossings, G : Grooms.

Small Cages. (8 subjects per group)

	Handled				Mother removed.				Undisturbed.			
	R	L	C	G.	R	L	C	G.	R	L	C	G
	81	108	18	1	50	540	2	1	54	520	1	0
	82	162	20	1	69	300	19	0	71	256	16	2
	90	97	12	1	47	320	1	2	39	540	0	2
	121	215	22	1	87	325	15	0	90	264	17	0
	96	90	17	2	55	180	10	3	50	295	9	1
	67	450	2	0	73	260	17	1	74	233	15	0
	45	470	2	3	90	275	18	0	87	110	21	0
	92	102	19	0	61	195	20	0	63	206	15	0
T	674	1694	112	9	532	2395	102	7	528	2424	94	5
M	84.2	211.8	14	1.1	66.5	299.4	12.8	0.9	66	303	11.8	0.6
SD	20.7	148.6	7.4	0.9	15.2	103.8	7.1	1.0	16.7	14o.8	7.2	0.9

Large Cage. (4 subjects per group)

	Handled				Undisturbed.			
	Rears,	Latency,	Crossings,	Grooms.	Rears,	Latency,	Cross.	Grooms
	83	87	20	0	41	260	11	1
	77	133	21	5	64	217	18	5
	83	66	23	0	71	92	22	0
	73	130	20	0	69	198	15	5
T	316	416	84	5	245	767	66	11
M	79	104	21	1.3	61	192	16.5	2.8
SD	4.2	28.5	1.2	2.2	12	61.8	4.0	2.3

* Latency : time in seconds to first crossing in each trial.

x Crossing: Crossing the barrier from one half the box to the other.

TABLE I7

Avoidance Trials (males)

The total number of trials required to learn an avoidance response to a criterion of two successive avoidances and the sum of the latency in seconds for all trials before the correct avoidance response, for each subject in Group II, tested at I00 days.

Group 2.:- Avoidance trials. a) Males.

Small Cages.

Handled		Mother removed		Undisturbed.	
Trials*	Latency x	Trials	Latency	Trials	Latency.
4	90 sec	3	52	3	65
4	79 "	4	65	4	52
4	30 "	4	80	4	60
4	33 "	5	44	4	54
T 16	232	16	241	15	231
M 4	58 sec	4	60.3	3.8	57.8
SD 0	26.8	0.7	34.4	0.4	5.1

Large Cages.

Handled		Undisturbed.	
Trials	Latency	Trials	Latency
4	63	3	22
5	97	5	68
3	51	4	99
5	95	4	118
17	306	16	307
4.3	76.5	4	76.8
0.8	19.3	0.7	36.3

* Trials : trials to criterion of two successive Avoidances of shock.

x Latency : Total time in seconds spent in shock compartment until criterion.

TABLE I8

Avoidance Trials (females)

The total number of trials required to learn an avoidance response to a criterion of two successive avoidances and the sum of the latency in seconds for all trials before the correct avoidance response, for each subject in Group II, tested at I00 days.

TABLE I8

Group 2. :- Avoidance trials. b) Females.

Small Cages.

	Handled		Mother removed		Undisturbed	
*	Trials	x Latency	Trials	latency	Trials	latency
	4	30 sec	5	62 sec	4	42 sec
	4	59	4	38	3	30
	4	43	4	55	4	61
	4	28	4	71	3	40
	4	36	3	160	5	164
	4	46	4	37	4	35
	4	51	5	42	5	58
	4	34	4	30	3	41
T	32	327	33	495	31	471
M	4	41.4	4.1	61.9	3.9	59
SD	0	10.1	0.6	39.3	0.8	41.0

Large Cages.

Handled.		Undisturbed.	
Trials	Latency	Trials	Latency
4	66 sec	3	32 sec
5	57	3	21
4	59	3	21
3	63	4	98
T 16	245	13	172
M 4	61.3	3.3	43
SD. 0.7	3.5	0.4	32.1

* Trials : trials to criterion of two successive avoidances of shock.

x Latency: Total time spent on shock compartment until criterion.

TABLE I9

Extinction Trials (males)

Total number of trials required to extinguish the avoidance response to a criterion of two successive no-responses,and the sum of the latency in seconds to the avoidance response in all trials,for each subject in Group II,tested at I00 days.

TABLE I9

Group 2 :- Extinction trials. a) Males.

Small Cages.

	Handled		Mother removed		Undisturbed.	
	* Trials	x Latency	Trials	Latency	Trials	Latency.
	13	142	17	137	6	72
	19	109	15	58	16	92
	21	58	13	99	18	104
	8	149	9	80	20	85
T	61	458	54	374	60	353
M	15.3	114.5	13.7	93.5	15.0	88.3
SD	5.1	35.9	3.0	29.o	5.4	11.6

Large Cages.

	Handled		Undisturbed.	
	Trials	Latency	Trials	Latency.
	21	102	19	9o
	9	75	14	148
	14	81	19	158
	16	86	15	95
T	60	344	65	491
M	15.0	86	16.3	122.8
SD	4.3	Lo.0	1.9	30.5

* Trials : trials to criterion of two successive no-responses of 30 seconds each.

x Latency : time in seconds up to but not including two criterion trials.

TABLE 20

Extinction Trials (females)

Total number of trials required to extinguish the avoidance response to a criterion of two successive no-responses, and the sum of the latenc in seconds to the avoidance response in all trials, for each subject in Group II, tested at Ioo days.

TABLE 20

Group 2 :- Extinction trials b) Females.

Small Cages.

	Handled		Mother removed		Undisturbed.	
	Trials	latency	Trials	latency	Trials	Latency
	19	100	8	63	29	61
	22	135	22	116	28	188
	3	66	20	90	29	61
	10	149	3	62	24	124
	26	209	24	118	29	58
	30	100	26	77	16	158
	16	113	13	101	29	61
	15	80	27	140	6	67
T	141	952	143	767	190	778
M	17.6	119	17.9	96	23.8	97.3
SD	8.1	42.4	8.3	26.2	7.9	48.8

Large Cages.

	Handled		Undisturbed.	
	Trials	Latency	Trials	latency
	14	92	29	64
	30	60	27	61
	18	140	22	109
	20	239	16	120
T	82	531	94	354
M	20.5	132.8	23.7	88.5
SD	5.9	67.6	5	26.3

* Trials : trials to criterion of two successive no-responses of 30 seconds each.

x Latency: time in seconds up to but not including two criterion trials.

TABLE 21

Elevated Maze (males)

The total time in seconds,and the number of errors to reach goal, on the elevated maze in five trials for each subject in Group II,tested at I00 days.The time spent on the elevated maze before the first consumption of water occurred is also shown,in seconds,for each subject

TABLE 21

Group 2 :- Elevated Maze. a) Males.

Small Cages.

Handled			Mother removed			Undisturbed.		
✱ time	x errors	‡ lst cons.	Time	errors	lst Cons.	Time	error	lst cons
330sec	18	300sec	420sec	14	350sec	560sec	17	520sec
650 "	7	560	360	10	280	490	11	480
220 "	5	203	450	8	410	310	12	250
240 "	10	210	210	7	180	220	4	120
1440	40	1073	1440	39	1220	1580	44	1370
360	10	268.3	360	9.8	305	395	11	342.5
172.4	4.95	224.3	92.5	2.7	85.6	136.1	4.6	164.7

Large Cages.

Handled			Undisturbed.		
Time	errors	lst cons.	Time	errors	lst cons.
450sec	11	430secs	335 sec	9	300 sec.
520	7	400	460	7	410
170	8	120	275	15	205
150	12	110	250	13	150
1290	38	1060	1320	44	1065
322.5	9.5	265	330	11	266.3
164.5	2.1	150.4	81.2	3.2	98.8

✱ Time : total time in five trials to reach goal.

x Errors : total errors in five trials.

‡ lst Cons. : time before subject lst consumes water.

TABLE 22

Elevated Maze (females)

The total time in seconds, and the number of errors to reach goal, on the elevated maze in five trials for each subject in Group II, tested at 100 days. The time spent on the elevated maze before the first consumption of water occurred is also shown, in seconds, for each subject.

TABLE 22

Group 2 :- Elevated Maze b)Females.

Small Cages.

	Handled			Mother removed			Undisturbed.		
	✱ Time	x errors	± 1st cons	time	errors	1stcons	time	error.	1stCon
	630sec	22	540sec	455sec	15	400sec	235	20	220sec
	485	23	410	465	17	410	610	27	540
	225	4	200	750	10	600	780	11	760
	790	21	650	620	11	540	650	4	600
	133	6	133	300	13	250	355	9	305
	700	5	600	690	2	608	600	13	500
	150	9	130	775	25	700	310	11	280
	480	8	420	210	21	180	655	15	610
T	3593	98	3083	4265	114	3688	4195	110	3815
M	449.1	12.3	385.4	533.1	14.3	461	524.4	13.8	476.9
SD	238.1	7.7	195.3	196.0	6.6	171.1	183.6	6.6	177.4

Large Cage.

	Handled			Undisturbed.		
	Time	error	1st cons.	time	errors	1st cons.
	385sec	10	210 sec	345sec	17	300 sec
	222	9	200	395	13	350
	710	15	680	550	11	465
	250	12	207	480	8	350
	1567	46	1297	1770	49	1465
	391.8	11.5	322.3	442.5	12.3	366.3
	193.8	2.3	205.4	78.6	3.3	60.6

✱ Time : total time in five trials to reach goal.

x Errors: total errors in five trials.

± 1st Cons. : time before subject 1st consumes water.

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C H A P T E R I

INTRODUCTION

Since Hunt's (1941) claim that he had introduced a new field into the laboratory study of the animal - its life history - there has been a spate of work in which the effects of many different kinds of variation have been studied. Though one may question the validity of Hunt's claim (see, for example, the early work of Conradi on singing birds, 1909) there is no doubt that this study of the effects of early food deprivation on subsequent hoarding has encouraged and perhaps given rise to a great number of other studies in this field.

The importance of influences in childhood has long been acknowledged by authorities as diverse as Rousseau and Freud. The authority of embryological studies also lent weight to the opinion that early influence, by affecting development at its most formative and plastic period, might have more widespread and radical effects than equivalent influences later in life. In particular, it was supposed that traumatic experiences at an early stage of life might have results which were both more persistent and more extensive than traumatic experiences at a later stage. Again, the embryological analogy with its critical periods before structures became determined seemed to support this view.

It is quite possible that all this is true, though it has been very imperfectly demonstrated. It is quite possible that there are psychological organisers which must act at certain critical periods of development; and it is quite possible that lack of these organisers will cause grave disorders in development. It is also possible that psychological lesions incurred early in life, by striking at the corner stones of psychological development, can cause very widespread effects.

For the demonstration of such general laws of psychological development work on animals is as useful as work on human subjects. That is the basic justification of undertaking such work. The specific details must be worked out with the species, but the general laws of development transcend the species.

One of the results of work on animals is that the notion of traumatic experience must be accepted with reservations. Work will be quoted in the review of literature contained in this thesis which demonstrates that severe shock in the earliest days of infancy increases the activity, resistance to subsequent stress, and learning activity of rats.

From this it is clear that we should not accept that any intensely unpleasant event in infancy or childhood necessarily causes lesions. In fact, the effects may be the opposite. Intense stimulation in infancy, provided that it does not exhaust the adaptive powers of the organism, may be beneficial to its subsequent resistance to stress.

It is proposed to show that work on animals as well as human subjects has helped to distinguish among sensory deprivation, sensory overload, emotional deprivation and stress. The concept which may enable us to link these apparently discrete conditions is that of adaptation level.

The original experiment described in Chapter VI of this thesis is an attempt to find out whether the effects on growth, activity, emotional behaviour, and learning of one form of stimulation - handling in infancy - persist into maturity in the white rat.

An attempt is also made to find out whether interaction between cage size and handling affects growth, activity, emotional behaviour and learning. This experiment was prompted by speculation that cage size is an important stimulus variable in the life of the rat which may interact with handling to increase or decrease its effects.

A third aim of the experiment is to discover whether removal of the mother from the pups is a form of stimulation which may significantly affect later behaviour.

When the experiment was conceived, it was hoped that the results would allow a conclusion, however tentative, about the nature of the effect of early stimulation. An important question appeared to be whether early stimulation has a developmental effect on the organism. It was thought that persistence of the effects of early stimulation on behaviour would support this viewpoint rather than a redintegrationist viewpoint. At the time, the possibility that handling is a special form of stimulation which achieves its effect mainly by taming was not considered seriously enough because of the large body of evidence which seems to show that the effects of handling on behaviour are not to be attributed to taming. But later, the question had to be faced : how much of the difference observed is the result of training and how much the result of stimulation? Then it had to be admitted that other forms of stimulation may permit more conclusive argument from results.

It will be seen that the effects of handling on behaviour do persist into maturity, but that the interpretation must remain doubtful in spite of the large body of evidence that handling has effects not directly attributable to taming.

CHAPTER II

OBSERVED VARIATIONS IN HUMAN INFANCY WHICH SHED LIGHT ON THE QUESTION OF CRITICAL AGE

Introduction

In this chapter the question of whether there is an age at which environmental variations have their greatest effect will be considered.

Another problem of some importance is whether the effects of variations at certain critical ages persist longer than at other ages.

Studies of the effects of (a) separation, (b) physical injury, and (c) extra practice will be considered.

(a) Separation

The extremely detailed studies by Spitz (1945, 1946, 1955) appear to make a strong case for the belief that there is a critical age in emotional development during which affective stimulation is vital.

A study of a large sample of children was made in one of Spitz'inquiries (1955) which revealed clearly that children over eighteen months are more resistant to emotional deprivation than children under eighteen months. After the age of eighteen months children are severely damaged but not killed by emotional deprivation, but children below the age of eighteen months are often killed by a lack of mothering. The comparison which led to this conclusion was made between ninety-one children from a foundling home who were deprived of maternal care after they had been breast fed for the first three months of life, and sixty-nine children from a penal nursery who were in daily contact with their mothers during the first year of life. There was a progressive deterioration of the foundling home developmental quotient,

whereas the penal home children developed normally, even though mothering was sometimes unsatisfactory. After five months of separation from the mother deterioration was often irreversible. Thirty-seven per cent of the foundling home children died in their first year.

Bowlby (1953) has laid special emphasis on complete or prolonged separation from the mother or established foster-mother during the first five years of life. He divided cases he had seen into those who stole and those whose emotional disturbance took other forms. The forty-four thieves were matched with an emotionally disturbed group for age and sex and were distinguished in a number of ways. The thief group contained a high proportion of 'affectionless' children; that is, children who were unable to enter into deep-rooted affective relations with others. There were none in the control group. The thieves had in 17 instances suffered complete and prolonged separation from their mothers during the first five years, whereas none of the control group had. It was found that the 'affectionless' thieves had a better hereditary record than the controls.

It is also noted (Bowlby, 1951) that not less than two-thirds of the children who presented persistent problems of maladjustment after evacuation during the war were under the age of five when first evacuated.

Goldfarb (1943) compared the mental development of children reared until the age of three in an institution before placement in foster-homes with the development of children who had gone straight from their mothers to foster-homes. Great care was taken to match the heredity of the two groups. Fifteen pairs were studied in great detail. In the institution babies were kept in their own little cubicles to prevent the spread of infection. Contact with nurses occurred only for feeding and cleaning. After the first nine months groups of fifteen to twenty were placed in

the care of a single nurse, till they were placed at about three years. The foster-homes in this study were also carefully matched and the testing was carried out six years after the children had been placed. The institution group was retarded in speech, intelligence, power of abstract thought, and social maturity.

A study by Theis (1924) indicated that children brought up entirely in an institution adjusted significantly less well as adults, than children who had spent the first five years at home before going into an institution, even though the homes were bad in 80% of the cases. This comparison is based on 179 cases.

There are large numbers of studies which all indicate the same thing : affective deprivation in childhood leads to persistent maladjustment. The studies quoted above indicate that the first five years are critical. In fact, Goldfarb's study indicates that mothering is not effective if commenced after the age of three, while Spitz attempts to quantify the reversibility, showing that there is a sharp decline till, after 5 month's separation in the first year, there is doubt as to the recovery of the child to normal development.

Bowlby (1953) states that there are three main developmental phases, three critical periods in fact, during the first five years of the child's life. During the first six months the child establishes a relationship with a clearly identified person, usually his mother. During the next 2 years, until his third birthday, the child requires his mother as an ever-present companion. During the fourth and fifth year the child becomes increasingly capable of maintaining a relationship with his mother during a short absence of a few days.

The concept of critical age suits well what we know about development. It has been demonstrated that during development of organs they are receptive to organisers

for limited periods, during which development may be profoundly affected, before they become determined and insusceptible to further developmental modification.

It is possible that certain experiences are necessary as organisers within certain periods of psychological development.

(b) Physical injury

Studies of physical injury occurring at various ages provide us with examples of accidental deprivation which sometimes illumine the problem of the importance of age. The accidents must be such that maturation is not affected. The studies must distinguish between the effect of the actual injury and the effect of the deprivation, where possible.

Studies of patients with congenital cataracts show the importance of early visual experience.

Miner (1905) reports that an exceptionally intelligent girl blinded by congenital cataract passed successfully through high school in spite of her handicap; yet after an operation to clear away the defect progress to simple recognition of the faces of four or five people with whom she was in daily contact took two years. This compares unfavourably with the progress of the human infant, who is capable of distinguishing several faces by the age of six months. It appears, therefore, that early learning to perceive visually is more rapid than late learning. This has been confirmed with chimpanzees, as will be detailed in chapter III.

