The influence of early handling on the temporal sequence of activity and exploratory behaviour in the rat

by

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ABSTRACT

The long and short term effects of brief handling of laboratory rats between birth and weaning have so far been shown to be mainly physiological in nature. Recent evidence indicates, however, that investigatory behaviour in adult animals may also be affected.

The area of exploratory behaviour is receiving increasing attention, but there have been comparatively few studies relating this to early experience. Following a brief review of each topic, a series of studies is therefore reported in which the behaviour of handled and non-handled rats is compared in a variety of experimental situations. These range from situations giving considerable opportunity for locomotor investigation to others in which responses to specific aspects of the environment can be observed. In addition, the behaviour of males and females is compared and responses to each situation recorded over a number of trials.

Results from these experiments indicate that a variety of tests can distinguish behaviourally between handled and non-handled animals, but that the locomotor measures were least satisfactory in this respect and also revealed fewer interactions between the variables of Handling, Sex and Trials, although females had higher locomotor scores than males. However, handled animals tended to approach novel objects more rapidly and to spend more time investigating them than did non-handled; they also scored higher on tests of home cage emergence. Statistical interactions in these situations were frequently found, indicating the complexity of the effects of early handling. In addition, differences between the groups tended to persist over repeated trials.

It is concluded that early handling is capable of producing effects upon subsequent investigatory behaviour, either in addition to or in place of the lower-level processes of emotionality and locomotor activity.

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I. INTRODUCTION

In common with other rapidly-expanding fields of research, the study of the effects of early experience on later behaviour has led to the emergence of various controversies. Some of these - such as the old issue of 'learned' versus 'innate' - are now unlikely to be revived, at least in their original form; but questions such as the necessity for various forms of early experience, the possible existence of 'critical periods', the physiological effects on the organism, and, occasionally, the irreversibility or otherwise of various possible changes continue to be of interest.

In spite of the fact that there now exists a considerable body of experimental evidence (particularly in relation to animal behaviour) on these issues - evidence which will be discussed briefly under the appropriate headings - it appears that very few workers have studied the later behaviour of the animals in much detail. In particular, it is unusual to find more than one experimental situation in use at the time when the animals are tested, so that little is known regarding differences in performance to be expected under a variety of conditions. Some of this information can, of course, be inferred by collating the results from different experiments run by different experimenters with different batches, strains or even species of animals; but the limitations of this approach are self-evident, however interesting such comparisons may be.

Another aspect of the testing situation which deserves greater emphasis than it has hitherto received is that of repeated testing in the same situation. It is rash to assume either that the behaviour of an individual animal on the second occasion of testing will necessarily correlate with its behaviour on the first trial (see, for example, Whimbey & Denenberg, 1967) or, perhaps even more importantly, that the differences between two experimental groups will remain comparable over a series of trials. If, as we hypothesize, there are situations in which the performances of two such groups show differential changes with repeated testing, then it may be actually misleading to draw conclusions on the basis of a single trial, quite apart from the loss of possibly informative findings which is entailed.

It may also be of interest to observe these differential changes in more detail; for example, we may be led to quite different conclusions regarding the nature of early experience, depending on whether the performance curves for an experimental group converge with, diverge from or remain parallel with those for the appropriate control group over several trials.

In particular, the research reported in this thesis has been designed to throw light on the following questions:

i) the extent to which different measures of behaviour are able to distinguish between handled and non-handled animals;

ii) the circumstances under which behavioural sex differences in non-sexual activities can be elicited;

iii) the changes, if any, which are likely to occur in the behaviour of the experimental groups as a result of repeated testing in a given situation;

iv) whether the differences between handled and non-handled animals can be regarded, on balance, as chiefly attributable to general factors such as changes in levels of emotionality and locomotor activity, or to more specific aspects of performance such as investigatory behaviour.

This thesis is accordingly concerned with the intersection of two major research areas: that of locomotor and exploratory behaviour, and that of early experience. Since review articles relating to each of these topics have recently become available, the relevant literature in each area will be briefly discussed before proceeding to the experiments, which deal with various aspects of exploratory behaviour in relation to early handling. Although the experiments are to some extent treated separately, each having its appropriate introduction and conclusions, it will be observed that they fall in some respects within certain groupings. For example, the first two experiments are obviously closely related, dealing as they do with two slightly different aspects of "home cage emergence". The third takes up the theme of locomotor activity (already present in Expt. 2) through the study of Y-maze performance, while the last three experiments are concerned with the question of investigatory behaviour and are not only related to each other but also refer back to Expt. 1, in which this aspect of behaviour is also important.

Finally, although each experiment concludes with a brief discussion of the findings and of specific points of interest relating to these, the section entitled 'General Conclusions' attempts to draw together the whole series of experiments, pointing out the possible relationships between them and discussing their wider implications.

Exploratory Behaviour

The nature of the relationship between activity (in particular locomotor activity) and exploratory behaviour has yet to be clarified. Berlyne (1960) has discussed this problem to some extent, emphasizing the difficulties encountered in attempting to decide whether an animal passing from point A to point B can be regarded as approaching B or avoiding A; and whether an animal which spends much time in one part of a given environment is engaging in more or in less exploratory behaviour than another animal which moves rapidly from one part of the environment to the next.

The approach/avoidance problem can be seen as closely related to that of knowing whether activity is occasioned by exploration or by fear (often equated in practice with 'emotionality' and defined in terms of open-field defecation, as in Hall, 1934 and Broadhurst, 1958). The relationships between these have been considered by several workers (e.g. Stone, 1932; Billingslea, 1942; Hess, 1953; Bindra & Thompson, 1953; Halliday, 1966, 1968; Lester, 1967a; Williams & Wells, 1970; Russell, 1973d). Although there are differences in the terminology used, several of these authors have employed some variation of a technique which may be described as 'free' exploration, in which the animal is allowed to enter or otherwise investigate a new environment in its own time. Since the animal may take some time to emerge into the unfamiliar environment, it follows that locomotor scores within a given period tend to be lower than in the 'forced' exploration situation (Hall, 1934; Broadhurst, 1957; Halliday, 1967 - and many other workers) in which the animal is placed directly in the experimental environment.

Evidence that locomotor activity is negatively associated with emotionality has been provided by Broadhurst & Eysenck (1964), using the Maudsley reactive and non-reactive strains in an open-field test. Non-reactive animals (low defecators) were found to have significantly higher ambulation scores than reactive animals. Females also scored higher than males; this was particularly noticeable in the initial phase of the test sessions. These authors are of the opinion that "There is little doubt that the ambulation of the rat in this situation is exploratory in character." It should, however, be pointed out that reactivity and exploration cannot be correlated in an entirely straightforward manner, since females scored higher than males on the ambulation measure, and yet no sex differences in reactivity were found.

Another method of producing differences in 'emotionality' is by the use of handling procedures similar to those described in the present series of experiments. It is generally found that handled animals are less emotional than non-handled controls (Denenberg, 1964). DeNelsky & Denenberg (1967a) report differences between handled and non-handled rats on a test of "visual exploratory behaviour", and also state that "The findings ... that handled subjects were more active then non-handled controls probably reflects (sic) the fact that the handled animals were less emotional. When activity in an open field is used as an index of emotionality, handled animals have been found to be significantly more active than non-handled controls (Denenberg, 1962)". The latter sentence is something of a non sequitur, but the conclusion parallels that of Broadhurst & Eysenck. No problems regarding sex differences were encountered, however, as only male animals were used.

A direct comparison of the effects of heredity (through the use of reactive and non-reactive strains) and environment (early handling) upon emotionality was carried out by Levine & Broadhurst (1963). These authors found not only that both heredity and environment produced significant effects but that there was an interaction between the two factors.

Other studies using handled and non-handled animals have shown that, although measures of behaviour which appears to be exploratory in character (such as Y-maze section entries, rearing, and alternations) are positively and significantly correlated (Wells, Lowe, Sheldon & Williams, 1969) in both groups of animals, these measures are negatively correlated with defecation scores;

unpublished data from the same experiment show that, in this instance, the correlations reach significance only for the handled group. It is interesting, however, that no significant differences between groups with respect to defecation scores were found, since this raises some doubts as to the nature of the effects produced by early handling.

The situation is further complicated by Halliday's (1966) suggestion that "rats tend to explore novel stimuli because they arouse low levels of fear". A similar position is adopted by Lester (1968, 1969), and contrasts with that of, for example, Montgomery (1955), according to whom fear and exploration would be mutually exclusive. These theoretical positions are reviewed in detail by Russell (1973d). Halliday reports an experiment in which rats were tested for 3 mins. on each of 4 successive days in either an enclosed or an elevated maze (the latter being considered more 'stressful'), and finds that activity declined significantly over trials in the enclosed maze but remained constant in the elevated maze. Similarly, the number of animals defecating in the enclosed maze decreased over trials, while the number defecating in the elevated maze remained constant. He argues from this that although both mazes had become familiar to the animals, the elevated maze had retained its capacity to evoke fear whereas the enclosed maze had not. However, this approach has been criticised by

M.H. Sheldon (1968, 1969), who finds that rats in an elevated maze spend a large proportion of their time apparently investigating the extra-maze environment (behaviour which would not necessarily be reflected in the measures employed by Halliday), and concludes that " ... behaviour in the two kinds of maze is so different that these comparisons do not justify the conclusions drawn from them." An ingenious experiment by Williams (1971) goes some way towards overcoming this difficulty: using an enclosed Y-maze constructed entirely of clear Perspex, he compares section entry scores and defecation in animals exposed to two different levels of illumination, and obtains results which he describes as " ... completely opposite to the expectation from Halliday's position." The defecation scores were higher for the group which experienced the higher level of illumination, indicating that this was the more 'stressful' condition (Broadhurst, 1957; Dixon & Defries, 1968); but a considerable reduction in the number of sections entered was observed for this group, whereas section entry scores for the group experiencing the low level of illumination (the less stressful condition) remained constant over trials.
It is interesting to note in this context that, according to Candland, Pack & Matthews (1967), defecation in a novel environment showed adaptation over a series of trials but heart rate did not, and that heart rate and defecation frequencies were not significantly correlated either for individuals or for groups. No sex differences

in defecation were found, but heart rate was higher in females than in males. Unfortunately, this latter measure is less frequently employed in the study of emotionality than are defecation scores, and it is not clear which of the two measures is to be preferred.

We have seen, therefore, that there is conflicting evidence as to whether a decrease in activity can be taken to indicate a less stressful environment or not. It is also possible that 'activity' may be indicative of different states of the organism on different occasions. Whimbey & Denenberg (1967) have found, for example, that the activity of rats tested in an open field is positively correlated with a measure of emotionality on the first day of testing but negatively correlated on subsequent days. Denenberg (in Ambroso, 1969, p.37) has suggested that activity on the first day can therefore be regarded as a hyperactivity phenomenon rather than as exploration as such. However, Williams (1971) has found that although the 'sections entered' measure in the Perspex maze showed the customary within-trials decline (Montgomery, 1952), an additional score of 'movement' recorded simultaneously showed no such decline. This is taken to indicate that the sections entered score is to some extent independent of general activity (even on the first day of testing) and that it does provide a reasonably sound measure of exploratory behaviour. Alternatively, Russell & Williams (1973) have suggested that the differences between Trial 1 and subsequent performance can be accounted for in terms of the differential habituation of approach and avoidance tendencies.

There is also the problem that a given hypothetical construct such as 'emotionality' can be assumed from radically different, if not incompatible, behaviours. For example, Candland (1958; cited by Halliday, 1966) has found that a population of emotional rats may be bivariate, consisting of some animals who " ... cower on a single square and deposit a large number of boli, while other animals race around the [open] field and also deposit a large number of boli". In other words, it seems that high activity scores may be both positively and negatively correlated with emotionality (defined in terms of defecation scores) within the same experimental group. This adds weight to Archer's (1973) criticism of the use of group means rather than individual scores in the study of emotionality (as in Whimbey & Denenberg, 1967).

Further difficulties are raised by the findings of Russell (1973a), who reports that rats selected as high defecators entered fewer maze arms than did low defecators, but that they also tended to choose the novel arm of the maze on their first opportunity to do so. In other words, it seems that emotionality may be a poor predictor of novelty-seeking behaviour. However, Williams & Russell

(1972), studying the behaviour of handled and non-handled rats over several trials in an open field containing a central stimulus object, suggest that exploration tends to increase as the suppressive effect of fear becomes less with habituation. According to this, the more emotional group would be expected to explore more on subsequent trials than on the first.

The review by Archer (1973) gives a comprehensive account of the evidence concerning relationships between emotionality and exploration. Citing many of the findings discussed above, he notes that 'emotionality' and 'exploration' have been considered by some workers to be inversely related, while some find a facilitatory effect of fear on exploration, others regard the relationship as U-shaped (exploration being high at intermediate fear states), and still others hold that fear may energize either ambulation or responses incompatible with ambulation; on the other hand, the two have also been regarded as independent concepts. It is therefore not surprising that the validity of emotionality as a concept is difficult to assess. Indeed, Archer prefers not to regard either emotionality or exploration as major motivational constructs, and we would add that although fear (or emotionality) may be one of the factors affecting an animal's activity, it is evidently neither the sole determinant nor entirely straightforward in its effects.

We have already cited evidence that measures which appear - intuitively - to represent aspects of exploratory behaviour tend to be positively correlated (Wells et al., 1969), but until an acceptable definition of exploration has been formulated, such an approach must be regarded as somewhat ad hoc. Berlyne (1963), for example, takes the view that exploratory behaviours are those which do not seem to be associated with any specific biological function. Apart from the inherently unsatisfactory nature of a definition which merely subdivides all behaviours into the two classes 'x' and 'not x', the absence of some biological function cannot necessarily be assumed (see also Fowler (1965) for a discussion of this point). Unfortunately, however, the description of exploratory behaviour which Fowler suggests - namely, instrumental responses bringing about a change in stimulation, together with orienting and investigatory responses elicited by this condition - does not really constitute a definition. In particular, the first part of the description could equally well apply to other activities such as grooming and thermoregulatory behaviour, and the second comes perilously close to a statement of the nominal fallacy that exploration is exploratory behaviour. Nevertheless, the idea of investigatory responses elicited by stimulus change is an important one, and will form one of the underlying themes of the experiments to be described subsequently; it is difficult to disagree with Fowler's assumption that responses of this kind have a part to play in a wide range of other activities.

One of the problems in employing activity as a measure of exploratory behaviour is that of distinguishing between emitted (or instrumental) and elicited responses; indeed, it is difficult to conceive of experimental situations in which components of both will not be present. However, there does seem to be some difference - if only of degree - between an experimental situation which allows the organism to act upon the environment in some way (as in sensory reinforcement studies) and one in which the environment apparently acts upon the organism (as in studies employing, for example, a brightly illuminated open field).

Even if locomotor measures can be shown to contain a strong component of exploratory behaviour, however, this is not to say that they are entirely independent of the organism's general activity. There is some evidence, for example, that certain forms of early experience may affect subsequent activity levels: Halliday (1966) reports that handled animals are more active in the home cage than are non-handled animals. On the other hand, Lawlor (pers. comm.) has found that rats gentled for 5 mins. per day on days 14-28 differed from controls on measures of response to novel objects, open-field activity and defecation, but that there were no significant differences with respect to activity in the home cage. This is in some ways a more informative finding, and suggests that psychological rather than physiological processes may be affected by this technique; it would also accord with the suggestion that early handling produces fairly gross changes in, for example, emotionality, whereas post-weaning handling affects behaviours which can be thought of as cognitive in nature (Denenberg; in Ambrose, 1969). At the same time, it must be noted that this interpretation is not satisfactory in cases where early handling produces differences in response to situations with a cognitive element (as may be the case in some of the experiments to be reported subsequently). Although this is not an area where clear-cut distinctions can be made, it is hypothesized that early handling may affect cognitive behaviour as well as producing effects on emotionality and/or activity, and that the extent to which these are revealed will be dependent on the exact nature of the testing situation employed.

We now turn to the problem of 'optimum levels', which has its historical roots in attempts to reconcile the observed behaviour of organisms (under conditions where the so-called biological drives are at low levels) with the predictions of theories of learning based upon drive reduction. Some workers responded to this challenge by postulating the concept of an exploratory drive (e.g. Berlyne, 1950); but following the publication in the early 1950's of a large number of papers showing that several species were capable of learning new responses in order to bring about an increase rather than a decrease in stimulation (see Leuba, 1955, for a selection of these), a change of emphasis was discernible.

The term 'optimum levels' is a rather unsatisfactory one, used here for the sake of economy to describe at least two major aspects of this change. Briefly, there is the concept of *optimal stimulation* as exemplified by Leuba (1955), who states that "the organism tends to acquire those reactions which, when over-all stimulation is low, are accompanied by increasing stimulation; and when over-all stimulation is high, those which are accompanied by decreasing stimulation". Leuba is also at pains to point out that there is nothing intrinsic either in the stimulus or in the current state of the organism by which intensity of stimulation could be defined as an absolute, but that the entire context of the stimulus situation must be taken into account. There are some similarities between this formulation and that of Dember (Dember & Earl, 1957; Dember, 1960), who states that "each individual can be thought of as having a preferred complexity level, or an *ideal* complexity level. The ideal complexity level is characteristic of the individual at a given moment in time and with respect to specific stimulus attributes".

It is apparent even from these short extracts that both Leuba and Dember place considerable emphasis on the stimulus aspects of the situation, and that although the condition of the organism is by no means neglected, their major aim appears to be the prediction of responses in terms of the immediate context of events. In other words, the organism's response could perhaps be regarded as being elicited by a given stimulus configuration.

Of even greater interest in the present context are those theories which place the emphasis squarely upon the state of the organism itself; these are best described as theories of optimal arousal. The history of the concept of arousal can be traced back to the turn of the century via attempts to classify emotional states, but one of the most influential formulations has been that of Hebb (1955), who relates the level of 'arousal function' (nonspecific cortical bombardment) to the level of 'cue function' (the more specific guiding role of sensation, which can be loosely interpreted as 'behavioural efficiency'). According to Hebb, this relationship can be expressed in the form of an inverted and approximately U-shaped curve, where maximal behavioural efficiency occurs at an intermediate level of arousal. At very low or very high levels of arousal, however, " ... the capacity of sensory stimulation to guide behaviour is very poor" (Hebb, 1966). In addition, the inverted U-shaped curve may take slightly different forms according to the aspect of behaviour in question.

Berlyne (1960), while accepting the importance of arousal as a theoretical concept, differs from Hebb in postulating that the organism behaves, within limits, in such a way as to reduce arousal and thus attain some optimum level. Thus, for Berlyne, boredom is regarded as a state of high arousal. Exploratory behaviour is interpreted as a way of reducing arousal (this has some similarities with those theories which postulate exploration as a method of reducing fear); alternatively, the organism may seek a temporary increase in arousal for the sake of the decrease which follows. Subsequently, however, Berlyne (1969) has cast some doubt on this latter suggestion; he compares several possible models relating reward-value to arousal increment, and suggests that, under certain circumstances, moderate increases in arousal may be rewarding. Correspondingly, and in common with some of the earlier theories, larger increases may be aversive.

Berlyne further postulates not only a reward system but also a parallel aversion system, both of which are affected by 'arousal potential' (roughly equivalent to 'amount of stimulation', in its broadest sense). For present purposes, the most relevant hypothesis arising from this is that " ... the most rewarding degree of arousal potential is higher at intermediate levels of arousal than at supranormal and subnormal levels. In other words, an animal will be most inclined to welcome arousing stimuli when its capacities for dealing with them are at their peak but will prefer less challenging and troublesome stimulation when arousal level is too high or too low for full efficiency" (Berlyne, 1969, p. 208). There is some experimental support for this view, including in particular a study by Haywood & Wachs (1967), who found that stimuli such as white noise and shock - interpreted as being strongly arousing - caused a decrement in novelty preference. Similarly, Williams, Wells & Lowe (1971), found that bar-pressing for response-contingent light was depressed by the administration of white noise, while control groups showed no differences in responding.