Senden (in Hebb, 1949) has assembled all the known cases of recovery of eyesight after congenital blindness as well as reporting his own observations. The later the age at which recovery occurs, the more difficult the progress towards effective discrimination.

Brain injury presents an interesting and special type of deprivation.

Even after injury to the brain, there are reports of high I.Q. among adult patients (Hebb, 1949). The loss of intelligence in Binet type tests appears to be smaller than the loss in non-verbal and puzzle-like tests. On the other hand, when brain injury occurs early in life, vocabulary tests and information tests show as great a deficit as puzzle and non-verbal tests. It appears that early injury prevents the development of function that equally extensive injury in maturity does not destroy. Hebb (1949) postulates that the first effort to understand is the greatest and demands the fullest resources of the brain. The first process of learning he calls primary learning. That is why, when presented with a new task (as in a puzzle) adults who are brain-injured reveal as much deficit as brain-injured children; but when presented with an old task (as in a vocabulary test), brain-injured adults who have already accomplished their learning do not reveal as much deficit as brain-injured children.

Strauss and Kephart (1955) state that 'the most typical test pattern which we see in brain-injured children involves low performance and high language achievement' (p. 209) which contradicts what Hebb has written. They state further that it appears that these children are 'low in perception and high in conception' (p. 209). The contradiction is explained by the observation that, though brain-injured children may use language in a grammatically and syntactically correct way, obtaining a high score, the concepts which the language supposedly represents are absent or distorted. Therefore, the apparently high achievement in conception is illusory. The dictum that conception is dependent on perception is not upset.

Though the case is not perfectly clear, the evidence of brain-injury at various ages indicates that early brain-injury, by hampering the process of primary learning has a greater effect on performance than late brain-injury.

The argument for critical age would only be fully supported if the brain could be subsequently repaired, which is unfortunately not possible.

(c) Practice

Very few studies have directly attacked the problem of the effects of extra practice at different ages. For example, the effects of extra practice and encouragement on intelligence could only be thoroughly studied if identical twins could be separated and reared in really different environments. Then we might know whether these effects are permanent.

Some studies of motor activity have been conducted.

Gesell and Thompson (1929) studied the effects of additional practice on cube-building and stair-climbing. At 46 weeks' practice in both activities was initiated in one identical twin 6 weeks before the other commenced practice. There was no apparent difference in the speed of development of these functions, since the second twin equalled the performance of the former at the end of 2 weeks' practice. The authors conclude that 'the time of appearance is fundamentally determined by the ripeness of the neural structures'.

McGraw (1935) experimented with the effects of practice in motor activities on a twin, Johnny, from the age of 21 days to 22 months. Jimmy, the other twin, was given no special practice. The author found that behaviour pattern controlled at an infra-cortical level could not be easily modified by practice. 'Activities of ontogenetic origin can be greatly accelerated through exercise of the performance,

but the degree to which they can be modified is dependent upon the state of maturation or plasticity of the behaviour pattern at the time the factor of exercise is introduced'.

Yet follow-up studies of Johnny and Jimmy (McGraw, 1939) indicated that Johnny, the twin who had been given extra practice, continued to show superior motor co-ordination.

It is also interesting that the twin given extra practice in the Gesell and Thompson experiment quoted above was less afraid of falling and had more assured balance 26 weeks after the training had ceased.

Dennis has made inter-cultural studies of restriction (1940). Hopi children are bound to the cradle during the first three months (except for about one hour daily), but show no motor retardation in the first year. He has also studied the effects of restricted practice on the reaching, sitting and standing of two infants (1935) compared to norms. The sample is too small for any conclusions of value.

It is possible to interpret the fact that the adult I.Q. of a child may be predicted more accurately on the basis of his parents' scores than on the basis of his own as an expression of the effects of practice (Anderson, 1939). The child from the poor environment is, in fact, suffering from restricted opportunities for practice as compared to the child from an encouraging environment.

The same interpretation is possible of differences among the scores of 'illiterate, poverty-stricken, anti-social mountaineers', Southern Negroes, and children reared in favourable environments (Hebb, 1949).

There is a fair amount of evidence for the proposition that development requires the convergence of maturation and experience at certain critical phases, and that if this convergence does not occur, the result may be an irreversible or hardly reversible defect.

(d) Reasons for animal studies

One of the reasons for studying animals is that experimental variation may be introduced into their life history under carefully controlled conditions. It is impossible to study the effects, to take an example, of rearing in complete isolation on human subjects. This may be done with animals. Groups can be matched and uncontrolled variables may be reduced to a minimum. The age at which variations are introduced may be carefully controlled. The animals can be kept in the laboratory for follow-up studies.

The ease and relative exactness of animal experiment does not require elaboration.

Animal experiments may also be used in refining an hypothesis and in suggesting new hypotheses. For example, the effects of separation under various conditions may be studied to test the hypothesis that separation leads to the emotional deprivation syndrome only after experience of nursing contact.

A careful study of the effects of variations may lead to the discovery of a phylogenetic pattern, which would strengthen, though it might not furnish sufficient argument for, our belief in a similar effect in man. As an example of this we may take the discovery that primates require a longer period of primary learning for visual discrimination than do lower mammals. This strengthens our belief that man requires a still longer period of primary learning than do other primates.

The fallacy to be avoided is a direct transfer of conclusions from one species to another. The discovery that dogs eat more rapidly in each other's company does not enable us to conclude that mice do, or that human subjects do. Conclusions from animal experiment can only be accepted for man if there is evidence for them from human studies as well.

C H A P T E R III

EXPERIMENTAL VARIATIONS IN THE INFANCY OF ANIMALS WHICH SHED LIGHT ON THE QUESTION OF CRITICAL AGE.

Introduction

In order to reap the fullest benefit from animal experiments, a careful study of the life history and development of the animal should be made. If we are to pursue the embryological analogy a little further, we might say that specific organisers have to be introduced at specific ages. A random selection of stimuli inflicted at a random selection of ages would not yield the information necessary for an accurate study of psychological development. A detailed study of development might suggest the ages of greatest susceptibility to certain variations.

The greatest amount of work in this field has been done on dogs, chimpanzees and rats. The work on rats will be discussed in subsequent chapters.

(a) Dogs

It has been suggested by Scott and Marston (1950), after a study of the development of seventy-three pups of seven breeds, that there are five periods in the growth of the dog : (i) neonatal (2 weeks), (ii) transition (2 weeks), (iii) socialisation (till weaning), (iv) juvenile (weaning to maturity), and (v) maturity. In the neonatal phase the animal is blind and unable to walk; sucking, yelping and withdrawal are the main features of behaviour. The transition period is entered when the animal's eyes open. Though there is no barking, fighting play is commenced which develops into dominance relationships in the phase of socialisation. During this period animals can be easily trained. Dominance

relationships in a group become fixed during the juvenile period and play diminishes.

It is probable that the critical periods of development occur just before and during the appearance of new patterns of behaviour. Unfortunately, there has been no systematic exploration of this hypothesis.

If we take the various phases and see what work has been done within each, the results are promising but limited as yet.

Levy's classic (1934) study of the sucking reflex of a number of pups attempts to evaluate the importance of deprivation of an activity-need in the neonatal phase. Deprivation leads to restlessness and irritability which is shown even in sleep. The deprived animals lose weight, search continually for objects to suck, or show searching and combative behaviour. Such a study would gain in importance if the effects had been followed into maturity.

Ross (1951) raised three groups of pups : bottle-fed, dropper-fed, bitch-fed. Both experimental groups showed more non-nutritional sucking and registered a higher sucking pressure on a manometer. These groups reduced their non-nutritional sucking when returned to the bitch but remained hyperactive during infancy.

The observations of those interested in training dogs show that the most effective period for establishing mastery, especially with wolf-descended dogs, is before the second month (Lorenz, 1952). Dogs caught early in the period of socialisation are more easily trained than those caught late.

Melzack (1952, 1954) has shown that pups which have been deprived of 'normal sensory experience' by early restriction in narrow cages, though their neural and sensory maturation is apparently not interfered with, show more diffuse behaviour and avoidance behaviour than their litter

mates reared in frequent contact with trainers and allowed considerable freedom in exploration. Ten to twelve months after derestriction the effects were still clear. It will be seen, since no variation is attempted at different ages, that we cannot draw any conclusion as to a critical age. This applies to most studies of infant environment. By not having an adult control they do not shed light on the importance of infancy as a condition for the effect.

Hebb (1955) explains the omission of controls at various ages in the preceding experiment. Animals which were restricted after a period of freedom became so wretched within a matter of days that the experiment was discontinued.

These observations are reinforced by further experiments of the same kind, reported by Thompson and Melzack (1961). The restricted animals were found to be alert, apparently curious, interested in the tiniest details, never bored. Their learning ability was severely retarded and their distractibility high.

Ivanov Smolensky (1954), quotes an experiment which shows that kennel dogs display a passive-defensive reflex not found in household littermates. Again, there was no adult control. Ribble (1944) states that babies who have been separated from their mothers and kept mainly to their cots in institutions show a fear of strange objects. It is an interesting observation reported by three different authors observing two species.

Thompson and Heron (1954) have imposed restriction of three different degrees of severity on twelve Scottish Terriers for a period of seven to ten months. Eight littermates were reared as pets. It was found that the restricted animals explored more in a familiar situation. The animals raised as pets soon adjusted to a new situation and settled down, but the restricted animals kept moving around. It has also been found that restricted mice explore more when

caged in adulthood. It is possible that the dogs would have behaved in the same way no matter what the age of restriction.

Though the work on dogs is highly interesting, it will be seen that it covers a limited area. There is nothing like a detailed experimental investigation of the organisers essential for psychological development at various ages.

(b) Chimpanzees

Though the development of the chimpanzee has been studied in some detail at the Yerkes laboratories, no detailed or organised attempt has been made to describe its psychological development.

This report will be confined to the work on the development of visual discrimination.

In the first place, it appears that once visual discrimination has reached a certain level of expectancy, fear responses are shown towards strange objects (Hebb, 1947). Before discrimination has developed, the infant chimpanzee responds positively or 'impulsively' to objects.

Riesen (1950) has studied the effects of being reared in darkness on the visual discrimination of the chimpanzee. In 1942 he blindfolded a chimpanzee at birth and released the blindfold at 16 weeks. It took the animal two weeks to develop normal discrimination. In 1945 he used three chimpanzees for his experiments. One female spent her first 16 months in darkness, with only forty-five seconds of electric light per day at feeding time. At 16 months, when exposed to long periods of light, she could not identify objects until she had touched them. This continued for an extremely long time. A male kept in darkness from the 16th to the 23rd month underwent degeneration of the optic nerve for an unknown reason. The prolonged darkness may have had

something to do with it. A control was reared normally.

These experiments were followed up, using another three chimpanzee subjects. One infant was reared in total darkness for seven months, another was permitted a plexiglass translucent mask which did not allow focusing for 1½ hours daily, and a third was permitted 1½ hours of normal white light each day. At seven months the third subject was found to be average in visual discrimination, but both the others were retarded, taking between thirteen and thirty days to establish normal discrimination. They could not follow a bottle with their eyes, recognise the attendant, or discriminate a pattern associated with shock until they had had many trials.

Another experiment in this series was conducted with a male chimpanzee placed in total dark from his 8th to his 24th month. He lost his ability to recognise objects, people and movements. Even when looking at the sun he did not close his eyes. Recovery of sight was partial, again suggesting physical damage to the eyes. Whether such physical damage invariably follows confinement in dark is an interesting question to which there is not at present an answer.

It should be noted that in this series of experiments there is no evidence of a critical age early in life. Indeed, they suggest that damage may be greater if the restriction is commenced later. Perhaps the periods of darkness suffered by the chimpanzees in this series of experiments were excessive.

The same author has studied the emotional effects of sudden light on a chimpanzee reared in darkness. (Riesen, 1961). Jerky movements of the eyes and of the limbs are observed which approach epileptic seizure.

Conclusion

Very few of the experiments quoted enable us to

assert that there are (a) critical periods, or (b) that the effects of early influences are more persistent.

Required for proof of (a) is the subjecting of animals at various stages of life to the same experimental variation; and required for proof of (b) are long-term studies.

A detailed knowledge of the life history of the animal is essential for effective planning of experiments to detect the most important variations and the appropriate ages.

C H A P T E R IV

EXPERIMENTAL VARIATIONS IN THE EARLY ENVIRONMENT OF THE RAT

Introduction

Probably because it is such a convenient animal to keep in the laboratory, there is an extensive literature on the effects of early experience on the rat.

The disadvantage of working with the rat is that, as Hebb showed (1937), primary learning is very rapid. Adaptation is extremely rapid, showing that adaptability is not always the criterion of the highest intelligence. A further disadvantage is that the social responses of the rat are very limited. A vast range of ontogenetic behaviour which is most likely to be affected by experience is thus eliminated.

But, as I have attempted to show, the general law of development, both psychological and physical, that formative phases are critical, may be tested with animals as well as men.

It is for this reason that we can profitably study the development of the rat as well as other animals, though it is possible to obtain more varied effects among higher than lower animals. This is in accordance with Dennis' (1937) conclusion that phylogenetically determined development is less susceptible to influence than ontogenetic behaviour.

The work on the development of rats has been divided into the effects of (a) handling, (b) stimulation other than handling, (c) housing, (d) food and water deprivation, and (e) social experience.

A. Handling

(i) a. Studies of the effects of handling before weaning.

Various techniques are employed in handling rats. Handling may simply consist of holding the animal for a certain period, as in the work of Levine (Levine, 1956, 1957a, 1957b, 1958, 1960), or it may consist of stroking the animal, as in the work of Weininger and others.

The effect of handling on avoidance learning has been studied (Levine, 1956), using a two-compartment Miller box of plexiglass. The conditioned stimulus was a 60 cycle hum and the grid in the starting compartment was wired to 110 volt A.C. source limited by a variable resistor. Handled rats were superior to controls in learning avoidance; they also extinguished the response more rapidly. Rats which had been shocked in infancy performed as well as the handled rats. That is, handling had the same effect as handling plus shocking.

In this study, as in all Levine's studies, testing occurred early in adult life (at 60 or seventy days).

Handled rats were also shown to be less emotional than non-handled rats. Emotionality was measured by a defecation count, by a count of the number of freezes, by a count of the number of hurdle crossings during pre-trial habituation to the Miller box, and by movement in the open field. Handled rats tend to explore more and defecate less than non-handled animals.

The lower level of emotional disturbance is probably the cause of handled animals taking better advantage of a short period of supply after deprivation (Levine, 1957a). Animals were placed on a deprivation schedule of eighteen hours followed by opportunity to relieve their thirst. The length of the relief period was varied. Water consumption was calculated per 100 grms. body weight so that there should be no bias in favour of the handled rats which were heavier

beyond the 0.01% level of chance. The results showed that there was no significant difference in water intake prior to deprivation, but that during short periods of relief (10 minutes) the handled animals drank significantly more ($p = 0.05$). During long periods of relief there was no difference in intake. After a period of adjustment the non-handled animals were able to use the short period as well as the handled animals.

Some confirmation of the interpretation that observed differences may reflect differences in resistance to emotional disturbance is found in the demonstration that handled rats shocked while relieving thirst recover normal drinking more rapidly than non-handled rats shocked under the same conditions (Levine, 1958).

A fact of doubtful significance is that destruction of the septal regions in between and below the hemispheres of the midbrain makes non-handled rats rather more vicious than handled rats. It seems that the effects of early taming are enduring (Levine, 1960).

Though handled and non-handled rats have the same volume of steroids (hormones) in circulation before shock, the volume rises more rapidly after shock in the handled rats and persists at a higher level for about fifteen minutes. The non-handled rats, on the other hand, achieve a high level of output more slowly and maintain it longer (Levine, 1960).

Handled rats develop a response to cold at an earlier age than non-handled rats, (Levine, Alpert and Lewis, 1958). On the experimental day the non-stressed animals were killed by cervical spinal separation and their adrenals were weighed and assayed for ascorbic acid content. The stressed animals were subjected to a temperature of $5^{\circ}C$ for ninety minutes before they were killed and their adrenals were weighed and assayed. Both the stressed and non-stressed groups contained handled and non-handled animals. The ascorbic acid

content of the adrenals was taken as an indicator of adrenalin output, since ascorbic acid is an essential constituent of adrenalin.

Animals tested on the tenth day of age showed no ability to respond to cold stress, but by the twelfth day of age the handled group showed significantly greater depletion of ascorbic acid. The non-handled group compared with the results of Jailer (1950) in showing 20% depletion of ascorbic acid by the sixteenth day, whereas the handled group showed 30% depletion. The handled group, therefore, not only began to respond to cold stress at an earlier age than the non-handled group, but also developed a greater response at the sixteenth day.

Handled rats are also more resistant to the physiological stress of glucose injection (Levine, 1957 a). At 70 days resistance to a 20% solution of glucose injected peritoneally at a rate of 7.5m.l. per 100 grams of body weight was tested. This is reputed to be sufficient to produce 21% mortality. Following the injection, subjects were placed in individual cages and deprived of food and water for 24 hours. Subsequently, survivors were watered for one hour and the water intake was recorded. The animals were then killed and the left adrenal gland was weighed. The non-handled rats had significantly larger adrenal glands after stress than the handled animals, and they also drank less water.

There are also a number of other physical differences between handled and non-handled rats (Levine, 1957 a, 1960). Handled rats show a significantly lower mortality rate after five days of deprivation of food and water than non-handled rats. Analysis of the brain tissues reveals a higher cholesterol content among handled rats, which may be taken to indicate white matter. Nerve pathways may mature more rapidly.