Most of these theories are, on the face of it, able to explain the differences in responding to a given level of stimulus input which are found when the performance of handled and non-handled animals is compared. However, any theory of optimum arousal as such suffers from the deficiency that it cannot explain how both groups are capable of adjusting their level of performance to deal with a new and possibly increased level of stimulus input even though the absolute differences between the groups may still be maintained. This has led Wells et al. (1971) to propose a dual arousal system incorporating both response to absolute stimulus input and also a mechanism which can monitor stimulus change and adjust arousal levels accordingly.

We therefore continue to stress the necessity of comparing the performance of handled and non-handled animals in a variety of stimulus situations and during more than one occasion of testing, since this is likely to provide greater insight into the ways in which the two groups, whose arousal levels have perhaps been 'set' at different values by the form of early experience which they have undergone, are capable of matching their performance in accordance with both intrinsic and extrinsic variables.

Early Experience

There are various possible approaches to the study of the effects of early experience in animals. For example, some workers have concentrated on the kinds of early environment or stimulation required to bring about a change in the organism's subsequent behaviour or physiology; the effects likely to be produced may or may not be specified. Related to this area of study are experiments attempting to establish the developmental stage at which such changes are most effective. Alternatively, greater emphasis may be placed on the nature of the effects obtained by a given experimental manipulation. Many workers have, of course, employed a combination of these approaches.

The section which follows does not attempt to give a comprehensive review of what is by now an extremely widely researched field, and one which has been covered in greater detail elsewhere (e.g. Newton & Levine, 1968; Ambrose, 1969; Denenberg, 1972; Daly, 1973), but rather attempts merely to draw attention to some of the relevant areas.

Enriched environment studies

Evidence from laboratory studies indicates that a wide range of modifications to the early environment will produce some effect on the organism, and that both deprivation and additional stimulation (as compared with baseline laboratory conditions, which are likely to vary between researchers) are capable of bringing about various changes. For example, rats reared in an environment containing additional visual and tactile stimuli have been found to score more highly on a test of three-dimensional discrimination than do animals with a lesser amount of perceptual experience (Meier & McGee, 1959). These and similar results obtained in 'free environment' studies by workers such as Forgays & Forgays (1952), Forgus (1954, 1955) and others owe much to earlier ideas put forward by Hebb (1949). Gibson & Walk (1956) have likewise shown that experience of geometrical shapes in the home cage during infancy improves subsequent discriminations involving such shapes. However, the degree of specificity of these effects is not altogether clear, as few workers have considered the possibility that prior experience with stimuli used in a discrimination test may have the effect of, say, reducing emotionality; thus in the Gibson & Walk experiment a control situation involving discrimination between other stimuli (geometric or otherwise) might have been desirable. A subsequent experiment by Gibson, Walk, Pick and Tighe (1958) is more satisfactory in this respect, and indicates that this kind of early experience may produce a general facilitatory effect on learning.

Although it is often assumed that the effects of an enriched environment operate at least in part through the visual modality, one of a series of experiments by Hymovitch (1952) indicates that performance on a 'closed-field' test can be affected by free-environment experience even in animals which have been blinded. It is also interesting that, in a subsequent experiment, no differences were found between free-environment and other experimental and control groups on a 10-unit T-maze, as it might have been expected that such experience would improve performance on a discrimination or other cognitive task.

The effects of an enriched environment may also depend to a large extent on the age, or perhaps developmental state, of the organism concerned. For example, an experiment often quoted in support of the effects of early experience on learning is that carried out by Bingham & Griffiths (1952). In fact, although performance on the Warner-Warden maze was improved for the 'enriched environment' groups, discrimination learning was not affected; and it is probably critical that the relevant early experience was not made available until the animals were 21 days old. Although a useful comparison of preand post-weaning effects has been carried out by Denenberg, Woodcock & Rosenberg (1968), showing that both kinds of enriched environment experience improved subsequent problem-solving, it is likely that the organism will make best use of such experiences from the time when its sensory faculties are in full operation, and that the imposition of a cut-off point at the time of arbitrarily imposed weaning is in itself somewhat arbitrary. Nevertheless, many studies concentrate almost exclusively on the post-weaning period, as do those by Cooper and Zubek (1958) on the learning ability of maze-bright and maze-dull rats, and by Forgus (1955), stressing the relationship between the quality of early experience and the nature of the task to be solved.

There is evidence, however, that animals reared in a visually complex environment show reduced locomotor activity but increased preference for complex visual stimuli as compared with controls (Nielsen, 1970). As suggested elsewhere, this indicates that locomotor scores do not provide an ideal measure of investigatory behaviour. The apparently anomalous finding by Zimbardo & Montgomery (1957) that 'free-environment' animals explore less than 'normal' controls could also be accommodated if it is borne in mind that exploration is here defined as the number of maze units traversed.

Few direct comparisons of pre- and post-weaning enriched environments have been carried out to date. However, an experiment of some complexity by Denenberg, Karas, Rosenberg & Schell (1968) shows - among several other effects - that a pre-weaning free environment may increase open field activity, whereas a post-weaning free environment improves avoidance learning.

Although this appears to be consistent with the findings discussed above, it is interesting that Denenberg and his co-workers have generally taken the view that avoidance learning (as used in the experiment cited in the previous paragraph) is more readily acquired by non-handled rather than by handled animals - or, in other words, by those animals which are usually regarded as being in some way deprived of stimulation.

There is also evidence from studies concerned with changes in brain weight (Riege, 1971) that enriched environments can affect fully mature rats as well as young ones; but effects are likely to be more pronounced in very young animals (Malkasian; cited in Rosenzweig, Bennett & Diamond, 1972). Since in this study the experimental procedure was initiated when the rats were only six days old, and measures of brain differences (such as increased thickness of cerebral cortex) were first taken at 14 days of age, it is unlikely that all sensory systems had reached an optimum level of functioning, or consequently that enriched environments must necessarily have their greatest effect after the animals have been weaned. Indeed, there is some evidence that early perceptual experience leads to a greater improvement in form discrimination than does later experience (Forgus, 1956).

The most clear-cut results in this area are probably those obtained by Denenberg, Woodcock & Rosenberg (1968) and by Forgays & Read (1962). Both studies found that either pre-weaning or post-weaning enriched environments could improve adult problem-solving performance, but Forgays & Read also state that such experience during the period immediately following weaning results in better performance than when it is made available either earlier or later.

It is therefore safe to assert that experience in an enriched environment will produce subsequent changes in behaviour. The factors mediating these changes, however, are by no means clear, particularly since in a 'free environment' situation it is virtually impossible to specify the nature of the experiences which the animals have undergone. Matters are not improved by studies such as that by Rosenzweig et al., cited previously, in which the enriched environment variable is apparently interacting with that of increased social experience; for the authors state that the brain measures which they customarily employ are not affected either by placing twelve rats in an empty cage for appropriate periods, or by putting a single rat in a large cage with play objects. This 'social facilitation' effect may also have influenced the results of other workers, such as Hymovitch.

We are also led to wonder what effects, if any, would result from similar procedures applied to species which are by nature solitary, rather than living in loose agglomerations as do rats under natural conditions.

Deprivation studies

The use of the term 'deprivation' immediately presupposes (as in the 'enriched environment' studies) that some baseline of experience can be identified which is normally common to all members of the species under investigation. In practice, however, this is often poorly specified.

Similarly, the 'deprivation' may assume a variety of forms, ranging through perceptual (or sensory), social, environmental, and perhaps in some cases emotional. As is the case in many areas of early experience, the consequences of such deprivations may affect development or behaviour in sometimes unforeseen ways; and furthermore, the effects may not be apparent until a later stage of development has been reached. An additional difficulty here is that of distinguishing between the variables of, say, social and sensory deprivation - a matter of some procedural difficulty - and indeed many investigators (see, for example, Melzack & Scott, 1957) have not attempted to do so.

In a sense, the perceptual deprivation rearing experiments are sometimes of less interest to the psychologist, since it is all too easy to produce some malfunction or degeneration in physical terms (Riesen, 1966), and although this will undoubtedly affect behaviour, the resulting information will only be of the most general kind. It would seem preferable to leave sensory systems intact wherever possible and to manipulate aspects of the environment instead, even where the possible effects on, for example, neural maturation are being considered (Rosenzweig, 1966).

In the studies on the rat, the emphasis has generally been on the effects of deprivation procedures on subsequent learning, an area surveyed by Gluck & Harlow (in Jarrard, 1971). The procedures described, unlike that of 'handling', are generally of long duration, beginning either at birth or after weaning and continuing until well beyond the onset of sexual maturity in the animals; however, the effect of restriction or enrichment tends to be greater when the treatment is carried out at some time between eye-opening and 60 days of age (Hymovitch, 1952; Gill, Reid & Porter, 1966; Nyman, 1967).

Social and maternal deprivation studies have been carried out on a somewhat wider variety of species, with particular emphasis on primates (Mason, 1960; Harlow, 1962; Green & Gordon, 1964), and including humans (Rheingold & Bayley, 1959; Dennis, 1960). Although there may be long-term effects on, for example, sexual behaviour which are attributable to early social deprivation, variables such as social responsiveness may be affected only in the short term, perhaps being modified by the nature of the experiences undergone during the subsequent intervening period before testing takes place (Rheingold, 1956; Rheingold & Bayley, 1959).

In some species, however, changes may be more persistent. Melzack & Scott (1957), using dogs as subjects, found that not only early learning but also responsiveness to painful stimuli were affected; and some maladaptive responses were still present two years after release from the restricted environment.

There are methodological difficulties in carrying out maternal deprivation studies in rats, but an experiment by Russell (1970) in which mothers were removed from litters for either one or ten hours per day on days 3 to 9 following birth found an increase in body weight and a decrease in defecation scores in the treated group on testing at 70 days. Open-field ambulation, however, was not affected. These findings contrast in some respects with those of Schaefer (in Newton & Levine, 1968), who reports that removal of the mother had no effects on offspring emotionality.

The difficulty here, as Russell points out, is that even positive results cannot necessarily be attributed to maternal absence per se. (Some of the additional factors which may be involved are discussed in the section on Handling). This objection applies, *mutatis mutandis*, to most of the deprivation studies which have been carried out to date, and indeed the mechanisms which are operating are likely to be difficult to clarify.