Handled infants are reputed to open their eyes earlier, achieve motor co-ordination more rapidly, grow body hair faster and become heavier at weaning.

It may be noted here that we have found no evidence for the four last-mentioned characteristics in our own experiments.

A mechanical handling device has been employed in treating two subspecies of deermice (King and Eleftherion, 1959). Large inter-specific differences were noted, but the differences between handled and non-handled subjects were small.

It has been shown that handled rats are more dominant than non-handled rats (Mezei and Rosen, 1960). The authors also confirm the finding that handled animals tend to remain dominant on retesting; but they do not find that handled animals are heavier than non-handled. They advance the hypothesis that handling raises the threshold for reactivity to novel emotional stimuli, and that the novelty of competing for food is more fear-arousing for the non-handled rats.

(i) b. Summary

The effects of handling before weaning are seen in (a) improved avoidance learning, (b) reduced emotionality, (c) more rapid consummation after water deprivation, (d) more rapid consummation after shock, (e) more rapid rise and decline of hormone level after alarm, (f) precocious resistance to cold, (g) heightened resistance to glucose injection, and (g) raised dominance status.

(ii) a. Studies of the effects of handling after weaning

It has long been known that animals which have had contact with the experimenter perform better in the laboratory. The survival rate of handled animals after a surgical operation for the removal of the parathyroid gland was known to be much higher than the survival rate of unhandled animals. The rates were, respectively, 75% and 15% (Greenman and Duhring, 1931).

Handled rats are reported to survive immobilisation in elastoplast for forty-eight hours much better than non-handled rats (Weininger, 1953, 1954, 1956). The same author reports that the handled rats, dissected after the period of immobilisation, showed less distension of the heart, fewer gastrointestinal bleeding points, and lighter adrenal glands. There was no difference in the weights of the livers, pancreas, or kidney. Non-handled rats produced more feces over a sample period, suggesting that they used their food less efficiently.

Growth, food utilisation and thyroid activity as a function of extra handling have been studied (Ruegamer, Bernstein and Benjamin, 1954). Animals were handled for ten minutes per day for five weeks after weaning. On the testing day the animals were injected intraperitoneally with 50 micro c.c. of radioactive isotope of iodine and killed twenty-four hours later. Observations showed that there had been no difference in their daily food intake, but that the handled group was heavier and had gained more per unit of food intake. It was also shown that the non-handled group had eliminated significantly more fecal pellets. The thyroids of the non-handled animals were found to be more radioactive. These results were interpreted as indicating that handled animals utilised their food more efficiently than non-handled animals and were less anxious.

Weininger has confirmed that handled rats are heavier (1954, 1956). He also maintains that they do more exploration in an open field test.

Bernstein has shown that an early-handled group is superior to late-handled and a non-handled group in learning a T-shaped discrimination box problem under hunger motivation. Unfortunately the late-handled group did not receive as much handling as the early-handled group (Bernstein, 1952), since the early-handled group was handled from 21 to 60 days and the late-handled group was handled from 50 to 60 days. He also showed that if the handling was interrupted the animals fared worse in extinction trials.

Barry has shown that rats handled between learn and relearn of a maze problem (interval 75 days) made fewer errors than non-handled rats (Barry, 1957).

The handling of rats for one day each does not appear to have any effect on their performance (Gertz, 1957). The animals, tested at the age of 120 days, were handled at 25, 54, and 83 days of age respectively. A non-handled group served as a control. The test consisted of a maze and a discrimination box problem. Gertz found no evidence for the hypotheses that handled animals explore more and are less emotional; the age at which handling is important; and handled rats perform better on problems.

All that can be said for this study is that it shows that single experiences of handling do not affect subsequent performance. Since the animals are handled a great deal in the experimental testing it is hardly surprising. It has been shown that three experiences of handling in the first five days will increase resistance to cold whereas the same number of handling experiences make no difference from ten to thirteen days (Levine, 1960).

A dissentient study found no difference in the subsequent performance of gentled, shocked and ignored rats (Scott, 1955). Treatment continued for 22 days (23rd to 44th day) and testing was commenced at 119 days. He found a significant

difference in weight between the shocked and the handled group, but not between the handled and the ignored group. Since he weighed the animals every sixth day, handling them at the same time, every animal was in fact a handled animal. This is too serious an objection to enable us to take his results very seriously. He found no difference in activity, food and water intake, resistance to twelve days of reduced diet, or resistance to a heat wave and the toxic effects of an injection of thiourea.

A dissentient study open to fewer objections investigated the hypotheses that (a) handling and other non-traumatic emotion-provoking stimuli early in life can raise the threshold for emotional reactivity; and (b) handling and other stimuli can raise subsequent resistance to stress (Ader, 1959). Groups of animals were stimulated in a variety of ways either from 23 to 53 days' of age or from 136 to 166 days' of age. Stimulation consisted of handling or swinging cage or varied stimulation or massed stimulation. At various ages the subjects were given cage emergence tests, were immobilised and their organs weighed and examined. No difference was found in the percentage increase of body weight or in the time required for emergence from cage. In the open field test it was found that the massed-stimulated group defecated most. In a Y-maze no differences of ability were discovered. No differences were found in the organs after immobilization or in the loss of body weight.

It is difficult to answer the objections which this experiment raises against the findings of others on the effects of handling.

It is interesting to note that the effects of handling have been obtained by Weininger with rats which have been caged solitarily. When animals are caged in groups, as in the work

of Ader, the effects of handling, at least after weaning, do not appear to be so prominent. That this may be so, is borne out by the investigations of differential amounts of handling (10, 5 and 0 minutes per day) under conditions of group housing (Winokur, Stern and Taylor, 1959). They could detect no differences in weight and body length. However, they confirm Weininger's finding that gastrointestinal damage is less among handled rats after immobilisation for forty-eight hours.

(ii) b. Summary

The effects of handling after weaning are similar to those obtained before weaning. They are (a) greater weight increases, (b) greater resistance to stress, (c) more effective food utilisation, (d) increased exploration, and (e) better performance on a T-maze. Dissentient studies are also quoted.

(iii) Comment

The effects of handling have been shown. What is the nature of the handling experience for the animal? Does it increase perceptual experience, reinforce the subjects relationship with the experimenter, or act as a stress? These hypotheses are discussed below.

(iii) a. Increase in perceptual experience

The experiments of Hymovitch (Hymovitch, 1952), indicate clearly that enriched perceptual experience at an early age is more beneficial to the maze-solving abilities of the rat than the same perceptual experience at a later age.

It has been stated that the magnitude of the facilitation by enriched perceptual experience is inversely related

to the age at which it is given (Hebb, 1949). Though it appears that handling at an early age (1 to 20 days) has a greater effect than later handling (51 to 70 days) (Levine, 1956), there is no evidence which has a direct bearing on the question of whether handling acts by enriching the perceptual experience of the animal. Such a question could only be answered by comparing the effects of handling on animals housed under various degrees of restriction.

If handling increases the exploratory tendencies of the animals as much as is claimed, it is possible that they enrich their own experience to a greater degree after handling.

In the experiment reported in this thesis, rats were housed in large and small cages in an attempt to arrive at some answer to the question of whether handling acts by enriching the perceptual experience.

(iii) b. Reinforcement of subject's relationship with experimenter

It is widely known from the work of Lorenz that greylag geese, jackdaws and other birds establish rapid social relationships at a very early stage of life. The process is so swift and final that he called it 'imprinting'.

Among mammals the process is less rapid, but there are nevertheless definite periods within which the most important social relationships must be established. Detailed studies have been made of dogs (Scott and Marston, 1950; Scott, Fredericson and Fuller, 1951). These show that there is a definite period of socialisation from three to ten weeks of age, during which a relationship must be established between the pup and the experimenter if it is to be strong and permanent. It is noticeable that rats which have been handled in infancy are often more docile and tractable at the commencement of testing in adulthood than non-handled rats are at the end of testing, by which time they have received more handling than the handled animals had.

Habituation to the experimenter is certainly an important factor in performance, even if it is not the main factor. Interruption of contact with the experimenter between learn and relearn of a problem has been shown to be important (Bernstein, 1952). Animals which were handled daily between tests relearnt the problem much more rapidly.

Handling provokes emotion in rats which have not had prior experience of it. They squeal, bite, defecate and urinate very readily. Emotional disturbance of this intensity certainly inhibits performance.

An experiment has been conducted to assess the importance of experimenter contact in developing resistance to cold (Levine and Lewis, 1959 b). The various stimuli, all administered from birth to the age of fourteen days, were shaking in the cage, movement of the cage to the shaker without shaking, two minute shock, and handling. It was found that all the experimental groups showed significantly greater depletion of adrenal ascorbic acid than the control when subjected to a temperature of 5° C for 90 days at the age of fourteen days.

This appears to indicate, at least as far as the scope of the experiment extends, that stimulation, or stress, is more important than mere experimenter contact.

This leads us to the supposition that handling acts as a stress, that some important and far-reaching adaptation to stress occurs, and that this adaptation is reflected in the growth and behaviour of the rat.

B

i) Experimental studies in which rats have been given early stimulation other than handling

A study already quoted (Levine, 1958) found that severe electric shock before weaning had the same effect as handling. The shocked or handled rats were equally superior to controls in adjustment to a shortened period of water consumption. In addition, both groups showed less emotional behaviour.

The effect of electroconvulsive shocks in late infancy on the learning ability of rats has been investigated (Porter, Stone and Eriksen, 1948). The convulsive shocks were administered between the ages of 21 and 30 days. After this, either ten or twenty days of recovery were allowed. The ten-day recovery group was given thirty trials on a Stone multiple T-maze. The twenty-day recovery group was run at the age of fifty days. In both tests it was found that the controls were superior to the experimental subjects in both time scores and rapidity achieving the criterion. No gross behavioural differences were observed. Differences were statistical. A second experiment was conducted in which half the convulsed group received 20 ma for .2 seconds and the remainder received 50 ma for .2 seconds. There was no observable difference in their later performance on the Stone multiple T-maze.

This, the earliest experiment in the field, strongly contradicts the later work. It should be remembefed, though, that subsequent work has been done in avoidance or escape learning, in which the subject is made to suffer another shock. This difference is probably important in explaining the apparent discrepancy. An explanation will be attempted later.

A subsequent investigation (Griffiths and Stringer, 1952) subjected rats to very intense stimulation from the day of birth till the age of 21 days. From the sixtieth day they were put through a battery of tests : the Warner-Warden maze, the Lashley discrimination apparatus, the open field test for emotional behaviour, and susceptibility to audiogenic convulsions. There were five groups, four of which were experimental groups which had been subjected to the intense infantile experience and the control. The four experimental groups had been treated as follows : (a) shocked, (b) temperature changed, (c) auditory stimulated (d) rotated.

This investigation found no significant difference in any of the tests conducted between the experimental and the control groups. It is not mentioned how frequently the controls were handled.

In the two investigations so far dealt with in this section, the amount of handling which the control groups received is not specified. This was later shown to be an extremely important factor. What one might conclude, therefore, is that intense stimulation in addition to handling will produce no added effects. However, that must remain doubtful until the range of the tests to which subjects have been submitted has been extended.

A subsequent attempt was made to introduce an adult control (Baron, Brookshine and Littman, 1957) in an effort to discover whether there are periods of heightened susceptibility to the effects of shock on later avoidance and escape learning. Only two shocks were administered to each experimental rat. Four groups of twenty-four subjects were used. The first group was weaned and shocked at 20 days. The second was weaned at twenty and shocked at 26 days. The third was an adult control group of which half was shocked two days before the test and half was not shocked. The fourth group was the control weaned at twenty days.

Testing commenced on the 120th day. It was found that subjects shocked at any time prior to the testing were superior to controls in escape learning under both high and low shock, and in avoidance learning under high shock only. It was also found that subjects shocked in infancy tended to extinguish more slowly under high-shock escape conditions.

The obvious criticism of the use of adult controls in this experiment is that they were traumatised two days before the test, while the shocked infants had been traumatised over ninety days before. Therefore, the experiment is not adequate to offer comment on whether there is such a thing as a critical period.

The work in this field, that is, dealing with the effects of early shock, seems to show that these effects are not as widespread as those of handling. But too little is known about the way in which the controls were treated. The amount of handling to which they were subjected is of the utmost importance in assessing this work.

An additional comment to be offered on the last experiment is that only two shocks were given to each rat. It may be that a larger number would produce a noticeable effect. The adult controls should be traumatised much longer before the experiment.

The question remains of how wide-spread the effects of early stimulation are, especially on the learning process. There is no evidence that shocked or handled rats perform better in a learning situation in which no second shock is administered. There is no evidence that rats shocked in infancy could, for example, do better in a discrimination problem or in a maze.

The point just raised is important in view of the conclusion of the above experimenters that rats subjected to shock at any time prior to the testing situation are superior

in learning escape under high shock and low shock, and in avoidance learning under low shock. This point has been expanded into a hypothesis (Kurtz and Pearl, 1960) that the experience of fear prior to the testing situation leads to its quicker arousal, and hence to quicker learning.

The hypothesis was borne out by studies conducted in a modified Miller box. All animals shocked prior to testing extinguished more slowly after learning the avoidance response.

(ii) Summary

Electroconvulsive shock was found to depress maze learning ability of rats tested 10 - 20 days later; but intense stimulation by shock, rotation, noise, and temperature change were found to have no effect on results of testing later in life. The difference between shocked and non-shocked rats on avoidance learning may be a function purely of the shock and not the age at which it is administered.

(iii) Comment

In these results there is no evidence of critical age or persistence of the effects of stimulation in infancy. It appears that all results can be explained in terms of the hypothesis of Kurtz and Pearl that prior shock is important in avoidance learning, not the age at which it occurs.

There is no evidence of broad developmental effects as a result of early stimulation.

C.

(i) Experimental studies in which the early perceptual experience of the rat is enriched

The commonest approach in this field is to provide some subjects with 'toys' and to limit the experience of other subjects as much as possible. One way in which to limit the visual experience of animals is to raise them in total darkness (Hebb, 1937). Those raised in darkness showed a reduced ability to discriminate among figures which lasted for only one hour! He also showed that the provision of 'toys' at an early stage of development facilitates problem solution at a later age (Hebb, 1947).

The effect of access to tunnels, inclined planes, swinging doors from the age of twenty-one days to fifty-one days has been investigated (Bingham and Griffiths, 1952). Controls were reared in laboratory cages with solid backs and sides. Another group was reared in squeeze boxes, that is, in cages the dimensions of which could be varied. At sixty-five days all the subjects were tested, commencing with the Warner-Warden maze. Testing was continued on the inclined-plane maze, the Lashley jumping apparatus, the open field test. Susceptibility to audiogenic seizures was determined.

The results showed that a wider and richer environment is favourable to the learning of mazes, but that there was no significant difference on the other measures.

An attempt has been made to investigate the effect of early free-environment experience on the rat (Forgays and Forgays, 1952). From the age of twenty-six days to the age of ninety days groups of rats were raised in seven different environments of varying degrees of freedom.

Testing on the Hebb-Williams maze was commenced at ninety days. It was found that the free-environment group with playthings was superior to all other groups. The order after that was : free-environment group without playthings, mesh-cage animals, mesh-caged animals reared between the

free-environmental groups and restricted groups.

A further test was conducted to determine how much the use of visual distance cues enabled the free-environment group to perform better than the other groups. Barriers were set up in the maze which eliminated the use of distance cues. It was found that the biggest drop in score was among the group which probably used these cues, that is, the free-environment group. It is concluded that there is an inverse relationship between the error scores in the Hebb-Williams test and the employment of visual distance cues.

There are two comments which must be made on the studies reported so far. In neither was an adult control used, so that while we do know that free-environment plays a rôle, we cannot be sure that the age at which this experience occurs has any bearing on the effect.

The second comment is that we do not know the amount of handling involved.

Hymowitz (1952) has investigated the effects of experimental variation of the conditions of infancy on problem solving in adult rats. He reports three experiments, two of which include the problem of the age at which the variation occurs.

In the first experiment rats were blinded early in life (17th) or late (78 days). Each group was subdivided into two : those reared in free-environment boxes six ft. x four ft. x six ins., and those reared in 'normal' cages of solid side and back with mesh front and top. At eighty days all groups were tested on the closed field test for their problem solving ability, and it was found that the free-environment group performed better regardless of the age at which blinding occurred.

In the second experiment rats were reared in different environments from the age of twenty-seven days : stove-pipe cages of diameter 8 ins., mesh cages, enclosed activity wheels, and one group was given a daily run in the free-environment box. At seventy-nine days they were compared for problem solution on the closed field, and for learning on the ten-unit enclosed T-maze. It was found that mesh-cage and free-environment rats were superior to the other two groups in the closed field, but that there was no significant difference between them on the maze. It is mentioned in the report that handling was kept to a minimum, but the free-environment rats were transferred daily from their home cages to the free-environment box. This meant a great deal of handling for one group. The purpose in rearing some rats in the activity wheel was to determine whether motor activity was important in maze learning and problem solution.

In the third experiment the problem of age was again tackled. One group was given stovepipe confinement early (30 - 75 days) and free-environment later in life (85 - 130 days). For the intervening ten days they were housed in normal cages. In a second group this treatment was reversed. There were two control groups, one reared for the entire period in the stovepipe cages and the other reared for the entire period in the free-environment box. The group which had early free-environment experience was significantly superior to the group with late experience.

In each testing situation there were two tests, a preliminary in which the animal had to reach a criterion of nine out of ten runs in one minute, before the final test was commenced. The aim was to eliminate timidity and greater exploration as factors. The effect was probably to eliminate the more transient effects. The experiment was planned with great care and merits careful study for its attention to the problem of adult controls and preliminary testing. The

author concludes from his investigation that differential opportunity presented early to various groups for perceptual learning was responsible for results which appear to be relatively permanent and possibly irreversible. His conclusion about the relative permanence and possible irreversibility of the results is based on the comparison of rats in which opportunity is presented early to those in which opportunity is presented late. Till more attempt at therapy is made, though, no conclusions can be arrived at concerning the irreversibility.

An attempt has been made to determine the relative effects of visual and proprioceptive experiences in infancy on the cognitive behaviour of mature rats (Forgus, 1954). Test criteria other than the Hebb-Williams 'intelligence' tests were used. Testing was commenced at eighty-four days. Groups of fourteen each lived in the experimental conditions from the age of twenty-four days till the testing was commenced.

The rats were tested on an elevated maze and the following observations were made : latency, emotionality, activity, variability. In addition, the rats were tested on a visual discrimination apparatus and they were given a reasoning test in which they had to find the shortest route to the goal.

On the elevated maze it was found that groups one and two were superior to the third group on all criteria, but that no distinction could be made between the performance of one and two.

On the visual discrimination apparatus group two was superior to group one, which in turn was superior to group three. Thus, the complex visual and poor proprioceptive experience of infancy seems to have sharpened the rat's visual activity.

On the reasoning test, groups one and two were not significantly different, but both were significantly superior to group three.

The author explains his results in terms of a hypothesis of Witkin, that reaction sets are built up. Group two would find the visual stimuli perceptually more prominent in terms of this hypothesis, and would build up reaction sets which depend more on visual stimuli than on other sensory experience.

The author set out to test a more refined hypothesis as a result of this investigation (Forgus, 1955). The hypothesis is, 'If two groups of animals, one reared in a complex visual and motor environment, and the other reared in a complex visual but relatively simple motor environment were to learn, partially, a complex open maze with visual cues present and were then tested for complete learning with visual cues greatly reduced, then the first group would be superior in performance on the second test'.

The groups were reared from the age of twenty-five days to the age of eighty-five days in the environments previously described and were then tested on an eleven-unit elevated T-maze. They were run to a criterion of one error or less per trial for two consecutive runs. Then the lights were turned out and the learning was completed. The experimenter could follow the rats by means of a luminous ring round their necks. They were run to a criterion of five correct runs in six.

The results show that group one runs faster, but that group two learns faster in the preliminary trials. The second group hesitated more at the choice points, but used more visual cues in the elimination of false choices. This is in accord with the findings of Witkin. After the lights

have been switched off, the first group achieved the criterion more rapidly.

Unfortunately, there was no control in which the learning was completed in the light.

Explanations might attempt to take account of differences of emotionality. In the 1954 experiment no significant differences between the two groups were detected. An explanation might also attempt to take into account the familiarity which probably results from the use of toys, but such an explanation could not account for the more rapid learning in the preliminary by the second group. It is noticed that the first group explores more in the preliminary, perhaps a polite way of saying that they make more errors, but that may be significant in explaining why they make less errors in the final, since the second group relies more on visual cues than on exploration for its solutions.

It seems that the hypothesis is a valuable one which might be subjected to further test.

(ii) Summary

Though the effects of early visual restriction are temporary, it appears from the results that visual or proprioceptive reaction sets in learning are retained long enough to show up in tests of learning ability on the elevated maze. The effects of small cages appear to be more injurious to the animal early in life than later, and it is suggested that the effects of severe restriction early in life are irreversible.

(iii) Comment

From these experiments it is not clear whether Hebb's findings on visual restriction apply to restriction in other modalities. It is possible that when an animal is placed in a situation in which he can make use of a preferred reaction set, such as a maze in which use may be made of visual, olfactory auditory and proprioceptive cues, differences will show up for

a long time. Animals in a freer environment may also learn to combine information from several sensory modalities, while animals in a restricted environment may develop almost exclusive dependence on the sensory modalities which they are permitted to use.

The emotional effect of a sudden increase in stimulation when an animal is released from a more restricted environment should also not be overlooked. This can adversely affect learning.

D.

(i) Experiments in which rats are subjected to early deprivation

Studies on the effect of infant deprivation on adult hoarding commenced in 1941 (Hunt, 1941). An improved and more detailed version of this experiment is reported in 1947 (Hunt, Schlosberg, Solomon and Stellar) and I shall deal with this only. An experimental group fed irregularly on mash for fifteen days after weaning at twenty-one days, and a control group supplied with mash at all times were used. At an unspecified age when they had reached 'maturity' they were tested in a hoarding apparatus in which cages had access to supply alleys which could be blocked. The first session was commenced on a hunger drive of twenty-three-and-a-half hours. The subjects were allowed to keep the supplies hoarded in their cages. By the fourth day hoarding activity had ceased. In four repeats of this experiment from 1941 onwards the probability levels for more hoarding among those deprived in infancy during the adult-deprivation series were .30, .60, .30 and 0.2. The .2 level was obtained when the rats were allowed access to pellets in infancy for a few days before being placed on the mash diet. The authors do not stress this point or attempt to make a distinction between the procedures. Instead, they multiply the p levels to get a p of .001, which is a highly doubtful procedure when different techniques are employed. It would, in my view, be much more profitable to stress the significance of the difference in procedure.

A subsequent experiment used three groups of twenty which were, respectively, a control on ad lib. feeding, a food-deprived group on alternating 12- and 24-hour cycles, and a water-deprived group on the same cycles (McKelvey and Marx, 1951). The deprived groups suffered deprivation for fifteen days from twenty-four to thirty-nine days. After this they

were placed on the ad lib regime. At one hundred and thirty days they were placed in the hoarding apparatus for four days of habituation with ad lib food, as well as water. Water pellets consisting of cylinders of cotton wool saturated with water were used.

The results contradict those of the previous experiment. No difference in the hoarding behaviour appeared, with the exception that the food-deprived males hoarded more. This is puzzling.

Perhaps the genetic factor is more important than early deprivation. In the previous experiment it was found that there were large inter-litter differences. It also seems that the low levels of probability that the effect is produced by the experimental variable were accurate, and that the authors should have accepted their lowest probability level instead of multiplying.

Relevant to the problem of experience is the finding that rats given access to storage alleys for twenty half-hour sessions hoard more under deprivation than rats given access to the same alleys for the same period when these alleys contained no food supply. (Holland, 1954). The rats used in this experiment were 145 days old at the commencement and 195 days at testing. We must conclude that there is no evidence that early deprivation is a factor in later hoarding, but that learning can play a part. At what age it is most effective we cannot say.

Rats kept on a deprivation schedule for ten days after weaning retain a faster rate of eating than controls, even after thirty weeks of unlimited feeding (Marx, 1952). The deprivation may be effected by limiting the feeding time or by limiting the amount of food. Subjects were observed after they had been placed on a deprivation schedule in adulthood. Differences disappeared by the seventh day. No differences in hoarding were observed.

Baker has shown that rats can adapt to a feeding schedule of thirty-six hours without any drop in weight, and that there is a perfect negative correlation between the length of deprivation and the amount consumed. That is, rats on a twelve-hour schedule ate more than rats on a twenty-four hour schedule; those on the thirty-six hour schedule ate least of all.

The question of whether they conserve weight by being less active or by digesting more efficiently has not been answered, though it could easily be done by counting the fecal pellets (or, more accurately, by weighing) and by recording activity. The important point for our purpose is that rats may adapt very well to a deprivation schedule without loss of weight. Perhaps hoarding is only affected when the schedule is irregular or when the point is reached when they begin to lose weight.

Spence and Lippitt found that rats which had learnt the locus of a water bottle under thirst drive subsequently went to the same locus when deprived of food. They were unable to learn that the alternate arm in the Y-maze contained food. The inquiry has been extended to deprivation in infancy (Christie, 1952). Two groups of rats were deprived from the first day to the fifty-fifth, first of milk and later of food and water. They were then set to learning the Y-maze; one group under hunger drive and the other under thirst. Both learnt the locus of the water bottle, though this was the irrelevant response for the hunger-motivated animals. In a subsequent test, a group of no deprivation history, allowed to explore the Y-maze while satiated, showed latent learning in producing the right response when deprived of either water or food. A group of deprivation history, allowed comparable exploration of the environment of the Y-maze while satiated, showed latent learning of the locus of the water only, whether hunger- or thirst- motivated.

These results are interpreted as showing a very strong cathexis to water. The effect is not peculiar to infantile deprivation. An interesting variation of this would be to deprive the infants first of food and subsequently of water, and to note whether they are still unable to learn the relevant response to hunger-drive. The association of the two in infancy may cause the hunger drive to act merely as a signal for the more powerful thirst drive.

When food delivery and bar-pressing in the Skinner box are at a distance from each other, what will be the reaction of rats deprived in infancy of food if they are placed in the box with a partner? This is the question asked by Littman (1956). Mowrer found, without investigating the life history of his subjects, that the more aggressive rats solved the problem by multiple bar-pressing. Littman, using sixteen experimental subjects fed irregularly for ten minute periods for fifteen days after weaning at twenty-one days, and sixteen control subjects matched for sex and weight, found that at 190 days there was no difference. He noted, though,, that the most active bar-pressers were five females of the experimental group. The conclusion which is drawn is that reduction of drive is equally effective in both the pressing and the delivery areas.

It has been shown that there is no difference in exploration, but that there is a difference in speed of consummation of feeding response in the open field situation among rats deprived in infancy (Mandler, 1958). A group of thirty-four males was weaned at twenty-one days and divided into a control group of sixteen, kept on a twelve-hour ad lib diet and a twelve-hour ad lib diet and a twelve-hour deprivation period, and an experimental group of eighteen kept on deprivation periods of six to sixty hours. At fifty days both were put on the control regimen until eighty days.

The mean weight of both groups became equal in this period.

At forty-four days a preliminary open-field test after twelve hours deprivation was conducted on a table two feet by seven feet on which a food pellet was placed at the end opposite to the rats. The animals were allowed ten minutes for exploration and consummation. At eighty-five days they were trained in a Skinner box on a twenty-four hour deprivation schedule. It was found that the experimental group learnt the response at a faster rate. There was no difference in the extinction rates.

Another experiment was run by the same author in which the controls were given continuous ad lib. From fifty-eight days the experimental animals were placed on an ad lib diet till the age of 106 days. The mean weights of the groups were equal. At 106 days both groups were given the open field test described above. Again, there was no difference in the exploration but the author reports that the eating of the experimental group was faster. At 107 days the training on the Skinner box was begun on a twenty-four hour deprivation period. Again, learning was faster for the experimental group.

The author concludes that the deprivation history of the experimental group is important. It is mentioned that the handling was kept to a minimum.

In conclusion, I wish to state that a general review of the evidence in this section tells us nothing which we may say relates specifically to the period of infancy as a critical period for effective stimulation or deprivation. None of the authors makes out a case for the 'critical period'.

(ii) Summary

There is some disagreement about whether deprivation early in life increases adult hoarding. But early

deprivation does appear to lead to faster learning in the Skinner box for a food reward. Early-deprived animals also appear to retain a faster rate of eating in adult life.

(iii) Comment

There is no evidence that the age at which deprivation occurs is important. It is possible that deprivation at any age prior to testing would lead to the results described.

E.

(i) Experiments in which rats are subjected to early variations of social experience

By 'social experience' in this section I wish to refer only to the contact which rats have with each other.

The earliest study deals with the frequency of grid-crossings in the obstruction apparatus of rats segregated before puberty as compared to rats raised in cohabitation (Jenkins, 1928). Male rats were used, since female rats show only periodical sexual drive. It was found that the male rats which were segregated were subnormal in the number of grid-crossings. According to the author the segregated rats showed homosexual tendencies.

Another study (Beach, 1942) indicates that males raised in isolation (not segregation) copulated more frequently than rats raised segregated or cohabited. Males without early sexual experience ejaculated more frequently. Zimbardo has, however, subjected the data in this study to a X analysis and has obtained a result of less than 1, which indicates a very high probability that the difference was obtained purely by chance. A subsequent study by the same author confirms this (Beach, 1958). Rats raised in isolation were found in this subsequent study to be no more active, sexually, than segregated rats.

A thorough study (Zimbardo, 1958) attempted to find out whether shocking young males approaching receptive females inhibited sexual behaviour in adult life.

Twenty hooded rats were used in a 2 x 2 design. Twelve shocked males were divided into six raised in isolation and six raised in cohabitation. Eight controls were divided in the same way. Electrodes were implanted in all the rats but only in the shocked group were they attached to the shock source so that shock could be administered whenever the males approached and faced a female at about one inch distance.

The test for the effect of this treatment was conducted at seventy-five days and again at one hundred and forty days. At seventy-five days each male commenced a series of three fifteen-minute sessions with a receptive female spaced two days apart. At one hundred and forty days a single ten-minute session was given. The measures were : mount latency, copulation latency, frequency of mounts, frequency of copulation, and the intercopulatory interval.

The results show that there was an immediate effect during juvenile training of reducing the speed of approach to the female in the training apparatus, but that there was no effect on adult sexual performance. On the other hand, males raised in isolation were significantly less active sexually than those raised in cohabitation, at both seventy-five and one hundred and forty days. A test in the original training apparatus showed that the experimental animals were inhibited by the shocking apparatus, but did not learn to avoid females.

It appears, therefore, that rearing in isolation and segregation have the same effects, but that cohabitation does increase sexual behaviour. The conditioned avoidance to the apparatus rather than to the female obeys the same principle as conditioned fear in a child hearing its mother scream in the pressence of a mouse. The child becomes frightened of the mouse, not of its mother.

It has been found that rearing animals in pairs or in isolation has no effect on their learning a brightness discrimination under thirst drive in a Y-maze at thirty, sixty or ninety days. (D'Amato, Jagoda, 1960). In the same study it was shown that age and acquisition are significantly and inversely related.

It has also been shown that twenty-three day old rats subjected to intense auditory stimulation in the presence of the mother do not differ from controls in susceptibility

to seizure, but do show less substitute behaviour, such as grooming.

In conclusion, it must be admitted that powerful social effects have not been demonstrated in the rat. It appears that familiarity with females increases sexual responsiveness, but that is no more than is to be expected. Testing in pairs has no effect on susceptibility to ulceration in conflict, and neither does weaning at as early as seventeen days. The rat is not upset by a change of cagemates and learns the Y-maze as well whether reared in isolation or company. There is no effect on his emotional behaviour. Dominance, though, appears to thrive on the submissiveness of the mother, which seems very human. No explanation is offered for this peculiar result. The presence of the mother reduces the tendency to groom the face in the presence of a loud noise when the rat tested is twenty-three days. Did the mothers perhaps stop the grooming reaction by grooming the young too frequently?

(ii) Studies of the effects of early removal from the mothers

A study designed to find out what effect the age of separation from the mother has on subsequent susceptibility to ulceration found no difference (Ader, Taum, Beels, 1960 a). Split litter controls were allowed to remain with the mother until day of testing, while the experimental groups were separated from their mothers at the ages of seventeen, twenty-two and thirty-five days respectively. No differences were found in rate of growth or in emotionality on the Hall open field test. Neither was any difference found when subjects were introduced in pairs or singly to the conflict situation in which they had to cross a charged grid to obtain food. Testing was at 120, 160, 200 and 220 days. A group separated

from the mother at fifteen days and introduced to hard food at twenty-two days was less efficient in getting food and suffered more ulcertation than its control when tested at one hundred days.

The effect of interruptions of contact with the mother was also studied (Ader, Beels, Tatum, 1960 b). Pups experienced daily removal of the mother in either the first ten or in the latter ten days before weaning at twenty-two days. Strangely enough, those experiencing the interruptions in the second ten days (interruptions totalled up to forty-eight hours) had significantly more ulceration in the test conflict than animals experiencing interruptions in the first ten days, or than control animals. Again, no difference was found when animals were introduced to the conflict in pairs. Changing the cagemates of some groups had no effect on them. There was no difference in the emotionality as measured on the open field test.

Uyeno (1960) has investigated the interaction of submissive and dominant heredity in the albino rat and early social experience with dominant or submissive mothers. Four groups were raised. Dominant stock raised by submissive foster-mothers; dominant stock raised by dominant mothers; submissive stock raised by submissive mothers; and submissive stock raised by dominant foster-mothers. Analysis of the data showed that all the rats of dominant stock were more dominant than the rats of submissive stock; but that rats of dominant stock were most dominant when raised by submissive mothers. The submissive stock showed no differences. The tests were conducted at thirty-five days of age, so we do not know whether these effects persist very long. Furthermore, contact with a dominant rat older than the subject at any stage up to maturity might tend to dampen the dominance of the subject more than contact with an older submissive rat. Therefore, we do not know whether infancy is the most

'favourable maturational status'.

(iii) Summary

It appears that segregated and isolated rats are less active, sexually, than rats raised in cohabitation.

Isolated rearing does not affect brightness discrimination in a Y-maze.

Separation from the mother at too early an age affects susceptibility to gastric ulceration. Social contact with the mother appears to be important in determining dominance.

(iv) Comment

Lack of sexual experience has an understandable effect on sexual competence. This effect is greater as the phylogenetic scale is ascended.

It is possible that the increased susceptibility to ulceration among animals subjected to too early separation from the mother may be due to actual damage sustained at the time. This damage may be exacerbated in test situations.

The finding that rats of dominant strain are more dominant if reared by submissive mothers than if raised by dominant mothers reminds one of Kahn's (1951) study of the effects of defeat at various ages on the aggressive behaviour of mice. Does the dominant mother inflict the equivalent of defeat on the infant rat? Yet Kahn (1954) found that offspring of submissive mothers appeared to learn submissive patterns of behaviour from them. There is not sufficient information for clarity on this point.