Handling

a) Terminology.

Many of the problems encountered in relation to enriched environment studies also arise in the handling experiments; in addition, the terminology can be confusing and is suceptible to changes in fashion. Some early experiments such as those by Weininger (1956) or McClelland (1956) employ variations of a procedure now often referred to as 'gentling' or stroking, and administer this treatment after weaning the experimental animals. By way of contrast, the 'handling' referred to by Levine, Denenberg or their co-workers consists in removing the young animal from the nest for a brief period each day between birth and weaning, transferring it to a separate container and then replacing it. In fact, the 'handling' aspect of this procedure tends to be minimal.

Since Levine's (1956, and subsequent) findings that 'handling' produces comparable results, in behavioural and physiological terms, to those which follow the administration of electric shock - a form of early experience previously considered 'traumatic' - some workers have referred to handling in terms of 'stress' (Levine, 1956; Denenberg, 1959). Some of the problems associated with this usage are discussed under the appropriate heading. A more moderate approach would be to refer to the procedure as 'early stimulation', or, better still, simply as 'early handling'.

b) Time of administration.

The term 'early handling', however, although generally accepted to refer to the time between birth and weaning, does not really specify when the procedure should be applied in order to produce given immediate or later effects. In many studies, the dependent variable is some measure of 'emotionality'; and it can be shown, for example, that handling a pregnant female rat reduces the subsequent emotionality of the offspring (Ader & Conklin, 1963). Here, the stimulus is being administered prenatally, although it cannot be stated with any certainty that the developing foetuses are being directly stimulated, since even when an effect on subsequent emotionality of the offspring can be demonstrated, this may well be mediated through effects on the mother herself. A similar argument can be applied to findings by Thompson (1957), who trained female rats on a shock-avoidance task, with the sound of a buzzer initially paired with the shock; the animals were then mated and exposed to the buzzer alone on several occasions each day of pregnancy. Again, effects on subsequent offspring emotionality were found, although in this case the experimental group were more emotional than controls.

Furthermore, there appear to be circumstances under which direct treatment of the experimental subjects, whether pre-natally or otherwise, becomes unnecessary: Denenberg & Rosenberg (1967) have found, for example, that the effects of early handling of 'grandmother' rats are still traceable in the offspring two generations later. Offspring emotionality can of course be affected by either environmental or genetic factors; and, as Ottinger, Denenberg & Stephens (1963) have shown, it may be independently related to both prenatal and post-natal emotionality of the mother.

At the other end of the scale, there are also difficulties in deciding at what point handling (or any other experimental treatment) should cease to be regarded as 'early'. Although this term might be regarded as referring to any time before the organism reaches maturity, it is in practice used chiefly to refer to the pre-weaning period in mammals.* Indeed, although in the previously-cited experiments by Weininger and by McClelland post-weaning stimulation was found to produce what may be described as the 'classical' effects of handling, there is evidence that post-weaning handling or shock can produce somewhat different effects from those obtained prior to weaning (Brookshire, Littman & Stewart, 1961; see also Denenberg, 1964). This point is discussed

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* In the case of rats, it is common laboratory practice to wean the animals at the age of 21 days. This procedure should be distinguished from the more gradual spontaneous weaning which would take place in a wild population.

more fully in the next section.

There have been several attempts to consider handling in terms of the 'critical period' hypothesis. By analogy with the embryological usage, this states that there may be certain periods during post-natal development when stimulation produces maximal effects, but that such intervention at other times will produce little or no effect (Scott, 1962).

As in many other contexts, the evidence concerning this theory is confusing, especially since one worker who reported that there is no evidence for a 'critical age' for handling did not administer this treatment until the animals were at least 25 days old (Gertz, 1957). There are some fairly straightforward findings relating age at handling to rapidity of adrenal ascorbic acid (AAA) depletion following exposure to cold (Levine & Lewis, 1959a), and showing that handling on days 2-5 can be as effective as handling on days 2-13; but in general, the more independent and dependent variables employed, the more confusing the situation becomes. This has led Denenberg (1962) to conclude that, since there may be as many 'critical periods' as there are possible combinations of variables, the term is somewhat lacking in explanatory value; and he suggests that it may be more useful to concentrate on the study of functional relationships among variables. It has also been shown (Denenberg, 1962; Ader, 1966) that the amount of handling per day, as well as the total number of days on which handling is administered, may produce important differences; this contrasts with the all-or-none effects often produced by intervention at the embryological stage.

Many workers prefer to avoid the term altogether whenever possible and employ an alternative such as 'sensitive periods' which has fewer unfortunate connotations (Sluckin, 1970).

c) Effects of handling.

A wide variety of effects, both immediate and subsequent, is reported to have been produced by the handling procedure. Many of these are listed in a comprehensive review by Daly (1973); they include increased body weight, more rapid development (e.g. eye opening, motor coordination and acquisition of body hair), greater resistance to physiological stress, improved performance on a learning task, increased activity and decreased defecation rate in a strange environment, earlier sexual development, and increased activity corresponding to greater stimulus variation. However, Daly also points out that there are several studies which find that handling has no effect on body weight (e.g. Denenberg & Karas, 1961; these and other authors have even reported reductions in weaning weight attributable to handling). Similar conflicts of evidence are cited with respect to defecation, performance on learning tasks and reaction to adult stress.

Daly also emphasizes the dangers of assuming that the handling procedure necessarily produces 'beneficial' results. This point will be further discussed in relation to the experiments reported subsequently.

It is perhaps worth noting that even when effects such as reduced emotionality can be attributed to 'handling', the relationship may be a curvilinear one. In other words, emotionality is not necessarily further reduced by increasing the number of periods of stimulation per day, but may return to the level shown by control animals (Ader 1966). There are, however, contradictory findings here too, and some workers take the view that the relationship is a monotonic one (Denenberg, 1964).

As we have previously indicated, pre-weaning handling is thought to produce effects which are qualitatively different from those produced by post-weaning handling (Levine, 1956; Seitz, 1954; Spence & Maher, 1962). There may also be differences between the effects produced by pre- and post-weaning shock (Lindholm, 1962). Denenberg (in Ambrose, 1969, p. 64 et seq.) suggests that post-weaning stimulation is likely to affect perceptual and cognitive processes, whereas pre-weaning stimulation produces somewhat gross effects in terms of subsequent emotionality, physiology and biochemistry.

He also proposes that post-weaning stimulation could be regarded as 'patterned physical stimulation' (as opposed to the 'unpatterned' characteristics of handling, shock, temperature change and so on), and that it is likely to be most effective if provided in the form of an enriched environment.

These distinctions are not to be regarded as absolute, since some effect can be obtained by administering a pre-weaning enriched environment, or, conversely, post-weaning shock. Indeed, Bruner comments in the same context that the organism's responses to novelty would probably need to be stabilized quite early on in order for exploratory behaviour and hypothesis testing to occur. This point has considerable relevance to the experiments which are to be reported here.

d) Mode of action of handling.

The main problem in attempting to discover how the handling procedure affects the young organism is that of ascertaining whether the treatment is affecting the animal directly or whether it is producing some change in the pattern of mother-infant interaction and is thus mediated through the behaviour of the mother.

Some possible mechanisms are discussed by Schaefer (in Newton & Levine, 1968), Russell (1971) and Daly (1973). These include: the direct action of tactile stimulation; hypothermia; maternal behaviour; and stress. Although many authors tend to assume that the first of these is chiefly responsible for the handling effect, it is not difficult to see that handling may also involve cooling, may occasion 'stress', or may through any combination of these factors affect maternal behaviour so that treated pups may elicit differing degrees and types of interaction from those elicited by untreated controls (Hutchings, 1967).

The same difficulties are inherent in investigations of other possible factors which may be involved. Russell (1970) has shown that removal of the mother, as opposed to removal of the offspring, also results in a reduction of the offsprings' subsequent emotionality; it has been found that removal of the young of various rodent species results in an increase in the production of ultrasonic calls, which in turn affects the mother's retrieval behaviour (Noirot, 1965; Sewell, 1970; Bell, Nitschke, Gorry & Zachman, 1971); and the proximity (without direct contact) of a strange male rat during the pre-weaning period can affect subsequent offspring emotionality, possibly through pheromonal influences on the mother (Williams & Wells, unpublished MS).

Russell (1971) points out that most existing experiments do not allow a distinction to be made between the effects of the various factors, and indeed there is likely to be considerable interaction between them. As Daly (1973) is led to conclude, most experimental treatments probably act through more than one mechanism in any case. No doubt until further clarification has been achieved the handling technique will continue to be employed, as it is in the experiments to be reported here, simply because it is a relatively straightforward and reliable method of demonstrating the long-term effects of early experience.

Stress

It is perhaps necessary to mention the use of the term 'stress' in relation to handling, particularly since there seems to be considerable confusion over terminology.

Some of the difficulties can be traced to early attempts to link animal experiments to the psychoanalytical literature through the study of early traumatic experiences. Thus Levine (1960) recounts that electric shock was initially chosen as a potentially stressful stimulus for the young rat, and only subsequently was it discovered not only that early handling produced similar effects but that the supposedly non-stressed group used as controls was the one in which 'adverse' effects were found.

As long as the term 'stress' is operationally defined, the rather all-embracing use which it sometimes receives is probably unimportant; but owing to the existing connotations of the word it becomes extremely difficult to make reliable predictions about events which the young organism may undergo. For example, under laboratory conditions at least, rat pups are trampled on, picked up, bitten, shaken about and briefly deprived of food and warmth by the mother herself as a matter of routine (see also Denenberg's remarks in Ambrose, 1969, p. 42); and yet none of these procedures is evidently to be regarded as stressful in experimental terms. What is more, although shock and handling by the experimenter are generally regarded as having a variety of desirable subsequent effects, none of the activities engaged in by the mother seems to achieve this unaided. If we attempt to reconcile these difficulties by assuming that shock, handling and so on produce their effects solely through the mediation of maternal behaviour, possibly by raising the mother's activities above some critical threshold (thus enabling them to be described as 'stressful'), the description of shock and handling themselves as 'stressful' to the neonate then becomes essentially meaningless.