General comment on the work on rats.

The most general observation is that animals are very seldom subjected to variation at different ages in the same experiment to determine the rôle of age, or tested at various ages to determine the persistence of the effects.

The most thorough study of the rôle of age was conducted by Hymowitz (1952) who found evidence for supposing that early restriction and blinding had greater effects than late restriction and blinding. Levine, Alpert and Lewis also showed that handling was more effective in producing resistance to cold if given in the first five days than from six to ten or eleven to fifteen days.

In addition, very little is known about the reversibility of the effects. Little therapy has been attempted. Again, the effect of therapy might be related to the age at which it is commenced.

These questions are of fundamental importance and can be investigated with the use of animals.

CHAPTER V

THEORETICAL CONTRIBUTIONS

Introduction

A number of effects of early deprivation, stimulation and stress have been dealt with. It is proposed now to deal with a number of theoretical positions which can, possibly, reveal links among these effects.

Pavlov's early work in the field will be mentioned, though the conceptual framework of his work is different from that of the others, predominantly American, considered.

The general adaptation syndrome as described by Selye is summarised because it deals with the effects of any non-specific stressor. It provides a link between the effects of a variety of forms of stimulation.

Hebb's emphasis on a phylogenetic order in the duration of primary learning is described as an example of the qualitative work which is necessary in this field. It is important in assessing the responses of higher and lower mammals to sensory deprivation and to stimulation.

Bruner's insistence that one of the major consequences of sensory deprivation is that it prevents the development of centrifugal control of sensory input is an important contribution to our understanding of the chaotic responses of sensory deprived animals to novel stimulation.

Though the relationship between sensory deprivation and the emotional deprivation syndrome described by Spitz is not clear, this is considered because it illustrates the fact that sensory deprivation is too broad a concept. In addition to sensory deprivation, the quality of the deprivation and the time at which it occurs must be taken into consideration.

Adaptation level as a concept for describing response to a level of stimulation was introduced by Helson and developed

by McClelland. Lindsley has proposed that the ascending reticular activating system is important as the mechanism of adaptation level.

(i) Pavlov : Reflex of natural caution

Pavlov (1955) divided the dogs with which he experimented into the weak type of nervous system and the strong type of nervous system. The weak type was characterised by rapid exhaustion of the cortical cells, susceptibility to inhibition with a rapid development of transmarginal inhibition and considerable external inhibition. There was evidence of a weak excitatory process finding expression in difficulty in establishing new conditioned connexions and of deficient active internal inhibition with a heightened tendency to passive protective external inhibition. The strong type of nervous system had a high functional limit to the working capacity of the cortical cells, with a strong excitatory process leading to rapid establishment of new conditioned connexions. Inhibition was of the active, internal kind.

The relationship between inhibition and excitation was also described by Pavlov in terms of equilibrium. Training, in his view, could contribute to equilibration, thus reducing excitability and increasing active internal inhibition.

A contrast was observed between half a litter of pups reared in a kennel and the other half reared in great freedom, as pets (cited by Ivanov-Smolensky, 1954). When the kennel dogs were released into a freer environment they displayed passive defensive behaviour, as though they had excessively weak nervous systems.

Pavlov commented that the puppies appeared to be provided with a reflex of natural caution. As soon as they commenced acquaintance with the new environment it was natural for them to wait for some time for the consequences of any new stimulation. They would abstain from new movements and repress existing movements. Only in the course of prolonged acquaintance with the environment would their

reflex of natural caution be gradually replaced by a new, special investigatory reflex.

It is also possible that stimulation may act by enabling the animal to acquire equilibrium, that is, to adjust excitability to the occasion.

It seems that the inherent temperament of the dog is important in determining its precise reaction to restriction. Thompson and Heron (1954) found, for example, that Scottish terriers reared in isolation in severely restricted cages appeared to be like prize bulls. They were alert, never bored, hyperactive, interested in the least thing.

On the other hand, the same dogs reared in groups under restriction might be of the passive-defensive type described by Pavlov.

Macmillan (1961) reports successful treatment of a child whose symptoms of withdrawal and passive-defensiveness were attributed to an undiminished cautionary reflex as a result of lack of stimulation in infancy.

The picture of the passive-defensive animal accords well with the descriptions of unhandled rats described by Levine (1960), and with the descriptions of hospitalism (Spitz, 1945).

Riesen (1961) reports that cats reared in the dark develop a tonic-clonic seizure when exposed to light and concludes that emotional disturbance is a prompt and dramatic consequence of incongruent sensory input.

It appears, therefore, that an animal which has had opportunities for exploration responds with equilibrium to new situations, an animal which has had fewer opportunities but has been reared in company with others responds by withdrawal, or passive-defensiveness, while animals which have been reared in restricted isolation may present various degrees of excitement. Animals appear to require company to learn when to be bored.

One must conclude, though, that the concept of a reflex of natural caution being gradually replaced by a special investigatory reflex does not appear to have high explanatory value. A reflex of natural caution is, rather, a description of the behaviour that develops when an animal is reared in restriction with company. There is no evidence for the belief that the animal is born with such a reflex, especially in view of the Thompson and Heron (1954) observations of hyperactivity and undirected curiosity among restricted, isolated dogs.

(B) Selye : Theory of Stress

A stressor is a 'preponderantly non-specific agent which both damages and stimulates defence'. With typical stressors, damaging and stimulating effects are about equally important. Examples of these are heat, cold, and various drugs. More specifically, an irritant may be defined as an agent which increases activity, while a noxa is a predominantly harmful stressor. In response, the body undergoes a triphasic adaptive reaction known as the G-A-S. The three phases are (i) alarm, (ii) the stage of resistance, and (iii) the stage of exhaustion. The stress response is 'the sum of all non-specific changes caused by function or damage. This includes the biologic phenomena necessary for the re-establishment of the normal resting phase' (Selye, 1955).

It is emphasised that the stress response is adaptive. It is not the cause of the vegetative disorders which follow, such as gastric ulceration or heart disease. Failure of the stress response, or part of the stress response, as in adrenalectomised rats, leads to increased ulceration, which may be reduced by administration of corticoids. Adrenalectomised rats, in spite of failing to show blood count changes and thymicolymphatic involution typical of the stress response, show an increase in organic damage. From this, it is concluded that the complete stress response is protective and adaptive.

But at the same time, many diseases are due to inappropriate non-specific stress. For example, excess of ACTH can cause latent tuberculosis to flare up.

The integrity of the pituitary-adrenal system is not essential for the effects of stress. Changes characteristic of damage occur more readily when there is a lack of adaptive hormones, e.g. ulceration, hemoconcentration, hypertension, shock. The stage of resistance can develop even

in adrenalectomised rats : they can be adapted to cold and survive temperatures of -18°C better than adrenalectomised and intact warm acclimated animals.

The first mediator of the stress response has not been determined and there is a possibility that it is multiple.

U.S. von Euler in an article in the same report mentions that no consistent change has been found in noradrenalin excretion during emotional stress though adrenalin figures are regularly elevated. Noradrenalin does not cause the apprehension and anxiety typical for adrenalin.

It is tempting in view of the work on aggressive and timid animals (Hess, 1951) and extra and intra-punitive types (Funkenstein, 1950) to speculate that stimulation in infancy may, among other things, alter the noradrenalin/adrenalin ratio, predisposing the stimulated animals to be more aggressive and less timid.

In applying the general adaptation syndrome to work on the effects of stimulation in infancy, certain questions must be answered.

The first question, which cannot be answered generally for all kinds of stress or stimulation, is whether early stimulation has a greater effect on the adaptation response than later stimulation. This is a repetition, in other words, of the question of critical age. The evidence has been reviewed already and shown to be rather scanty.

The second question is whether, once a stage of resistance is achieved, it persists. Again, the question cannot be answered for all stressors regardless of kind. Resistance to certain bacterial stressors, for example, can last for several years. Resistance to cold or to altitude is lost rather rapidly. The persistence of the effects of handling, investigated as the experimental part of this thesis, is a small part of this problem.

The third question is whether one kind of stress can prepare an animal for a stress of a different kind. The answer is a qualified yes when the first stress affects the general level of adaptability of the organism, as when pups are reared as pets instead of in a kennel, or when rat pups have their resistance to cold precociously raised by handling (Levine, Alpert and Lewis, 1958). Caution is needed here before accepting it as a general rule that a stress can raise the general level of resistance.

(C1) Hebb : Primary and secondary learning

When one compares the recovery of vision by a rat raised in darkness (Hebb, 1937) to the recovery of a chimpanzee (Riesen, 1950) or to the recovery of human subjects with congenital cataracts (Miner, 1905; Senden, 1932), one is impressed by the rapidity of the rat and the slowness of the primate.

There is another fact which is relevant here. Bilateral ablation of the occipital lobes of the cerebrum of the rat produce only partial defects in vision, while in the dog these effects are extensive and serious and in primates there is apparently complete blindness (in Fulton, 1951).

It appears, therefore, that the greater the cortical representation of vision, the longer it takes to acquire. The higher we go on the phylogenetic scale, the longer the period of learning that is necessary in infancy and the higher the achievement that is possible in maturity.

Hebb concludes (1949) that for primates the first steps of learning are steps of gradual increment. In fact, the animal is first learning to perceive. This can be demonstrated even with perceptions which are normally regarded as immediate, such as the perception of pain (in Hebb, 1955). It appears that animals have to learn to perceive pain just as they have to learn to see. Only after an animal has learnt to perceive can configuration or gestalt learning occur.

Furthermore, if we take the kinds of learning at which various species are most efficient, there is no evidence that higher species can learn more rapidly than lower. If the material is simple, the feeble-minded person learns as fast as the genius. The rat can learn a simple maze as fast as a man (Lashley, 1929). In other words, evolution has not changed the rate of formation of simpler habits, at least within certain ranges.

Basic to Hebb's schema is the hypothesis that all complex learning in maturity is transfer of training. The superiority of the higher animals lies in the building up of more complex concepts in primary learning and in the more rapid and extensive configurational use which may to made of these concepts by higher animals. The explanation of the more exclusive associations and of the slower primary learning lies in the relationship between the sensory projection areas and the association areas of the cortex.

The length of primary learning is roughly proportional to the ratio

$$\frac{\text{total association cortex}}{\text{total sensory cortex}}.$$

In other words, the larger the association cortex, the longer the period of primary learning. 'We can then regard the stage of primary learning as the period of establishing a first environmental control over the association areas' (Hebb, 1949, p. 125).

When widely different species of vertebrates are compared, a hierarchy of psychological complexity can be discerned which corresponds with an increase in the size of the cerebrum and a rise in internuncial neural tissues compared to afferent neural tissues.

This also appears to correspond to a freeing of the animal from the contemporary stimulus and an increase in direction by inner phase sequences.

If we assume that the differences which we observe between the behaviour of rats which have been restricted early in life and rats which have had a freer environment, are due to interruption of primary learning, it is easy to understand their inefficiency in maze performance.

The process of secondary learning occurs when there are well-established phase sequences which can be set off by stimulation.

Hebb's theory is difficult to apply to the effects of handling, but its relevance to the question of cage size is obvious. The animals which live in the larger cages might have increased opportunities for primary learning. Whether this is so, and whether the particular forms of primary learning can be revealed by the tests in the experiment dealt with in this thesis, is another question.

Hebb's theory is a rich one, capable of explaining a large range of phenomena. In applying his work to the effects of restriction we must note the caution which he adds to an observation on the work of Thompson and Heron (Hebb, 1955) that 'perceptual restriction in infancy produces intelligence of a low level, but it may not, by itself, produce emotional disorder'.

There seems to be little doubt at this stage that perceptual restriction in infancy damages the ability of the organism to learn. Sensory deprivation, even in maturity, produces hallucination and a loss of ability to solve problems (Heron, W., 1961), showing that throughout life the mammal is more dependent on his environment than we realise.

It is possible, though, that animals may learn to be dependent on each other. The isolated pups reared by Thompson and Heron (1954) appeared quite ordered, emotionally, whereas animals which are isolated after they have made contact with others are thoroughly wretched.

(D) Bruner : Perceptual development as perceptual differentiation

Bruner (1961) proposes that continued contact with a rich sensory environment permits the differentiation of sensory modalities and of events within modalities. Sensory deprivation prevents differentiation. He proposes further that contact with rich sensory environments makes the development of strategies for creating usable information, strategies such as class identity and reversibility, possible.

He draws attention to the finding that there are numerous centrifugal fibres which set the sensitivity of peripheral receptors in the muscles, the retinal cells, the organ of Corti. If these fibres are severed, the cortical control of the peripheral sensorium is destroyed (Granit, 1955).

It is possible that animals which have been reared in a highly restricted sensory environment do not acquire this ability to eliminate sensory input from certain structures when their attention is directed elsewhere. The distractibility and hyperactivity of the Scottish terriers described by Thompson and Heron (1954) might be explained on this basis.

The tonic convulsive reactions of the cats reared in darkness (Riesen, 1961) might be the result of complete inability to gate or reduce visual stimulation by centrifugal control.

It is clear that we are enabled to perceive anything only by not perceiving everything, and one mechanism which enables us to achieve perceptual differentiation is centrifugal control.

When we contrast the listless reactions of restricted animals which have company and a fair sensory input with animals which suffer severe sensory deprivation and are hyperexcitable on testing in a new sensory environment, we are

prompted to the conclusion that in the former case we are restricting the use of abilities which the animal has already developed, resulting in lethargy or withdrawal. In the latter case we are preventing the formation of selectivity. In other words, the former case would be one of deterioration of function while the latter would be prevention of function.

Naturally, more work is required to answer this question.

(E) Spitz : Stress and deprivation unified

As a result of her studies of the effects of contact and effective deprivation in a foundling home, Spitz (1955) has drawn up a table of comparison of the G-A-S (general adaptation syndrome) and the E-D-S (emotional deprivation syndrome). This table is given below.

	G-A-S	E-D-S
1)	Tension	Weepiness
2)	Excitement	Demanding attitude
3)	Loss of appetite	Loss of appetite, loss of weight
4)	Resistance to evocative stimulus increases	Social sector increases
5)	Adaptibility to other agents diminishes	Arrest and regression of D.Q.
6)	Libido subnormal	Absence of autoerotic activity
7)	Depression of nervous system	Withdrawal, insomnia, decreased motility
8)	Adaptation stops	Regression of D.Q. irreversible
9)	Resistance ceases	Infection liability
10)	Arteriosclerosis of brain vessels	Facial rigidity, atypical finger movements
11)	Breakdown	Morbidity increases
12)	Death	High mortality rate (37%)

This highly interesting comparison shows us clearly that emotional deprivation acts as an acute and persistent stress.

Once more we are faced with the question posed by Hebb. Is emotional dependence acquired, and does deprivation only act as a stress after that dependence has been acquired? All the children in this study had been breast-fed or nursed by their mothers for three months before separation. Naturally, we do not advocate experiments in which human infants are deprived of contact throughout their lives, but the differences between animals which have acquired an affectional response to a nurse and animals which have been raised without maternal contact could be studied.

Studies of this kind help us to clarify our hypotheses about the effects of sensory deprivation, the effects of stress, and the effects of perceptual enrichment in infancy. It may be that a combination of the factors of emotional deprivation and sensory deprivation produced the retardation and regression observed by Spitz. The effects of one of these at a time might be quite different. For example, infants reared under restricted with close maternal contact might not be emotionally deprived, but they might well be retarded. Infants reared under conditions of frequent sensory stimulation might not be mutually retarded, but they might well suffer some or all effects of the emotional deprivation syndrome.

The studies of Igel and Calvin (1960) on the development of affectional responses of the dog indicate that pups separated from their mothers at birth were able to develop affective contact with cloth surrogate mothers. The studies of Harlow and Zimmerman (1959) of affectional responses in the infant monkey indicate that infant monkeys respond in the same way.

Therefore, it is possible that emotional dependence is acquired and that the E-D-S would only occur in infants which have developed this dependence prior to separation. It also seems clear that in the cases of hospitalism dealt with by Spitz (1945) we are dealing entirely with the E-D-S and not with the effects of sensory deprivation. The institution children may present a combination of syndromes.

The rats reared in isolation by Weininger (1953, 1954, 1956) may be suffering from a combination of sensory deprivation and emotional deprivation. Handling such animals may have an important effect on their performance for both reasons.

The rats handled under conditions of group housing (Winokur, Stern and Taylor, 1959; Ader, 1959) do not show the same effects. There is no difference between controls

and handled groups. This is suggestive that something like an emotional deprivation stress is occurring.

Rats handled in infancy (Levine, 1956, 1957, 1958, 1960) may present a clear case of adaptation to stress and development of dependence on the experimenter. These animals are notably tame throughout their lives and may develop a permanent resistance to excitement at a slightly higher level than unhandled rats.

(F) Helson, McClelland and Lindsley : Adaptation level.

Helson (1948) has shown that receptors reach an adaptation level as a result of contact with stimuli of a certain level of intensity for a finite period of time, and that discrepancies from this adaptation level produce positive effect if they are small, negative affect if they are too large. He also found that the natural adaptation level of different receptors varies - some readily giving rise to pleasant discrepancies and other readily giving rise to unpleasant discrepancies. For example, sweet taste gives pleasure over a large range of intensity, while bitter taste gives rise to displeasure over a large range of intensity.