Turning for the moment to the use of 'stress' in the investigation of the subsequent effects of early experience, we find that the situation is even less well defined. Procedures subsumed under this heading include food deprivation, often terminal (Bovard, 1958; Levine & Otis, 1958); injection of noxious agents such as leukaemia cells or glucose in sufficient quantity (cited in Levine, 1960); exposure to cold for varying periods (Woods, 1957; Levine, Alpert & Lewis, 1958; Levine & Lewis, 1959b); administration of electric shock (e.g. Levine, 1962); intense auditory stimulation (Woods, 1957; Bloom, Daniel, Johnston, Ogawa & Pratt, 1973); rectal distension (Bloom et al., 1973); or various kinds of surgical intervention (Woods, 1957; Bloom et al., 1973). The list could, of course, be extended.

So far, the issue would appear to present few problems from the intuitive or anthropomorphic point of view, even though the techniques are not always effective (Griffiths & Stringer, 1952); no doubt few experimenters would care to submit themselves to such procedures without some compelling reason. However, consideration of some other procedures which have been designated as 'stressful' may give rise to some confusion. A major example is the handling procedure itself (albeit mostly used as an initial experimental treatment), which has come to be regarded as stressful only with the advantage of hindsight. Among the original assumptions that were proved wrong were, firstly, that handling would be ineffectual and would therefore provide a suitable control for the procedures involved in the administration of shock (c.f. Levine, 1960); and secondly, that handling per se would be reinforcing (Candland, Horowitz & Culbertson, 1962).

Similarly, and especially in view of the evidence indicating that organisms will seek out and even learn new responses in order to encounter novel stimuli, it is perhaps surprising to discover that novelty is also to be regarded as stressful and that rats which have not been given the benefit of handling find it particularly aversive (Denenberg & Grota, 1964; Levine, 1967). Few workers seem to have observed, however, that rats in the wild state exhibit a considerable degree of 'neophobia' (Barnett, 1958); this makes it difficult to argue that handled animals are being exposed to a level of stimulation commensurate with that experienced by wild strains and that the non-handled group are correspondingly deprived.

Clearly, what is needed here is some independent definition of 'stress'; and indeed, such a definition can perhaps be provided by a physiological rather than a psychological approach. Thus we may wish to say that 'stress' can be defined as any procedure which results in an increase in levels of circulating corticosteroids; this would certainly include treatments such as heat or electric shock applied to the neonate rat (Haltmeyer, Denenberg, Thatcher & Zarrow, 1966) and early handling (Denenberg, Brumaghim, Haltmeyer & Zarrow, 1967); and, as Levine (in Ambrose, 1969) points out, it is particularly interesting that the effects of stimulation can be observed during the period when central nervous system organisation is presumed to be occurring. (See also Levine & Mullins, 1966; Levine, 1968).

The particular relevance of this finding is that such stimulation in infancy may well produce permanent changes in CNS organisation, thus affecting neuroendocrine mechanisms which in turn result in differential patterns of adrenocorticotrophic hormone (ACTH) secretion. 'Stimulated' animals are therefore predisposed to respond in a different manner to stress later in life; and Levine (1962) has found that ACTH secretion and steroid responses to stress are indeed affected in adult animals which have undergone handling in infancy. In handled animals, for example, the steroid response to an electric shock is more rapid but less persistent than in non-handled animals. This could well be a process of positive feedback leading to eventual tissue damage. However, it is not immediately obvious whether early physical stimulation produces long-term changes in the corticoid response per se, since the usual experimental procedure is either to measure the response within minutes (by sacrificing the animal) or to measure responses which occur in adulthood to some further stimulus.

The technique described in the previously-cited paper by Bloom et al. (1973) has some advantages, since it involves measuring changes in glucagon levels in response to stress by means of blood sampling procedures; but even here, there are difficulties in relating this to the study of ongoing behaviour since the animals (primates, in this case) have to be "lightly restrained", and, for technical reasons, the method is not entirely suitable for use with small mammals such as rodents.

Even though techniques such as these may provide some insight into what constitutes a stressful stimulus, we must still bear in mind that the perception of 'stress', or painful stimuli, will depend on the past history of the individual organism, as Melzack & Scott (1957) have clearly shown. Considerations such as these have led

Levine (in Newton & Levine, 1968; Levine & Mullins, 1966) to formulate a theoretical mechanism to account, at least in part, for the differential responding of handled and non-handled animals. This will be discussed briefly in the next section.

Although it must be accepted that a surprising variety of stimuli can affect the organism in a surprising variety of ways, it is still not altogether clear what role (if any) the concept of stress has to play, especially since there must come a point at which stress - for example, the administration of electric shock - ceases to be beneficial either in its immediate or in its subsequent effects: namely, when the organism is either seriously incapacitated or killed. Many discussions on the subject therefore contain the implicit assumption of the ubiquitous U-shaped curve relating stress to a variety of indices and generally concluding that 'moderate' amounts of stress are likely to be beneficial; but it is doubtful whether the concept has any great explanatory value here, particularly in view of the difficulties in relating it to other measures such as defecation and changes in heart rate, which in turn are found not to correlate with each other (Candland, Pack & Matthews, 1967), but which might have appeared on the face of it to be equally valid responses to aversive stimulation.

Theoretical approaches

There have been comparatively few attempts to assimilate the research on early experience into a theoretical framework. This may perhaps be attributed to a general disenchantment with all-embracing theories, or possibly to the realisation that there is a considerable body of sometimes conflicting evidence to be accommodated. Some attempts, however, have been made. One of the earliest is a formulation by Glanzer (1958), who states that " ... the increase or decrease of activity with respect to parts of the environment is a function of the difference between the average amount of information the individual is accustomed to and the current rate of flow of information from the environment". This can be stated as follows:

$$\frac{dA}{dt} = f\left(\frac{I}{t} - \frac{dI}{dt}\right)$$

where A = amount of activity

I = amount of information processed during the organism's life history

t = time measured from birth of organism

Glanzer argues that this formulation can account for the differential effects of early and late experience (the greater effect being produced early in life), and also for the observed effects of ageing: namely, that the organism tends to stay in a limited area, thereby receiving less information and consequently requiring less.

The argument may well be valid as far as it goes, and it is welcome to find some consideration given to the other end of the life-span; but given the inherent difficulties of substituting values for I in the equation, the perhaps rash assumption that amount of activity is related to amount of information, and the even more dubious one that t should be measured from the birth of the organism, it is doubtful whether this approach is likely to find much practical application. Its chief value is likely to be as a compact descriptive statement of some of the major variables which must be considered, and as a suggestion regarding the ways in which these variables may interact.

Like Glanzer's theory, that of Sokolov (1960; described briefly in Newton & Levine, 1968, p. 176) relies on a process of matching current and prior events; but in this case, a greater variety of early experience is thought to result in the setting up of a greater number of 'neuronal nets' with which subsequently occurring stimuli can be found to correspond. Relating this theory to the early handling experiments, Levine (op. cit.) points out that Sokolov would predict a greater degree and speed of habituation in the handled animals, and that this appears to be supported by behavioural evidence.

The theoretical position most favoured by Levine, however, is the 'hormonostat' model, which is based, at least in part, on suggestions by Yates & Urquhart (1962). According to Levine (in Ambrose, 1969, p. 47), a critical concept of this model is the notion of the controlling 'setpoint', values of which may vary between individuals and which may be modified by various aspects of early experience. The 'hormonostat', which is taken to be a central nervous system mechanism, operates by assessing the quantity of circulating corticosteroids and comparing them with the setpoint; if the concentration is too high, adrenocorticotrophic hormone (ACTH) and consequently adrenal output diminishes, whereas if the concentration is too low, ACTH is released and more steroids are produced.

The most relevant features of the model for present purposes are, firstly, that the setpoint is not fixed at any given level, and can vary both according to the demands of the environment and according to the inner states of the organism; and secondly, that the setpoint may be modified by early handling and similar procedures so that it is enabled to vary in a gradual manner between maximum and minimum values. In non-handled animals, by contrast, the response to the environment tends to be of an all-or-none form with few gradations.

This is perhaps one of the more interesting theories to have emerged so far, although once again the behavioural correlates of the steroid response are not always easily ascertainable (*pace* Levine, who does cite a little evidence of such correlations). The fact that there may be considerable variability between individuals may also cause problems in view of the necessity of sacrificing the animals in order to obtain the relevant measures, thus rendering them unsuitable for either behavioural or long-term physiological comparisons.

A more serious objection is raised, however, by the findings of Hodges & Jones (1963, 1964) that the release of ACTH appears to be independent of changes in blood corticoid concentrations; though perhaps procedural differences may be sufficient to account for this.

In common with most theories, those we have referred to are perhaps valuable as source of suggestions for further research rather than as completely satisfactory explanations in their own right; but as we have already implied, it is no doubt a little premature to expect such explanations at this stage in our knowledge.

II EXPERIMENTAL INVESTIGATION

General Methodology

Since all the studies reported below follow the same general procedures with respect to early handling and animal husbandry, a brief section describing these is included here in order to avoid subsequent repetition.

a) Subjects

Ss were hooded rats bred in the Department of Psychology, Bedford College, from random-bred stock initially obtained from the MRC. In all experiments, equal numbers of males and females were used.

b) Housing

The animals were maintained under laboratory conditions with a temperature range of 72° - 75°F and in normal daylight supplemented in winter by artificial light between the hours of 08.30 - 17.30. They were housed in white plastic cages measuring 220 x 175 x 370mm, with metal grid floor and similar top which contained a food hopper and water bottle. Each cage rested on a plastic tray containing wood shavings, which could be replaced for cleaning purposes without undue disturbance to the animals. Pregnant females were also provided with hay as nesting material. Diet consisted of 41B pellets and water, available at all times, supplemented by fresh greens and chopped carrot several times a week.

c) Handling procedure

At birth, complete litters were allocated at random either to the 'handled' or to the 'non-handled' group, but litters containing fewer than 6 animals were not used. Each day between birth and weaning (which occurred for all Ss at 21 days), the following procedure was employed: each cage containing 'handled' animals was removed singly from the shelf and placed on a table, and the mother transferred to a spare cage. Ss were then taken individually and at random from the nest and were each placed in a small plywood compartment measuring 70 x 130 x 140 mm. When each member of the litter had been thus treated, Ss were replaced singly in the nest in the same order and the mother returned. The total 'operation time' for each animal was approximately 30 seconds per day. 'Non-handled' animals were undisturbed during this period apart from routine laboratory procedures of cleaning and feeding.