McClelland (1953) speculates that the sweet taste is relatively blunted (has a high threshold) compared to bitter taste (has a low threshold), and that discrepancies in sweet taste are small, producing pleasurable effect, compared to discrepancies in bitter. This leads him to the hypothesis that receptors have a natural adaptation level near their thresholds, though this is constantly being modified by stimulation. Three factors will affect the size of the discrepancies that yield positive or negative affect - the lower threshold, the upper threshold, and the Weber fraction.

Haber (quoted in McClelland, 1956) has found that a hand adapted to water at physiological zero temperature will perceive a temperature change of $1^{o}C$ in either direction as more pleasant than larger or smaller discrepancies. It is possible that organisers have natural optimum discrepancies from optimum levels of adaptation near the threshold for a receptor which give maximum positive effect.

Alpert (quoted in McClelland, 1953) has shown that when the adaptation level of the eye to light is high above the threshold, decreases in intensity are perceived as pleasant

while increases are unpleasant; and when the adaptation level is low, increases as well as decreases are perceived as pleasant. In other words, the hedonic curve may be shifted by changes in the adaptation level of the receptors.

From this work with single receptors it is a considerable step to the work of Hebb (1949) on the production of fear by discrepancy from expectation. Once a chimpanzee has learnt to recognise another, fear is produced by showing it a detached head, or by showing it a deeply anesthetised animal which it may take to be dead. Animals reared in darkness do not show fear reactions until they, too, have formed expectations.

It is assumed that these qualitative observations are on a continuum with the observations of the functioning of single receptors, even though dimensions for quantitative analysis have not beeen isolated.

Interesting observations show that a rat will seek variation in its path to food once it has learnt the route well, that it will often prefer a path with obstructions to a path without and that it may prefer seeds which are difficult to crack to those which are easy, (from McClelland, 1953). These lead McClelland to the conclusion that confirmation of expectations of too high a level of probability leads to negative affect as does confirmation of expectations of too low a probability (fear of the strange) (boredom). It is when expectations are at a moderate level of probability that confirmation is likely to produce maximum affect. As examples we might take the effects of seeing a complete stranger unexpectedly walking into one's house, seeing a friend who comes every night, and seeing a friend who comes occasionally.

It is obvious that a great deal of work has to be done in analysing the relationship between the hedonic effects of discrepancies from adaptation level of single

receptors and the hedonic effects of discrepancies from expectation. The two are not necessarily identical. It is possible that the expansion of the term 'adaptation level' to cover the reaction of a five months' chimpanzee to a stranger may cause the loss of a useful precision rather than an increase in understanding.

Lindsley (1961) lays great stress on the evidence of centrifugal control of the senses, showing that various receptors may be turned on and off by the central system. The ascending reticular activating system (ARAS) lies on the path from the senses and on the path to the senses 'at the crossroads of input and output systems' (p. 175). He suggests that ARAS achieves and maintains an appropriate adaptation level, and that disturbance of this level produces the cortical effects which lead to the hallucinations and disturbances of affect and cognition observed during isolation on radical sensory deprivation of adults. Vernon et al (1961) produce evidence in favour of an adaptation-level theory by discovering that subjects isolated for 72 hours do better on tests than subjects isolated for 48 hours; but Heron (1961) found progressive deterioration. Vernon's subjects were allowed to move around in a cubicle, but Heron's were immobilised. To achieve adaptation to more complete sensory deprivation could quite reasonably be expected to take much longer.

An application of adaptation-level hypothesis to the differences between handled and undisturbed rats might be as follows. The handled rats build up an expectation of moderate level of probability about the consequences of or the nature of handling. Consequently, they show less disturbance during handling when testing commences, adjusting more easily to each fresh variation in the situation. The discrepancy between expectation and event is not as great for them as for the undisturbed animals. The Weber fraction

is lower and chances of raising the adaptation to meet the demands of the situation are more likely.

If we accept this explanation, then the interest of our experiment will lie in demonstrating the relative permanence of such an adaptation level.

Conclusion

The adaptation-level theory is possibly at its most useful in describing emotional differences between stimulated and restricted animals. The general adaptation syndrome is a contribution to insight into the manner of achieving an adaptation level to stimulation, though, as Selye is very willing to admit, it is a commencement only.

The rôle of stimulation in learning to create useable information is dealt with by Hebb and Bruner. The rôle of primary learning in achieving perceptual differentiation is emphasised.

Since the consequences of handling appear to be both emotional and cognitive, both of these types of theory will have to be borne in mind when discussing interpretations of its effects.

C H A P T E R VI

EXPERIMENTAL REPORT

A. EXPERIMENT

a) INDEPENDENT VARIABLES

The present experiment on the effects of stimulation in infancy and housing conditions was conducted on white rats of the Wistar strain bred in the Department of Psychology of the University of Cape Town from stock obtained from Medical School.

(i) Handling

The stimulation employed was handling, since it has been extensively reported that handling is effective in increasing the rate of maturation, raising resistance to stress, reducing emotional behaviour and improving the learning ability of rats (Levine, Chevalier and Korchin, 1956; Weininger, 1953; et alia).

(ii) Housing

Housing conditions also have an important effect on the learning ability and emotional behaviour of rats (Forgays and Forgays, 1952; Forgus, 1954, 1955).

A previous experiment conducted in this department by the author failed to obtain the expected differences between handled and undisturbed rats which were housed in large cages after weaning. It was hypothesised that a possible cause of this failure was the interaction between handling and housing. The rationale of this is that the stimulation of housing in a large cage might compensate for the lack of stimulation among the undisturbed or non-handled animals, raising their performance to the level of the handled animals. That is, the difference between handled and undisturbed animals was thought of as being mainly caused by sensory deprivation. It was felt that housing in a small

cage presents practically no opportunity for an animal to develop its powers of adaptation - to raise its adaptation level, in the terms of McClelland - and that the function of handling under such conditions might be to present the animal with an opportunity for bringing into play the powers of adaptation described by Selye (1955). Housing in a large cage might, it was speculated, present the animal with more proprioceptive and visual experience and call into existence a wider range of adaptive behaviour.

(iii) Removal of mother

A second hypothesis suggested by this unsuccesful attempt to discover differences in the activity, learning ability and emotional behaviour of handled rats compared to undisturbed rats, was that the agitated behaviour of the mother when returned to the cage after separation for handling of half of a split litter might so stimulate the non-handled half of the litter as to cancel out any effects of the stimulation of handling. It was observed that the mother licked the pups, transferred them from one corner of the cage to another, and often trod on them in her agitation when returned to her cage. The experimental evidence of Ader, Beels and Tatum (1960) indicates that separation for a total of 24 hours during the nursing period can increase susceptibility to gastric ulceration. Perhaps, it was thought, separation from the mother for a shorter period (a total of six hours before weaning), might have measurable effects on emotional behaviour, activity and learning.

b) DEPENDENT VARIABLES

(1) Persistence of effects

The most important part of the present experiment was an investigation of the persistence into maturity of the effects of handling in infancy and a comparison of the effects on activity, emotional behaviour and learning at

three different ages to discover if there is any trend of increase or decrease of the effects.

It is important to discover whether the effects of infantile stimulation have a limited duration in the life of an animal or whether they continue to be important throughout the life of the animal. A survey of the literature shows that this problem has seldom been attempted. Only one experiment (Thompson and Melzack, 1956) follows the effects of variations introduced early in life into maturity. It was found that Scotties brought up in isolated restriction retained their characteristic hyperactivity and retarded learning ability well into mature life.

A review of the ages at which rats have been tested for the effects of handling on behaviour and growth shows that the work is limited to the early life of the rat. The animals in Levine's various experiments (1956, 1957, 1958, 1960) were tested between 60 and 70 days of age. Weininger (1953, 1954, 1956) tested his animals at nearly sixty days. Ruegamer, Bernstein and Benjamin (1954) tested their animals at 56 days. Gertz (1957), who tested his animals at 120 days, gave them only one experience of handling each, so that his negative results have a limited significance. Scott (1955), who began testing his animals at the age of 119 days, handled his animals once a week for weighing, which largely destroys the value of his experiment and the importance of his negative result. Ader's (1959) early-handled group was tested at 68 days and his late-handled group at 181 days; but this was only 15 days after the experience of handling had ceased.

From this it will be seen that experiments have aimed largely at demonstrating the qualitative effects of handling on growth, resistance to stress, activity and learning ability. The problem of permanence has been left untouched.

It is to this problem that we address ourselves in this experiment, assuming that if the effects of handling on

physical growth and hormonal balance are as extensive as is claimed in the literature, they should continue to affect behaviour throughout life.

2) Effects Tested

(i) Each animal was weighed at 25 days and at the age of testing (50 days, 100 days, or 220 days).

(ii) Each animal was given pre-shock preliminary runs in a Miller box and counts were taken of rears, crossings from one compartment to the other, latency to first crossing, grooms, defecation, and urination.

(iii) Each animal was trained to avoid shock by crossing from the starting compartment to the adjacent compartment in the Miller box. The conditioned stimulus was a buzzer. After reaching a criterion of two successive avoidances, each subject was put through extinction trials until reaching a criterion of two successive no-responses of 30 seconds.

(iv) Each animal was trained to run an elevated maze for a reward of water.

Weight was recorded because it was reported that handled animals increased in weight more rapidly than non-handled animals (Weininger, 1955, 1956). Avoidance training and the measures used in the preliminary runs were reported to show up differences between handled and non-handled rats (Levine, Chevalier and Korchin, 1956; Levine, 1956). In these experiments it was found that handled animals were more active and less emotional, and that they achieved successful avoidance more rapidly.

An elevated maze was used in this investigation since it is useful in distinguishing between animals from more restricted and less restricted environments (Forgus, 1954, 1955). It is found that animals with more extensive visual and proprioceptive experience are better able to learn the elevated maze than animals from restricted environment.

c) HYPOTHESES TESTED

(i) That the interaction between stimulation by handling and stimulation by housing reduces differences between handled and undisturbed rats in scores of activity, emotional behaviour and learning when the animals are housed in large cages and increases them when the animals are housed in small cages.

(ii) That the removal of the mother is an important variable to control in experiments dealing with the effects of handling before weaning.

(iii) That handling in infancy produces effects on growth, emotional behaviour, activity and learning which persist into maturity.

Experimental design

A total of 126 subjects of both sexes, representing five types of treatment, was divided into three groups, each group to be tested at a different age. Each group included all five kinds of treatment.

The five treatments were :

(1) handled and housed in small cages (8"x 12"x 6") (sh)

(2) handled and housed in large cages (57" x 10" x 10") (lh)

3) undisturbed and housed in small cages. (su)

4) undisturbed and housed in large cages. (lu)

5) mother removed daily for equivalent of handling period of fifteen minutes; but untouched by hand and housed in small cages. (sm)

Distribution of subjects in groups and treatments

		Subjects	Sub-Groups (Treatments)					
Group	Age at testing	Sex	sh	lh	su	lu	sm	Total
Group I	50 days	males	10	5	10	5	10	40
II	100 days	males	4	4	4	4	4	20
		females	8	4	8	4	8	32
III	220 days	females	8	5	8	5	8	34
	Total		30	18	30	18	30	126

PROCEDURE

Subjects

Mothers of the same age, 110 days, were selected for breeding. Immediately they had given birth, the number of pups per litter was brought down to six by removal of the surplus. This was done to eliminate the rôle of nutrition and competition from the results. A previous study had shown a negative correlation of .78 between size of litter and weight at weaning.

The mothers were handled before giving birth in order to tame them so that they would not be too agitated

when they were removed from their pups during the experimental treatment.

Treatment

Complete litters were assigned at random to one of three treatments : (i) handling, (ii) removal of the mother without contact with the experimenter, and (iii) ignored, or non-handled.

Handling followed the following procedure as nearly as possible :

After the mother had been removed from the litter and placed in another cage, the pups were picked up individually between the thumb and index finger of the left hand and transferred to the palm of the right hand. They were stroked along their backs from the base of the skull to the tail with the index finger at a rate of approximately one stroke per second. After thirty seconds each pup was transferred to a small (3" x 3") compartment in a cardboard box. After nine minutes the pup was restored to its home cage and the mother was returned. On the return, the pup was handled in the same way as on removal. The mother was returned approximately fifteen minutes after removal.

The second treatment type merely had the mother removed for fifteen minutes each day.

At twenty-five days the pups were weaned, weighed, sexed, and assigned either to large cages measuring 57" x 10" x 10" or to small cages measuring 8" x 12" x 6". Both the large and the small cages had chicken-wire front and top and solid backs and sides. Droppings and waste fell through the mesh or grid floors into trays of sawdust which could be removed and cleaned without handling the animals.

The rats were housed four per cage and were identified by ear markings. The temperature was thermostatically controlled at 70°F.

Feeding and watering was ad lib. Food was supplied in the form of rat cubes and vegetables two to three times per week.

Distribution of subjects

There were three distinct groups to be tested at three different ages.

Each group was made up of five sub-groups :

(i) Handled animals housed in small cages (sh).

(ii) Handled animals housed in large cages (lh).

(iii) Animals which had been subjected to removal of the mother, and which were housed in small cages (sm).

(iv) Undisturbed or ignored animals housed in small cages (su).

(v) Undisturbed or ignored animals housed in large cages (lu).

It was decided to keep each group unisexual since, though males and females are both affected by handling, standard deviations might be smaller with groups of one sex only. Therefore, group I, tested from the age of 50 days, consisted of males only; group II, tested from the age of 100 days, consisted of females mainly, with some males to test the supposition that the sexes are equally affected (a supposition which is richly supported by the literature); and group III, tested from 220 days, consisted of females only.

The numbers were as follows :

(i) In group I the sh, sm, and su groups contained ten subjects each and the lh and lu groups contained 5 subjects each, making a total of forty subjects.

(ii) In group II the sh, sm and su groups each contained eight females and four males, and the lh and lu groups contained four males and four females each, making a total of fifty-two subjects.

(iii) In lot three the sh, sm and su groups each contained eight females and the lh and lu groups each contained five females, making a total of thirty-four subjects.

Testing

All groups were tested in the same way.

(i) Each animal was weighed.

(ii) Each animal was given one 3 minute session per day for three days in a glass-walled box 24" x 10" x 12" divided into two equal compartments by a perspex wall, in which was set, at a height of 5 " above the grid floor, an aperture 3" x 3". The aperture was kept open during the preliminary trials and closed by a one-way door during avoidance trials. Illumination by a 40 watt lamp 6 foot away. Observations were made of rears, crossings from the starting chamber into the other, latency before the first crossing, grooms, and elimination.

(iii) After the preliminary habituation trials, avoidance learning was commenced at the rate of two spaced trials per day.

The animal was placed in the starting chamber with the aperture closed and a buzzer was sounded for five seconds. After an interval of five seconds the grid was electrified by a 12 volt current from two Eveready Ignitor dry cells through an induction coil. If the rat had not escaped through the aperture into the adjacent chamber within fifty seconds, it was assisted through.

Each animal was removed to his home cage immediately he had completed the avoidance action.

The number of trials required to establish avoidance and the latency of each reaction was recorded. The criterion was two successive avoidances.

(iv) Extinction trials were commenced immediately. The criterion for extinction was two successive no-responses for thrity seconds. Two spaced trials were run every day.

(v) An elevated T maze consisting of two pieces each three feet long was used under illumination of a 100 watt lamp ten feet above the maze. The animals were run once per day after a water deprivation of 21 hours for five trials. The reward was ten seconds' consumption before return to cage, in which the animals were watered. Time scores were taken.

B. RESULTS

The effects of handling, removal of the mother, and cage size which were tested may be divided up as follows :

Rate of growth, measured by increase in bodily weight;

activity, measured by rears, crossings of the barrier in the Miller box from one compartment to the other, and latency to 1st crossing in each trial;

emotionality, measured by grooms, urination and defecation counts;

avoidance learning, measured by the number of trials required to achieve a criterion of two successive avoidances in the Miller box and by the latency to the avoidance response in each trial;

extinction of the avoidance response, measured by the number of trials required to achieve two successive no-responses of thirty seconds, and the latency to response in avoidance trials; and

maze learning on an elevated maze, measured by time to reach goal, time to consume water, and errors.

In addition, the persistence of the effects of handling was observed by comparing differences between handled and undisturbed subjects at three different ages; and by tracing differences between handled and undisturbed subjects through the three preliminary trials at each age level.

Rate of growth

Scott (1955) suggested that increases in body weight should be in terms of ratio of increase rather than absolute body weights for each group. This suggestion has been adopted by Weininger (1956) and Ader (1959). The aim of this treatment is to eliminate the effects of any accidental differences. This suggestion has been adopted and weight increase has been presented as a ratio of weight at

age of testing over weight at weaning multiplied by ten. (Wt/W25 x 10).

In no case did F analysis of weight increase as a function of either cage size or handling yield significant differences.

Activity

As in the work of Levine, Chevalier and Korchin (1956) and Levine (1956), all subjects were put through preliminary habituation trials in a Miller box before avoidance learning. The finding that handled animals are more active was confirmed by their higher scores on rears and crossing-the-barrier, and by their smaller latency to the first crossing in each trial.

At all three ages a difference better than the 1% level of confidence was found between handled and non-handed animals in the number of rears (Group I : $F = 18.2$, group II : $F = 13.3$, group III : $F = 11.4$).

A difference in the crossings was found between handled and undisturbed males at 100 days ($F = 14.7$, $P < .01$), and between handled and undisturbed females at 220 days ($F = 21.7$, $p < .01$). No difference in the crossings of handled and undisturbed females was found at 100 days or between handled and undisturbed males at 50 days.

A difference between the latency of handled and undisturbed males was found at 100 days ($F = 13.9$, $p < .01$) and between handled and undisturbed females at 220 days ($F = 17.4$, $p < .01$). No difference was found for males at 50 days and for females at 100 days.

The trend is, therefore, for the older group of each sex to reveal larger differences between handled and undisturbed animals.

No activity measure was affected by cage size or removal of the mother. There was no significant interaction between handling and housing.

Emotional behaviour

In all cases the undisturbed animals showed more signs of emotional disturbance during actual handling, while being transferred from their home cages to the testing apparatus. They made more attempts to escape and to bite, and they occasionally defecated while being held. This merely shows that early handling is effective in training animals well into maturity.

In the testing situation itself, the Miller box without shock, no difference between handled and undisturbed animals in either urination or defecation appeared. As in the findings of Ader (1959), defecation was found to be atypical (eleven subjects out of one hundred and twenty-six). Urination (seven subjects only) was also atypical.

The undisturbed males groomed more than the handled males at 50 days ($F = 5.4$, $p < .05$) and the undisturbed females more than handled females at 220 days ($F = 4.75$, $p < .05$). No differences appeared at 100 days.

Grooming of animals tested at 50 days ($F = 5.3$, $p < .05$) and 100 days ($F = 8.9$, $p < .01$) was increased by housing in large cages.

Interaction between handling and learning was found at 50 days ($F = 4.53$, $p < .05$) and 220 days ($F = 6.0$, $p < .05$), but not at 100 days.

Removal of the mother had no affect on emotional behaviour.

Avoidance learning

Group I ($F = 4.26$, $p < .05$) and group II ($F = 8.1$, $p < .01$) reveal differences between the handled and the undisturbed group in the number of trials required to establish

an avoidance response to a criterion of two successive avoidances. Only group III ($F = 8.03$, $p < .01$) showed a difference in latency before avoidance between the handled group and the controls. Where there are differences, they show that the handled group required fewer trials to establish avoidance and that the latency before avoidance response was less for the handled group. No significant effect was due to cage size. There was no significant interaction.

Removal of the mother did not affect scores in avoidance learning.

Extinction trials

Only in group III did handled animals extinguish the avoidance response in fewer trials than undisturbed animals ($F = 5.2$, $p < .05$). No other differences of significance were found, so that not much reliance can be placed on this isolated finding.

Cage size did not affect extinction.

No interaction was found between handling and cage size.

Removal of the mother did not affect extinction.

Elevated maze

Handling, cage size and removal of the mother did not affect any of the scores on the elevated maze.

No interaction was found between handling and cage size.

Sex difference

The performance of 16 males and 24 females in group II was analysed for sex differences in performance.

Differences were found in rears ($F = 6.8$, $p < .05$), crossings ($F = 7.49$, $p < .01$), and grooms ($F = 8.2$, $p < .01$) in the preliminary trials. There was also a difference in the number of trials required to establish extinction of the avoidance response ($F = 7.1$, $p < .05$).

It appears that the females in our sample were significantly more active in the preliminary, rearing up more frequently and crossing more rapidly and more often.

The females also required more trials to extinguish response, confirming the picture of greater activity and excitability.

The males groomed more frequently. Grooming is sometimes interpreted as an indication of hesitation and uncertainty and is called 'displacement'. In view of the finding that animals from the larger cages also groom more frequently than animals from the smaller cages, interpretation is difficult.

No interaction of any significance was found between sex and handling. We may, therefore, safely assume that males and females respond in the same way to handling, though their absolute scores may differ. The division of the available animals in this experiment so that groups were unisexual is, therefore, justified. Sex differences would have reduced the possibility of attaining significant results by increasing the variability in each group.

A separate analysis of male and female results in group II reveals that in one measure, crossing-the-barrier, the handled males crossed more frequently than the undisturbed males, but no difference was found between handled and undisturbed females. This was the only instance of a significant difference in one sex and not in the other.

Persistence

Bar diagrams of the mean difference between handled and undisturbed animals on activity measures show the difference in each trial at all three ages. There is no pattern common to all three ages. Apparently, therefore, there is no trend towards diminution of the differences as the undisturbed animals become habituated to handling (Appendix 1-3)

When the F values for the differences between handled and undisturbed animals at different ages are compared (see graphs) (Appendix 9-15), the measures of activity show a consistent increase in the differences between handled and undisturbed animals with age.

Grooms, on the other hand, yield a V-curve of differences. (Appendix 12) The same curve is observed for avoidance trials (Appendix 14) and latency in avoidance learning. (Appendix 13) Trials to extinguish avoidance yields what appears to be a flattened version of this curve (Appendix 15)

No other F values are plotted since the differences are insignificant and, therefore, statistically not reliable.

Product-moment coefficient of correlation between grooms and trials to learn avoidance is +0.59 ($t = 5.6$, $p < .01$), indicating that their covariance on the graphs is not accidental.

Product-moment coefficients of correlation for activity measures are :

rears - crossings = + 0.74 ($t = 8.4$, $p < .01$)

rears - latency to crossing in preliminary trials = - 0.64 ($t = 6.3$, $p < .01$)

crossings - latency = - 0.78 ($t = 9.1$, $p < .01$).

Again, the indication is that these measures are associated and that their covariance on the graphs is not accidental.

A. Summary of the results of analysis of variance

Table I.

F values for differences between handled and undisturbed animals.

TESTS	GROUPS			
	I	II		III
A. Preliminary	(50 days)	(100 days)		(220 days)
	male	male	female	female
Rears	18.2**	20.1**	6.3*	11.4**
Crossings	1.6	14.7**	1.2	21.7**
Latency	1.1	13.9**	2.8	17.4**
Grooms	5.4*	0. 3	0.3	4.75*
B. Avoidance learning				
Trials	4.26*	0.2	0.1	8.1**
Latency	3.8	0.1	0.6	8.03**
C. Extinction				
Trials	0.1	0.1	2.4	5.2*
Latency	1.6	0.1	1.9	1.5
D. Elevated maze				
Time to goal	2.8	0.2	0.8	2.53
Time to 1st consumption	1.6	0.2	1.2	2.4
Errors	0.3	0.1	0.4	1.0
E. Weight increase	1.2	0.3	0.1	2.3

* = 5% level
** = 1% level

Table II

Combined F values for Group II (Male and Female)

A. Preliminary	
Rears	13.3**
Crossings	3.9
Latency	8.96**
Grooms	0.3
B. Avoidance learning	
Trials	0.1
Latency	0.3
C. Extinction	
Trials	1.9
Latency	1.2
D. Elevated maze	
Time to goal	0.6
Time to 1st consumption	1.0
Errors	0.5

Table III

F values for differences between animals reared in large and small cages.

TESTS	GROUPS		
A. Preliminary	(50 days)	(100 days)	(220 days)
Rears	0.37	2.9	0.9
Crossings	3.08	0.6	0.2
Latency	2.06	1.9	4.9*
Grooms	5.3*	8.9**	0.25
B. Avoidance learning			
Trials	0.69	0.2	0.5
Latency	0.1	0.9	0.12
C. Extinction			
Trials	0.1	0.1	2.6
Latency	0.5	0.0	0.1
D. Elevated maze			
Time to goal	0.24	1.6	2.86
Time to 1st consumption	0.2	1.9	2.15
Errors	0.3	0.4	1.1
E. Weight increase	0.8	0.5	1.0

Table IV

F values for interaction between cage size and handling.

TESTS	GROUPS		
A. Preliminary	I (50 days)	II (100 days)	III (220 days)
Rears	1.2	1.6	2.0
Crossings	0.3	0.59	3.8
Latency	0.7	1.7	3.6
Grooms	4.53*	3.4	6.0*
B. Avoidance learning			
Trials	0.69	0.7	0.2
Latency	0.6	0.5	0.33
C. Extinction			
Trials	0.5	0.1	0.1
Latency	2.1	0.5	0.1
D. Elevated maze			
Time to goal	0.4	0.1	0.1
Time to 1st consumption	0.02	0.3	0.1
Errors	0.4	0.0	0
E. Weight increase	0.2	0.4	0.62

Table V.

F values for Sex differences in Group II (100 days)

A. Preliminary	
Rears	6.8*
Crossings	7.49**
Latency	1.7
Grooms	8.2**
B. Avoidance learning	
Trials	0.3
Latency	1.3
C. Extinction	
Trials	7.1*
Latency	0.2
D. Elevated maze	
Time to goal	3.4
Time to 1st consumption	3.8
Errors	1.5
E. Weight increase	9.44**

Direction of Difference :

Females were more active as shown by greater number of rears and more crossings from one compartment to other. They groomed less than males, but required more trials to extinguish avoidance response.

Table VI

F values for Interaction between Sex and handling in Group II (100 days)

A. Preliminary	
Rears	0.0
Crossings	0.6
Latency	0.79
Grooms	0.1
B. Avoidance learning	
Trials	0.1
Latency	0.8
C. Extinction	
Trials	1.1
Latency	1.5
D. Elevated maze	
Time to goal	0.1
Time to 1st consumption	0.1
Errors	0.0
E. Weight increase	0.3

TABLE 23

Weights (females)

The weights in grams of thirty-four subjects at 220 days and 25 days, and the ratio of the weight at 220 days to the weight at 25 days, multiplied by ten.

TABLE 23

Group 3 :- Weights in grams.

Small Cages. (eight subjects per group)

Handled			Mother removed			Undisturbed.		
220 days	25days	Ratio*	220days	25days	Ratio	220days	25days	Ratio
196	39gr	50	188gr	40gr	47	218gr	30gr	73
185	37	50	185	39	47	178	32	56
195	34	57	185	38	49	175	34	51
196	35	56	196	40	50	180	35	51
214	40	54	200	39	50	187	36	52
194	39	50	180	29	62	191	40	48
177	37	48	183	27	68	188	35	54
197	42	48	207	41	50	199	36	55
T 1554 gr	303gr	413	1524gr	293gr	423	1516 gr	278 gr	440
M 194 gr	M 38gr	M 52	M 191gr	M 37gr	M 53	M 190gr	M35gr	M 55
SD 9.9	SD. 2.5	SD.3.3	SD.5.8	SD. 5.1	SD7.3	SD. 13	SD. 2.8	SD7.2

Large Cages. (5 subjects per group)

Handled			Undisturbed		
220 days	25 days	Ratio	220 days	25 days	Ratio.
185 gr	31 gr	60	186 gr	37 gr	50
189	36	53	211	36	59
227	39	58	216	32	68
188	38	49	189	35	54
196	37	53	196	28	70
T 984 gr	181 gr	273	998 gr	168 gr	301
M 197 gr	36 gr	55	200 gr	34 gr	60
SD 15.5 gr	2.8	3.9	11.9	3.25	7.7

* Ratio : W 220 / W50 x 10)

TABLE 24

Preliminary trials (females)

The total number of rears, the total latency in seconds to crossing the barrier, the total number of crossings, and the total numbre of grooms for each subject in three trials of three minutes eaxh. The subjects belonged to Group III, tested at 220 days.

Group 3 : - 3x3 min preliminary rums in conditioning apparatus without shock.

Small cages. (8 subjects per group)

Handled				Mother removed				Undisturbed.			
Rears	* latency			x crossings			Grooms				
R.	L.	C.	G.	R.	L.	C.	G.	R.	L.	C.	G.
116	152	14	0	68	165	12	5	34	540	0	10
88	155	16	1	86	290	6	3	70	235	8	1
86	115	16	0	45	520	1	5	57	520	1	3
118	66	24	1	100	125	24	3	51	540	0	5
86	110	16	1	63	540	0	4	56	540	0	4
94	66	18	0	37	540	0	5	76	540	0	4
79	390	7	0	63	470	1	5	48	520	1	2
57	270	7	0	85	380	10	0	78	126	12	0
T 724	1324	118	3	547	3030	54	30	470	3561	22	29
M 90.4	165.5	14.8	0.4	68.4	378.8	6.8	3.8	58.8	445	2.8	3.6
SD 18.4	104.3	5.3	0.5	19.9	157.5	7.82	1.7	14.1	155.4	4.3	3.7

Large Cages. (5 subjects per group)

Handled				Undisturbed.			
Rears	latency	crossings	grooms	rears	latency	crossings	grooms
51	170	7	3	46	265	5	2
64	130	8	0	82	136	11	1
85	170	14	2	85	220	14	2
73	186	14	4	58	245	5	0
93	92	19	4	39	365	6	4
T 366	748	62	13	310	1231	41	9
M 73	149.6	12.4	2.6	62	246	8	1.8
SD 14.8	32.7	4.4	1.5	18.6	73.9	3.6	1.4

* Latency : time in seconds to first crossing in each trial.

x Crossings: crossing the barrier from one half the apparatus to the other.

TABLE 25

Avoidance Trials (females)

The totals number of trials required to learn an avoidance response to a criterion of two successive avoidances, and the sum of the latency in seconds for all trials before the correct avoidance response, for each subject in Group III tested at 220 days.

Group 3 :- Avoidance learning.

Small Cages. (8 subjects per group)

	Handled		Mother removed		Undisturbed.	
	* Trials	x latency	trials	latency	trials	latency.
	4	122 sec	4	60 sec	15	660 sec
	6	141	5	175	4	61
	3	50	7	88	12	588
	3	29	3	39	5	76
	5	62	6	120	15	670
	6	183	9	367	5	121
	5	45	4	56	15	617
	5	41	7	182	4	54
T	37	673	45	1087	75	2847
M	4.6	84.1	5.6	136	9.4	356
SD	1.12	53.07	1.87	100.7	4.98	279.5

Large Cages. (5 subjects per group)

	Handled		Undisturbed.	
	trials	latency	trials	latency
	4	71	15	642
	8	362	9	426
	3	23	6	123
	3	38	3	67
	3	24	5	131
T	21	518	38	1389
M	4.2	103.6	7.6	278
SD	1.95	130.4	4.17	221.1

* Trials : trials to criterion of two successive avoidance of shock.

x Latency : total time in seconds spent in shock comp until criterion.

TABLE 26

Extinction Trials (females)

Total number of trials required to extinguish the avoidance response to a criterion of two successive no-responses of thirty seconds, and the sum of the latency in seconds to the avoidance response in all trials, for each subject in Group III, tested at 220 days.

TABLE 26

Group 3 :- Extinction trials.

Small Cages. (8 subjects per group)

Handled		Mother removed		Undisturbed.	
Trials *	latency x	trials	latency	Trials	Latency
18	94 sec	7	61	30	58
21	129	21	114	29	185
2	60	19	88	30	58
9	143	2	60	25	121
25	203	23	116	30	58
30	94	24	75	17	155
15	107	12	99	30	58
15	74	26	142	6	64
T 135	904	134	755	197	757
M 17	113	16.8	94.4	24.6	94.6
SD 8.27	42.35	8.19	27.07	8.23	48.5

Large Cages. (5 subjects per group)

Handled		Undisturbed.	
Trials	latency	Trials	Latency
13	89	30	58
30	58	30	58
17	143	30	108
30	99	30	125
25	249	24	116
115	638	144	465
23	127.6	28.8	93
6.9	66.57	2.41	29.1

* Trials : trials to criterion of two successive no-responses of 30 seconds each.

x Latency: time in seconds up to but not including two criterion trials.

TABLE 27

Elevated Maze (females)

The total time in seconds,and the number of errors to reach goal for each subject in Group III,tested at 220 days,in five learning trials on the elvated maze.The time spent on the elevated maze before the first consumption of water occurred is also shown,in seconds, for each subject.

TABLE 27

Group 3 :- Elevated maze

Small Cages. (8 subjects per group)

Handled			Mother removed			Undisturbed.			
* Time	x	± errors	lst cons.	time	errors	lst cons.	time	errors	lst Con
740sec		28	690sec	560sec	13	560sec	900 sec	6	900sec
595		24	580	570	18	480	490	14	410
335		22	270	900	10	900	900	11	900
900		5	900	665	27	485	475	20	475
243		5	223	520	21	480	900	20	900
355		8	235	660	21	625	900	46	900
900		21	900	900	23	900	730	18	630
194		11	169	880	14	880	355	17	340
T 4262		124	3967	5655	147	5310	5650	152	5455sec
M 532.8		15.5	495.9	706.9	18.4	663.8	706.2	19	681.9
SD 261.3		8.6	289.7	151.5	5.3	183.8	216.3	11.3	231.0

Large Cages. (5 subjects per group)

Handled			Undisturbed.		
Time	error	lst con.	Time	errors	lst cons.
321 sec	11	270 sec	397 sec	9	367 sec
222	6	192	452	14	442
755	20	755	555	28	555
272	9	257	790	13	790
435	11	435	365	13	310
T 2005	57	1909	2559	77	2464
M 401.2	11.4	381.8	511.8	15.4	492.8
SD 190.5	5.7	203.1	153.3	6.5	169.7

* time : total time in 5 trials to reach goal.

x lst cons : time before subject consumes water.

± errors : total errors in 5 trials.

Group 1 :- Analysis of variance of rears (h and u groups only)

Scores in rears.

Cage size		Handled	Undisturbed	Sum and Mean
small (20rats)	T	732	525	1257
	M	73.2	52.5	62.8
Large (10 rats)	T	355	300	655
	M	71	60	65.5
Sum		1087	825	1912
Mean		72.1	55.0	63.7

SH^2 54,286 SU^2 29,531 LH^2 25,511 LU^2 18,290

Total sum of squares : 5,759.9

Sum of squares among groups : 2,491.8

Sum of squares within groups : 3,268.1

Table of Variance.

Source of variation	sum of squares	df.	estimate of variance
Between groups	2,491.8	3	830.6
Within groups	3,268.1	26	125.7

$F : \frac{830.6}{125.7}$; 6.607 (signif. at 1% level)

Sum of squares for cage size : 46.8

Sum of squares for treatment : 2,291.2

Sum of squares for interaction: 153.8

Cage size : F : 0.37 (not signif.)
Handling: F : 18.227 (1% level)
Interaction: F: 1.2 (not signif.