At 21 days of age Ss were separated from the mother and re-caged with like-sex litter-mates (i.e. with animals of the same experimental group). At approximately 40 to 50 days they were dye-marked for individual identification and caged in groups of 2 to 4 animals under the same conditions. Testing was begun in all cases when animals were approximately 90 days old.

EXPERIMENT 1 : Rearing up within the Home Cage

Introduction

Although the existence of behavioural differences between handled and non-handled animals is well established (c.f. Levine, Chevalier & Korchin, 1956; Denenberg, 1962; Denenberg & Grota, 1964), the exact nature of these differences remains unclear. In particular, two major aspects require clarification: the characteristics of the experimental situations which elicit these differences, and the extent to which the differences persist over time. In some situations it seems likely that differences between the two groups will not be observed; in the open field situation, for example, some workers have found the non-handled (or, where relevant, the reactive) group to consist of a bi-polar population in which some animals 'freeze' in response to the experimental situation while others exhibit a form of hyper-activity which appears random rather than systematic (Candland, 1959; see also Ambrose, 1969, p. 36). In these circumstances, the average score for such a group would tend to resemble that of the handled or non-reactive group, although differences in variance might well be found.

Similarly, even if differences between groups are found, these differences may vary from day to day in a complex manner (Whimbey & Denenberg, 1967), and can be caused to 'appear' and 'disappear' according to the presence or absence of given stimuli (Levine, pers. comm.; Wells et al., 1969; Wells, Williams & Lowe, 1971). Even in cases where the stimulus situation is not changed between trials, the pattern of responding to changing degrees of familiarity, or the choice of greater or lesser stimulus variation, may well differ between the handled and non-handled groups. (DeNelsky & Denenberg, 1967a, 1967b).

Few investigators, however, have attempted to ascertain whether the behaviour thus affected is exploratory in nature or whether the experimental treatment has produced changes of a more general kind (such as differences in activity levels or in emotionality); although Levine (in Ambrose, 1969), considering the effects of infantile stimulation on various dependent variables, comes to the conclusion that " ... infantile stimulation does not affect cognitive function per se, but ... has a major role in altering some characteristic of the organism which is related to emotional reactivity."

The present experiment therefore employs a modified version of a technique described by Williams & Wells (1970) in which an aspect of the animal's behaviour with respect to the already familiar home cage is studied. It is argued that this type of measure is likely to prove less stressful than tests employing a strange environment such as the runway or open field, and will therefore not only be a more sensitive method of eliciting behavioural differences (Hunt & Otis, 1963), but will lead to the inference that any such differences will be less dependent on general factors such as emotionality.

Method

Subjects were male and female black hooded rats, bred from MRC stock, of whom 50% had been subjected to the handling procedure previously described. For the purpose of this experiment, only cages containing 3, or at most 4, animals were used, and the numbers were equalised for sex and experimental condition to give a total of 24 cages with 6 cages in each sub-group.

On each of 4 successive trials, each cage was pulled out a distance of approximately 300mm from the shelf. A door measuring 110 x 160mm in the metal grid top of the cage was opened, and a record taken of the amount of time, in seconds, required for all three animals in the cage (or the first three, if four were caged together) to rear up at least once. The definition of 'rearing' was that both front paws should have left the floor of the cage simultaneously. Testing was carried out in alternating sequences of three cages of handled and three cages of non-handled animals, and the inter-trial interval for any given cage was approximately 15 minutes.

Results and Discussion

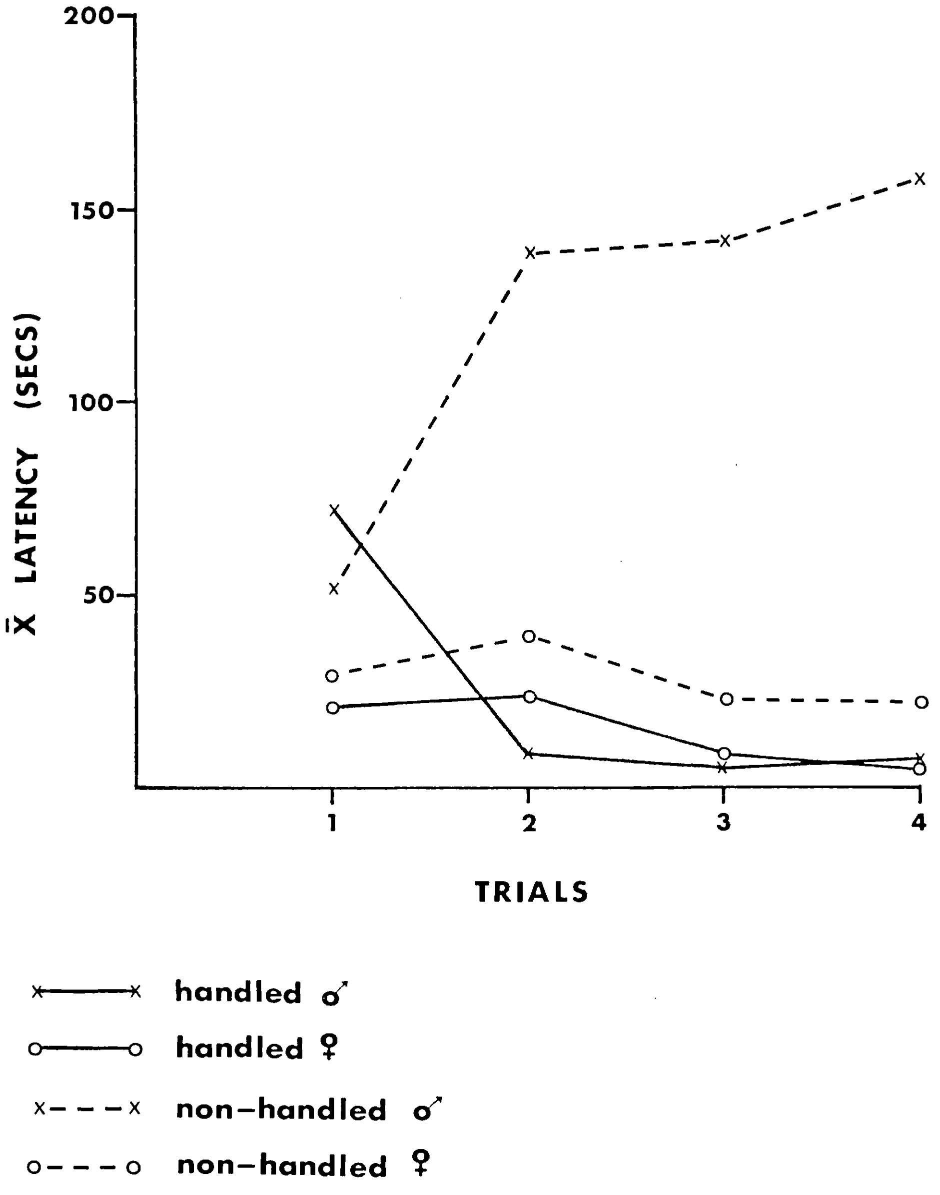
An analysis of variance was carried out on the combined latency scores for each group of rats per cage, and the results are set out in Table 1. Of the three main effects of Handling, Sex and Trials, the first two are significant beyond the .01 level, while the third fails to reach significance. The Handling x Sex, Handling x Trials and Handling x Sex x Trials interactions are also significant. The nature of these interactions, as well as the direction of the main effects, is illustrated in Fig. 1. This shows that in general the latency for the non-handled males is markedly longer than that for any other group, although the non-handled females also have higher latencies overall than either of the handled groups. It seems likely that a ceiling effect has been obtained in the later trials for the handled group; this is borne out by observation at the time of testing, which indicated that most handled animals had reached the rearing criterion as soon as the cage was opened.

The direction of the sex differences (females rearing before males) is in agreement with the findings of several workers (Meyers, 1965; Hughes, 1968; Broadhurst & Eysenck, 1964; Gregory & Liebelt, 1967; Williams & Wells, 1970) employing various measures of exploratory behaviour, but contradicts those of Lester (1967b). It should be borne in mind, however, that this difference is largely contributed by the scores of the non-handled animals, and that the sex differences in scores as far as the handled animals are concerned are almost negligible (hence the Handling x Sex interaction). It is interesting to speculate why the handling procedure should have eliminated sex differences in this instance, but no obvious explanation presents itself.

The higher-order (Handling x Sex x Trials) interaction is also of some interest, since the non-handled males appear to be demonstrating a totally different kind of adaptation to the experimental situation from that shown by the other groups. In other words, while the latencies of the other groups tend to become shorter with successive trials, those of the non-handled males tend to become longer. It would therefore seem that there is little hope of their overcoming the supposedly detrimental effects of 'not having been handled' by successive familiarisation with the experimental situation. It is interesting to compare this result with other findings (e.g. Wells et. al., 1969; c.f. also other experiments in the present series) where some adaptation has apparently occurred. A reconciliation of these differing findings may lie in the nature of the test situation: in a highly familiar situation such as the home cage, the non-handled animal is under little pressure to explore the environment, and its best strategy may indeed be to refrain from investigation, whereas in a relatively unfamiliar test apparatus the choice between exploring a test stimulus and refraining may be much less distinct. Relevant to this argument is a report by A.B. Sheldon (1969) that rats in an unfamiliar environment tend to prefer a familiar to an unfamiliar stimulus, but that preference shifts to an unfamiliar stimulus after habituation to the environment. It is possible, for example, that one of the effects of the handling procedure is to change not only the level of preference for a given stimulus situation but also the rate of adaptation to that situation.

FIG. 1.

Rearing up within the home cage.