Group 1:- Analysis of variance of grooms (h & u groups only)

Scores in grooms.

Cage size		Handled	Undisturbed	Sum and Mean
small (20 rats)	T	5	27	32
	M	0.5	2.7	1.6
Large (10 rats)	T	16	14	30
	M	3.2	2.8	3.0
Sum		21	41	62
Mean		1.4	2.7	2.1

SH^2 5 LH^2 58 SU^2 105 LU^2 42

Total sum of squares : 81.9

Sum of squares among groups : 37.7

Sum of squares within groups : 64.2

Table of Variance.

Source of Variation	Sum of squares	Dif.	Estimate of var.
Among groups	37.7	3	12.6
Within groups	64.2.	26	2.5

$F : \frac{12.6}{2.5} : 5.0$ (signif. at 1%)

Sum of squares for cage size : 13.1
Sum of squares for treatment : 13.4
Sum of squares for interaction : 11.2

Cage size F : 5.3 (signif. at 5% level)

Treatment F : 5.4 (signif. at 5%)level)

Interaction F : 4.53 (signif. at 5% level)

TABLE 30

Group I :- Analysis of variance of avoidance trials (h and u groups)

Scores in trials.

Cage size		Handled	Undisturbed	Sum and Mean
Small cage(20rats)	T	40	58	98
	M	4.0	5.8	4.9
Large cage(10rats)	T	20	23	43
	M	4.0	4.6	4.3
Sum		60	81	141
Mean		4.0	5.4	4.7

SH^2 179 SU^2 398 LH^2 84 Lu^2 111

Total sum of squares : 109.3
Sum of squares among groups : 19.5
Sum of squares within goups : 89.8

Table of Variance.

Source of variation.	Sum of squares.	Df.	Estimate of Var.
Among Groups	19.5	3	6.5
Within Groups	89.8	26	3.45

$F : \frac{6.5}{3.45}$: 1.9 (not signif.).

Sum of squares for cage size : 2.4
Sum of squares for treatment : 14.7
Sum of squares for interaction: 2.4

Cage size: F : 0.69 (not signif.).
Treatment: F : 4.26 (signif. at 5% level).
Interaction : F:0.69 (not signif.).

TABLE 31

Group 2 :- Analysis of variance of rears in preliminary (h and u groups).

Scores in rears.

		Handled	Undisturbed	Sum
Cage size	Small (24)	1002	720	1722
	Large (16)	546	462	1008
	Sum	1548	1182	2730
sex.	Male (16)	558	409	967
	Female (24)	990	773	1763
	Sum	1548	1182	2730

SH^2 87354 SU^2 46334 LH^2 38802 LU^2 27374

Total sum of squares : 13,541.5

A/ Analysis of cage size and handling.

Sum of squares among groups : 4,489.5
Sum of squares within groups: 9,052

Table of variance.

Source of variation.	sum of squares.	DF.	estimate of variance
Among groups	4,489.5	3	1496.5
Within groups	9,052	36	251.4

$F : \frac{1496.5}{251.4}$: 5.95 (signif. at 1%)

Sum of squares for cage size. : 735.
" " " " handling : 3,348.9
" " " " interaction : 405.6

F cage size. : $\frac{735}{251.4}$: 2.9 (not signif.)

F handling : $\frac{3,348.9}{251.4}$: 13.3 (signif.at 1%)

F interaction : $\frac{405.6}{251.4}$: 1.6 (not signif.).

B. Analysis of sex difference.

Sum of squares among groups: 4,977.2
" " " within " : 8,564.3 (estimate of variance:237.9)
" " "for sex difference : 1,628.
" " " for interaction : 0.3

F. sex : $\frac{1,628}{237.9}$: 6.8(signif. at 5%)

F. interaction : $\frac{0.3}{237.9}$: 0.0 (not signif.).

TABLE 32

Group 2 :- Analysis of variance of latency in preliminary (h and u groups).

Scores in seconds.

		Handled	Undisturbed	Sum.
Cage size	Small (24)	2201	4149	6350
	Large (16)	1451	1892	3343
	Sum	3652	6041	9693
Sex	Male (16)	1542	2850	4392
	Female (24)	2110	3191	5301
	Sum	3652	6041	9693

SH^2 612,693 SU^2 1,657,907 LH^2 360,437 LU^2 491038

Total sum of squares 773,219

A. Analysis of cage size and handling.

Sum of squares among groups : 199,994
" " " within " : 573,225

Table of variance

Source of variation	sum of squares	d.f.	estimate of variance
Among groups	199,994	3	66,665
Within groups	573,225	36	15,923

F. : $\frac{66,665}{15,923}$: 4.2 (signif.at 5%)

Sum of squares for cage size : 29,726
" " " " handling : 142,683
" " " " interaction : 27,589

F. cage size : $\frac{29,726}{15,923}$: 1.9(not signif.).

F handling : $\frac{142,683}{15,923}$: 8.96 (signif at 1%)

F interaction : $\frac{27,585}{15,923}$: 1.7 (not signif.).

B. Analysis of sex difference.

Sum of squares among groups : 183,225.
" " " within " : 589,994.
" " "for sex difference: 27,606
" " " for interaction : 12,936

F sex : $\frac{27,606}{16,388}$: 1.7 (not signif.).

F interaction : $\frac{12,936}{16,388}$: 0.79 (not signif.)

Group 2.:- Analysis of variance of crossings in preliminary (H and U groups)

Scores in crossings.

		Handled	Undisturbed	Sum.
Cage Size	Small(24)	177	110	287
	Large(16)	118	100	218
	Sum	295	210	505
Sex.	Male (16)	99	50	149
	Female(24)	196	160	356
	Sum	295	210	505

SH^2 3115 SU^2 1628 LH^2 2076 LU^2 1454

Total sum of squares : 1897.4

A. Analysis of cage size and handling.

Sum of squares among groups. : 234.0
Sum of squares within groups : 1663.4

Table of variance.

Source of variation	sum of squares	d.f.	estimate of variance
Among groups.	234.0	3	78
Within groups	1663.4	36	46.2

F : $\frac{78}{46.2}$: 1.69 (not signif.).

Sum of squares for cage size. : 26.7
" " " " handling : 180.7
" " " "interaction : 26.6

F eage size : $\frac{26.7}{46.2}$: 0.6 (not singif.)

F handling : $\frac{180.7}{46.2}$: 3.9 (not signif.)

F interaction : $\frac{26.6}{46.2}$: 0.59 (not signif.)

B. Analysis of sex difference.

Sum of squares among groups : 496.7
" " " Within " : 1400.7 (estimate of variance :38;9)
" " "for sex difference: 292.6
" " "for interaction : 23.4

F sex diff. : $\frac{292.6}{38.9}$: 7.49 (signif. at 1%)

F interaction : $\frac{23.4}{38.9}$: 0.6 (not signif.)

TABLE 34

Group 2 :- Analysis of variance of grooms in preliminary (h and u groups).

Scores in grooms.

		Handled	Undisturbed	Sum
Cage size	Small(24)	18	12	30
	Large(16)	17	29	46
	Sum	35	41	76
Sex	Male (16)	21	25	46
	Female (24)	14	16	30
	Sum	35	41	76

SH^2 38 SU^2 28 LH^2 67 LU^2 149

Total sum of squares : 137.6

A. Analysis of handling and cage size.

Sum of squares among groups : 35.9
" " " within " : 101.7

Table of variance.

source of variation	sum of squares	d.f.	estimate of var.
Among groups	35.9	3	11.96
Within groups	101.7	36	2.83

F : $\frac{11.96}{2.83}$: 4.2 (signif at 5% level)

Sum of squares for cage size : 25.3
" " " " handling : 0.9
" " " " interaction : 9.7

F cage size : $\frac{25.3}{2.83}$: 8.9 (signif at 1% level)

F handling : $\frac{0.9}{2.83}$: 0.3 (not signif.)

F interaction : $\frac{9.7}{2.83}$: 3.4 (not signif).

B. Analysis of sex difference.

Sum of squares among groups : 26.5
" " " within " : 111.1 (estimate of variance : 3.09.).
" " "for sex difference: 25.3 : 0.3
" " " interaction : 25.3
" " F sex difference : 3.09 : 8.2 (signif.at 1% lvl)

F interaction : $\frac{0.3}{3.09}$: 0.1 (not signif).

TABLE 35.

Group 2 :- Analysis of variance of extinction trials.
(h and u groups).

Scores in trials.

		Handled	undisturbed	Sum
Cage size	Small(24)	202	250	452
	Large(16)	142	159	301
	Sum	344	409	753
Sex	Male (16)	121	125	246
	Female (24)	223	284	507
	Sum	344	409	753

SH^2 4046 SU^2 6032 LH^2 2794 LU^2 3381

Total sum of squares : 2078

A. Cage size and handling.

Sum of squares among groups : 114
" " " within " : 1964

Table of variance.

Source of variance	Sum of squares	D.F.	Estimate of var.
Among groups	114	3	38
Within groups	1964	36	54.6

$F : \frac{38}{54.6}$: 0.7 (not signif.).

Sum of squares for cage size : 0.1
" " " " handling : 106
" " " " interaction: 7.9

F cage size : 0 (not signif.)
F handling : 1.9 (not signif.)
F interaction : 0.1 (not signif.)

B. Analysis of sex difference and handling.

Sum of squares among groups : 474
" " " within " : 1604 (estimate of variance : 44.6).
" " "for sex difference : 318
" " " interaction : 50

F Sex : $\frac{318}{44.6}$: 7.1 (signif. at 5% level)

F interaction : $\frac{50}{44.6}$: 1.1 (not signif).

Group 3 :- Analysis of variance of rears in preliminary (h and u groups).

Scores in rears.

Cage size		Handled	Undisturbed	Sum and Mean.
Small (16rats)	T	724	470	1194
	M	90.5	58.8	74.6
Large (10rats)	T	366	310	676
	M	73	62	67.6
Sum	T	1090	780	1870
Mean	M	84	60	72

SH^2 68242 SU^2 29206 LH^2 27900 LU^2 20950

Total sum of squares : 11.802
Sum squares among groups : 4,649.5
Sum of squares within groups : 7,152.0

Table of variance.

Source of variation	Sum of squares	d.f.	estimate of variance
Among groups	4,649.5	3	1549.8
Within groups	7,152	22	325.1

$F : \frac{1549.8}{325.1}$: 4.77 (signif. at 5% level)

Sum of squares for cage : 304
" " " " handling : 3,696
" " " " interaction : 650

F cage size : $\frac{304}{325.1}$: 0.9 (not signif.)

F handling : $\frac{3,696}{325.1}$: 11.4 (signif at 1% level)

F interaction : $\frac{650}{325.1}$: 2.0 (not signif).

Group 3 :- Analysis of variance of latency in preliminary (h and u groups).

Scores in seconds.

Cage size		handled	undisturbed	sum and mean
Small (16rats)	T	1324	3561	4885
	M	165.5	445	305.2
Large (10rats)	T	748	1231	1979
	M	149.6	246	197.9
Sum	T	2072	4792	6864
Mean	M	159	292	268

SH^2 306,166 SU^2 1,778,301 LH^2 117,760 LU^2 330371

Total sum of squares : 720,502
Sum of squares among groups: 407,089
Sum of squares within groups: 313,413

Table of variance.

Source of variation	sum of squares	d.f.	estimate of variance
Among groups	407,089	3	104,471
Within groups	313,413	22	14,246

$F : \frac{104,471}{14,246}$: 7.3 (signif at 1% level)

Sum of squares for cage size : 71,000
Sum of squares for handling : 284,553
" " " " interaction : 51,536

F cage size : $\frac{71,000}{14,246}$: 4.9 (signif. at 5% level)

F handling : $\frac{284,553}{14,246}$: 17.4 (signif at 1%)

F interaction : $\frac{51,536}{14,246}$: 3.6 (not signif.)

TABLE 38

Group 3 :- Analysis of variance of crossings in preliminary (h and u only)

Scores in crossings.

Cage size		Handled	Undisturbed	Sum and Mean
Small (16rats)	T	118	22	140
	M	14.8	2.8	8.8
Large (10rats)	T	62	41	103
	M	12.4	8	10.3
Sum	T	180	63	243
Mean	M	13.8	4.8	9.3

SH^2 1962 SU^2 210 LH^2 866 LU^2 403

Total sum of squares : 1170
Sum of squares among groups : 635
Sum of squares within groups : 535

Table of variance.

Source of variation	Sum of squares	d.f.	estimate of variance
Among groups	635	3	212
Within groups	535	22	24.3

$$F : \frac{212}{24.3} : 8.7 \text{ (signif at 1\% level).}$$

Sum of squares for cage size : 15.
Sum of squares for handling : 526.6
Interaction : 93.4

F cage size : 0.2 (not signif.)

$$F \text{ handling} : \frac{526.6}{24.3} : 21.7 \text{ (signif. at 1\% level)}$$

$$F \text{ interaction} : \frac{93.4}{24.3} : 3.8 \text{ (not signif.).}$$

TABLE 39

Group 3:- Analysis of variance of grooms in preliminary (h and U)

Scores in grooms.

Cage size		Handled	Undisturbed	Sum and Mean
Small (16rats)	T	3	29	32
	M	0.4	3.6	2
Large (rats10)	T	13	9	22
	M	2.6	1.8	2.2
Sum	T	16	38	54
Mean	M	1.2	3	2.1

SH^2 3 SU^2 171 LH^2 45 LU^2 25.

Total sum of squares : 132
Sum of squares among groups : 44
Sum of squares within groups: 88

Table of variance.

Source of variation	Sum of squares	d.f.	Sum and Mean.
Among groups	44	3	14.7
Within groups	88	22	4

$F : \frac{14.7}{4} : 3.7$ (not signif.).

Sum of squares for cage size : 1
" " " " handling : 19
" " " " interaction : 24

F cage size : $\frac{1}{4}$: 0.25 (not signif.)
F handling : $\frac{19}{4}$; 4.75 (signif. at 5%)
F.interaction: $\frac{24}{4}$: 6.0 (signif. at 5%)

TABLE 40

Group 3 :- F analysis of variance in mean no. of avoidance trials (h and u)

Scores in trials.

Cage size		Handled	Undisturbed	Sum and Mean
Small (N16)	E	37	E 75	E 112
	M	4.6	M 9.4	M 7
Large (N10)	E	21	E 38	E 59
	M	4.2	M 7.6	M 5.9
Sum	E	58	E 113	E 171
Mean	M	4.5	M 8.7	M 6.6

SH^2 181 SU^2 901 LH^2 107 LU^2 376

Total sum of squares : 440.
Sum of squares among groups : 126
" " " within " : 314

Table of variance.

Source of variation	sum of squares	d.f.	estimate of Var.
Among groups	126	3	42
Within groups	314	22	14.3

$F : \frac{42}{14.3}$: 2.9 (not signif.).

Sum of squares housing : 7
Sum of squares handling : 116
Sum of squares interaction : 3

F housing : $\frac{7}{14.3}$: 0.5 (not signif.).

F handling : $\frac{116}{14.3}$: 8.1 (signif. 1% level)

F interaction : $\frac{3}{14.3}$: 0.2 (not signif.).

TABLE 41

Group 3 :- Analysis of variance of mean latency in avoidance trials (h and U).

Scores in seconds.

Cage size	Handled	undisturbed	Sum and Mean
Small (N16)	E 673 M 84.1	E 2847 M 356	E 3520 M 220
Large (N10)	E 518 M 103.6	E 1389 M 278	E 1907 M 190.7
Sum Mean	E 1191 M 91.6	E 4236 M 325.8	E 5427 M 208.7

SH^2 79,145 SU^2 1,637,987 LH^2 138,634 LU^2 630,419

Total sum of squares : 1,353,403.
Sum of squares among groups : 376,539
Sum of squares within groups: 976,864.

Table of variance.

Source of variation.	Sum of squares.	D.F.	Estimate of Variance
Among groups	376,539	3	125,513
Within groups	976,864	22	44,403

F : 2.8 (not signif.).

Sum of squares housing : 5,282
" " " handling :356,616
" " " interaction : 14,641

F housing : $\frac{5,282}{44,403}$: 0.12 (not signif.)

F handling : $\frac{356,616}{44,641}$: 8.03 (signif at 1%)

$F_{\text{interaction}}$: $\frac{14,641}{44,403}$: 0,33 (not signif.)

Group 3 :- Analysis of variance of extinction trials (hand u groups)

Scores in trials

Cage size	handled	undisturbed	sum and mean
Small (16)	E 135 M 17	E 197 M 24.6	E 332 M 20.8
Large (10)	E 115 M 23	E 144 M 28.8	E 259 M 25.9
Sum Mean	E 250 M 19.2	E 341 M 26.2	E 591 M 22.7

SH^2 2825 SU^2 5391 LH^2 2883 LU^2 4176

Total sum of squares : 1841
Sum of squares among groups : 48.7
Sum of squares within groups : 1354

Table of variance.

Source of variation	sum of squares	d.f.	estimate of variance
Among groups	487	3	162.3
Within groups	1354	22	61.5

$F : \frac{162.3}{61.5}$: 2.6 (not signif.)

Sum of squares housing : 163
" " " handling : 318
" " " interaction 6

F housing : $\frac{163}{61.5}$: 2.6 (not signif.) 5% level

F handling : $\frac{318}{61.5}$: 5.2 (signif. at 5% level

F interaction : 0.1 (not signif.).