200
150
100
50
X̄ LATENCY (SECS)
1
2
3
4
TRIALS
handled ♂
handled ♀
non-handled ♂
non-handled ♀

SOURCE	df	SS	VE	F	p
Handling	1	76106.34	76106.34	13.44	< .01
Sex	1	62781.51	62781.51	11.09	< .01
H x S	1	43733.06	43733.06	7.72	< .025
Subjects within groups	20	113265.06	5663.25		
Total	23	295886.25			
Trials	3	1149.12	383.04	0.41	N.S.
T x S	3	4071.62	1357.21	1.46	N.S.
T x H	3	31773.28	10591.09	11.39	< .001
T x S x H	3	26624.78	8874.93	9.54*	< .001
T x S within groups	60	55793.44	929.89		
Total	95	415298.49			

* The linear and quadratic trend components of this interaction are significant ($F = 20.37$, df = 3;60, $p < .001$; and $F = 6.59$, df = 3;60, $p < .025$ respectively).

TABLE 1

Analysis of latency scores for rearing up within the home cage.

Note:

i) The calculations for this and all subsequent tables have been corrected to two places of decimals.

ii) Analyses may be affected by the failure of some Ss to reach criterion within the time allocated. The maximum number of such scores (24%) occurs in the data analysed in Table 2.

iii) The latency measures analysed in Tables 1 and 2 represent joint scores for 3 Ss per cage.

EXPERIMENT 2 : Total Emergence from the Home Cage

Introduction

In this experiment the animals were given an opportunity to leave the home cage, and the latency for this was recorded. Since in order to do this they had first to rear up in the cage, the results from this and the previous experiment are logically related and must to some extent be considered together. It is hypothesized, however, that the measure used here is likely to be a less sensitive indicator of behavioural changes between the groups as it places more emphasis on the locomotor aspects of exploration.

Method

The same animals were used as in the previous experiment, and, as before, only cages containing three or four animals were used. In this case, however, cages were taken from the shelves and transferred to the experimental room. During testing, each cage was placed in an open field apparatus 4 ft. in diameter and illuminated from above by two 60w lamps. A door in the metal grid top of the cage was opened, and the time taken for 3 animals to emerge from the cage was recorded.

The criterion for emergence was that the animal should have climbed with all four feet on to the top of the cage. Animals which had emerged were not replaced in the cage until a latency measure for 3 Ss had been obtained, but were not prevented from returning of their own accord. Trials were terminated either when this criterion had been reached or at the end of 4 minutes. The intertrial interval was approximately 45 mins.

Results and Discussion

Latency scores per cage were analysed as in the previous experiment; the results are shown in Table 2. The main factors of Handling and Sex were significant beyond the .001 level, but no other factors or interactions reached significance. Fig. 2 illustrates that handled animals emerged more quickly than non-handled animals, and that females emerged more quickly than males. No significant changes over successive trials were observed; this, together with the lack of significant interactions, provides an interesting contrast to the previous experiment. In both cases, however, the non-handled males were clearly the slowest to emerge, and as before some Ss failed to reach the emergence criterion at all. A sequence of emergence behaviour is illustrated in Plates 1 to 6.

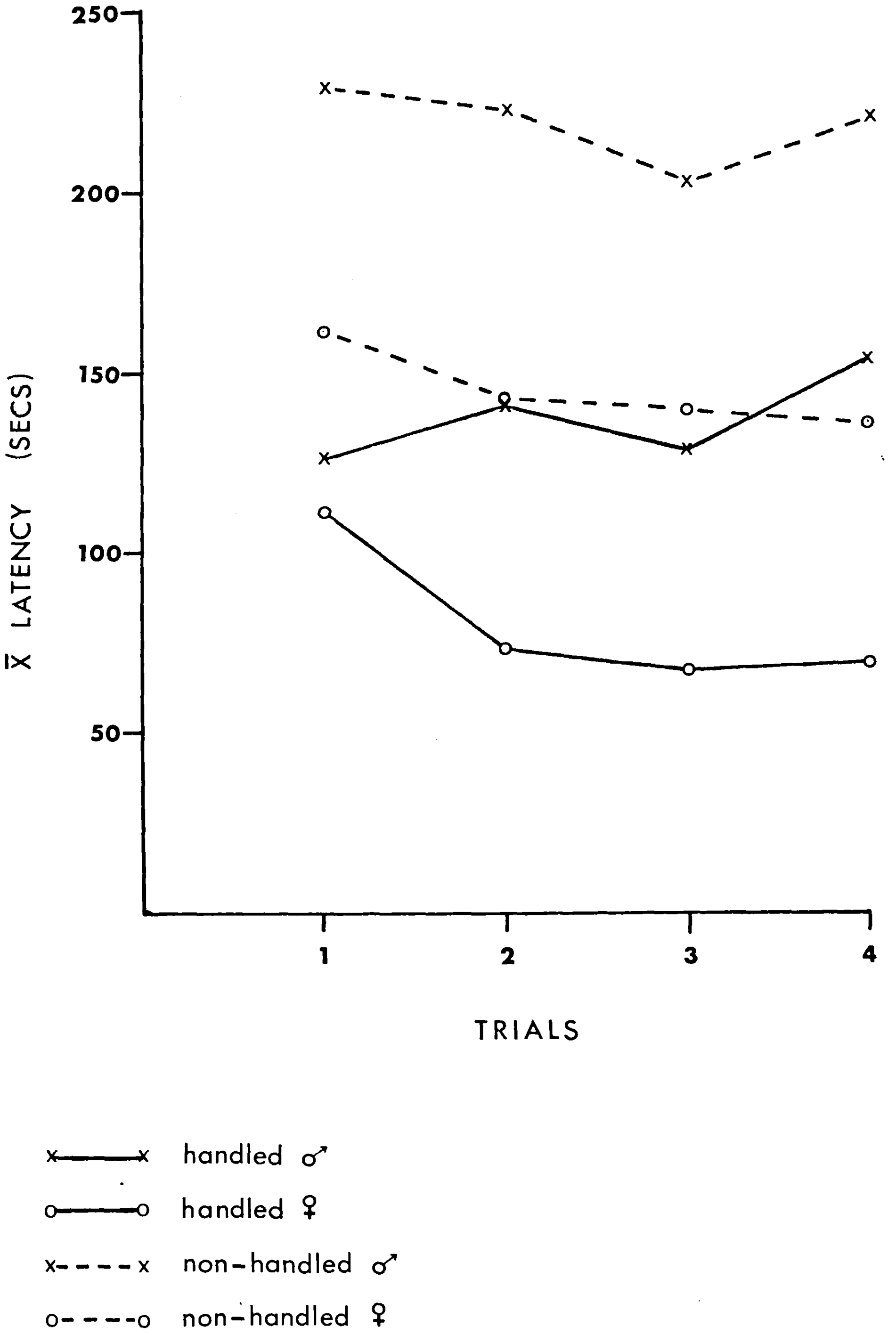
The relatively straightforward differences between the handled and non-handled groups, and between males and females, lead to the conclusion that this experimental measure is more likely to contain a strong component of some general factor (such as locomotor activity or emotionality); Denenberg (in Ambrose, 1969, p. 35), for example, remarks: "When working with measures of emotionality we get big main effects. Interactions are not significant... When looking at measures of exploratory behaviour, however, the situation is much more complicated." Defecation scores (the usual measure of emotionality) are, of course, hardly a practical proposition when the home cage behaviour of group-caged animals is under consideration; but it is interesting that interactions are in fact found in the previous study, since rearing up within the home cage might be thought of as a prelude to sensory rather than motor exploration.

Additional support for this argument is provided by the fact that some workers (e.g. Broadhurst & Eysenck, 1964; Hughes, 1968) have reported that females score higher than males on largely locomotor measures such as ambulation in the open field (although the measure employed by Hughes is difficult to assess since several aspects of exploratory activity are combined under one heading). This sex difference, however, is not observed in an operant situation such as bar pressing for light reinforcement (Wells et al., 1969), and is apparently eliminated by handling in the case of the rearing measure.

The handling procedure is evidently an even more important determinant of behaviour than the sex of the animal in both the home cage measures reported here, although it seems to act in somewhat simpler fashion on home cage emergence than was the case in the rearing measure, where a marked Handling x Sex interaction was found. It should be noted, however, that the findings of this latter study are not entirely compatible with those of an earlier report (Williams & Wells, 1970), and the distinctions that might be made on tho basis of a comparison between the two sets of data presented here may prove to be of less consistency than the rather massive effects of handling in all cases.

FIG. 2

Total emergence from the home cage.


250
200
150
100
50
X̄ LATENCY (SECS)
1
2
3
4
TRIALS
x——x handled ♂
o——o handled ♀
x- - - -x non-handled ♂
o- - - -o non-handled ♀

SOURCE	df	SS	VE	F	P
Handling	1	125715.38	125715.38	11.15	< .01
Sex	1	102573.38	102573.38	9.10	< .01
H x S	1	2128.17	2128.17	0.19	N.S.
Subjects within groups	20	225544.40	11277.22		
Total	23	455961.33			
Trials	3	5706.08	1902.03	1.12	N.S.
T x S	3	6760.38	2253.46	1.33	N.S.
T x H	3	614.04	204.68	0.12	N.S.
T x S x H	3	2335.75	778.58	0.46	N.S.
Trials x Subj. within groups	60	101612.25	1693.54		
Total	95	572989.83			

TABLE 2

Analysis of latency scores for total emergence from the home cage.

Plates 1 - 6

A sequence of home cage emergence

Plate 1.

Plate 2.

Plate 3.

Plate 4.

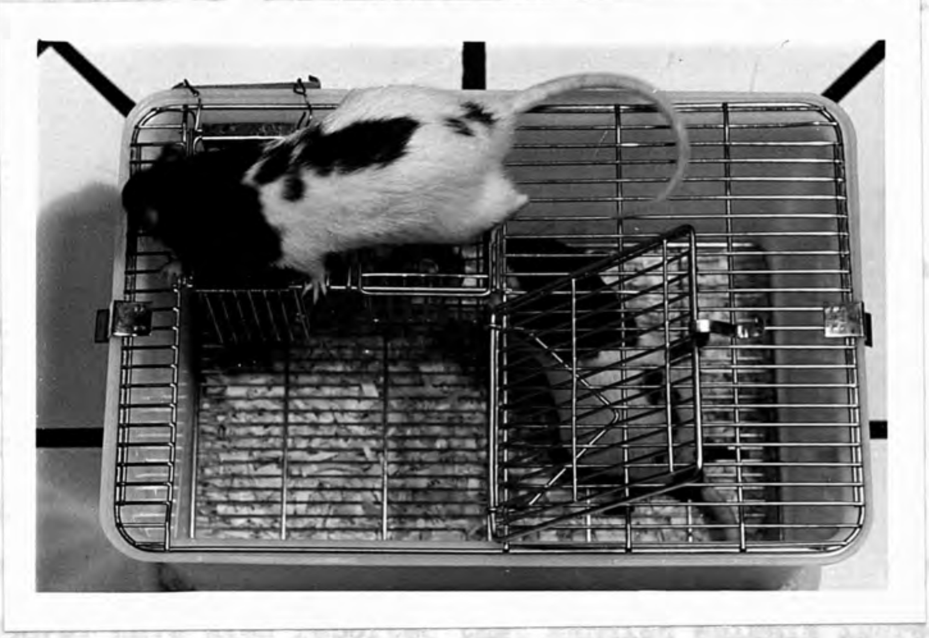


Plate 5.

Plate 6.

EXPERIMENT 3 : Y-Maze Performance Before and After Habituation

Introduction

There is some evidence available that handled and non-handled rats differ behaviourally when first confronted with a novel stimulus situation, but that these differences tend to disappear with time provided that there are no further stimulus changes (Wells et al., 1969; Levine, pers. comm.). DeNelsky & Denenberg (1967a, 1967b) have also reported that handled animals increased their activity as stimulus variation increased, while non-handled controls showed a corresponding decrease. According to these authors, this effect may be demonstrated independently of possible effects of handling on emotionality (see also Whimbey & Denenberg, 1966). On the basis of this finding, they hypothesize that " ... providing a stimulus situation which offers a minimum of potential variation, or which is extremely familiar to the animal, would result in a greater amount of exploratory activity by non-handled than by handled animals."

If this kind of interaction between early experience and stimulus environment can be shown to occur, it would indicate that the groups are influenced by varying kinds or degrees of stimulation rather than that one group has undergone a generalised suppression or enhancement of performance as compared with the other (c.f. Wells et al., 1971). It is therefore proposed that the handled and non-handled groups should be tested both on initial exposure to a simple experimental apparatus (a Y-maze) and after a considerable period of habituation.

Method

Subjects were 20 male and 20 female hooded rats bred from MRC stock. Half of each group had been subjected to the handling procedure previously described; all were otherwise reared under normal laboratory conditions. Testing was carried out when Ss were between 90-100 days old.

The apparatus used was a symmetrical Y-maze with plywood floor and walls of hardboard, measuring 0.26m in height, 0.45m along each arm and 0.11m across the width of each arm. A similar maze, but with the walls constructed of Perspex, is illustrated in Plates 7 and 8. The maze was divided into sections by a line drawn at right angles halfway along each arm and by a triangle drawn at the intersection of the three arms. A section entry was defined as follows: a) when the animal's head and three of its feet had crossed one of the lines halfway along an arm; and b) when at the junction of the arms the animal's head and three of its feet had crossed the line at the entrance to a second arm.

Six identical mazes were used in an overlapping sequence. Ss were placed singly in an arm of the maze facing the choice point, and on the first day of testing were left in the maze for 1 hour. During the first and last minutes of this hour, the following measures were recorded: i) number of sections entered, and ii) number of times S reared up on its hind paws, having touched the ground with a fore-paw since last rearing up. In addition, a record was made of whether defecation or urination had occurred either during the first minute or after the full hour had elapsed. (The second observation would, of course, be inclusive). Ss were then removed from the mazes and replaced in their home cages, and the apparatus was cleaned with an odour-removing disinfectant.

After an interval of approximately 24 hours, each S was re-tested for 1 min. in the same apparatus, with measures recorded as described above.

Results and Discussion

It was initially established that there were no significant differences between either the handled and non-handled groups or between males and females at the end of the first hour of testing on either the sections entered or the rearing measure; in fact, in all cases the scores had virtually reached zero, and are therefore not considered further.

The data for the first minute of Day 1 and for the Day 2 test were then subjected to a three-factor analysis of variance, the sections entered and rearing scores being analysed separately. The results of these analyses are given in Tables 3 and 4. On the sections entered measure, significant differences were found between sexes, with females scoring considerably higher than males, and between trials, as all groups showed a significant increase from the first trial to the re-test 24 hours later (see Fig. 3). However, there were no significant differences attributable to the experimental treatment, although the Handling x Sex x Trials interaction is significant at the .025 level and indicates that the scores for the handled females and the non-handled males increased over the trials compared with those for the non-handled females and handled males.

The rearing measure, however, produced significant differences on all three main factors (Handling, Sex and Trials), with the only significant interaction being that between these three factors. Fig. 4 illustrates that in this case handled animals scored higher than non-handled, and females higher than males, and that there was a tendency for scores to increase from the first to the second trial. However, the presence of a significant three-way interaction indicates that most of this tendency is in fact contributed by one group, that of the handled females, and the graph shows that the handled males have, if anything, the opposite tendency.

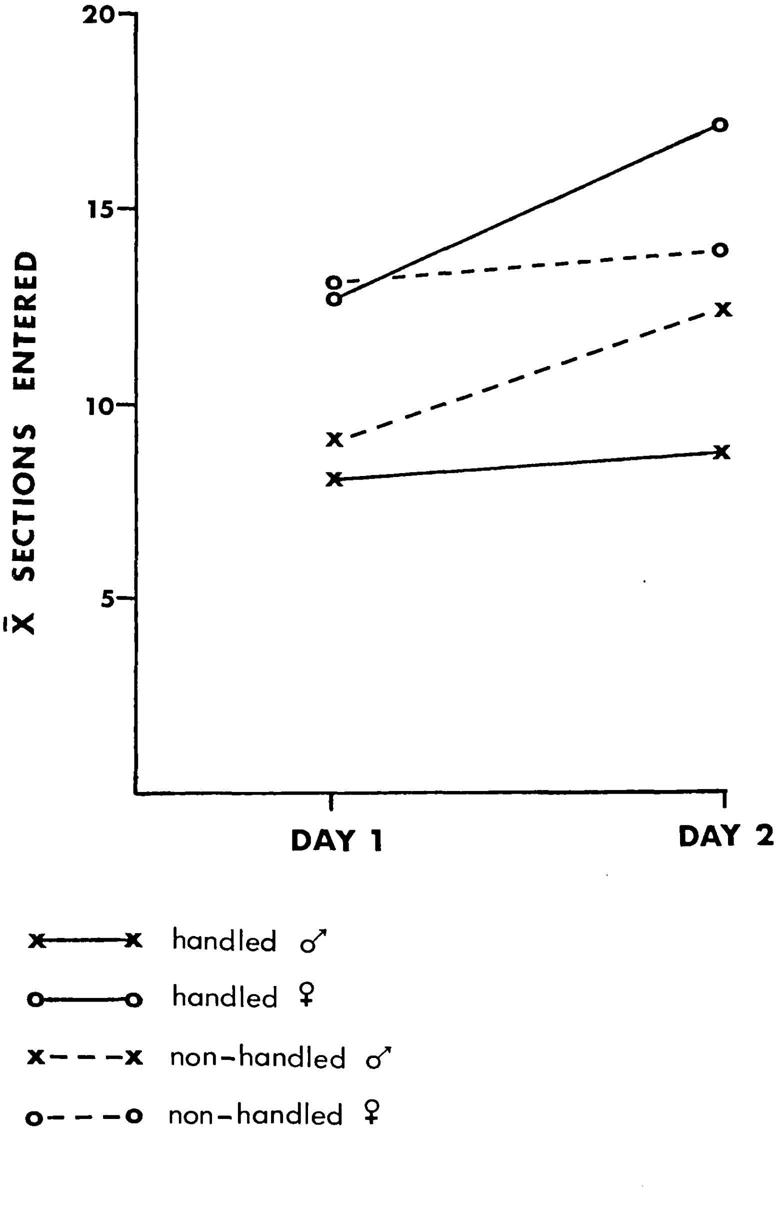
Defecation scores during the time of testing were extremely low for both groups; in the first minute of Trial 1, scores were recorded for 5 of the non-handled group only, and no animal defecated during the re-test. Scores at the end of the habituation period were sufficient for analysis, but no significant differences between the groups were found (X^2 = 0.17, df = 1, N.S.).

The prediction regarding the behaviour of handled and non-handled groups in a highly familiar situation is not entirely fulfilled with respect to either measure, since, as we have seen, the tendency is for all groups to show increased scores on the second trial rather than for the handled group to show a decrease. An explanation in terms of learning theory would probably require a system similar to that proposed by Broadhurst & Eysenck (1964) and involving the interaction of fear responses and inhibitory factors. This would possibly account for the recovery of locomotor activity after 24 hours, and perhaps even the increase reported here, but the lack of sensitivity of the defecation measure produces difficulties for an explanation in terms of fear or emotionality. However, the hypothesis put forward by DeNelsky & Denenberg cannot be rejected outright, since a negative result can always be dismissed on the grounds that the reduction of stimulus variation, or (as in this case) familiarisation with the experimental situation, was not sufficient.

An interesting feature of these results is that the rearing measure is apparently able to discriminate between the handled and non-handled groups where the locomotor measure fails. This gives support to the contention that handling may affect areas of investigatory behaviour rather than activity per se, and is also in agreement with the findings of Experiment 4 (Berlyne box, taken in this case to be a measure of locomotor activity for reasons which are given subsequently), and also Experiments 1 and 2 (rearing within and emergence from home cage). It is perhaps to be expected that sex differences should be more pronounced in the case of the locomotor measure; this point will be discussed in greater detail elsewhere.

FIG. 3

Y-maze performance before and after habituation: 'sections entered' measure.


20
15
10
5
X̄ SECTIONS ENTERED
DAY 1
DAY 2
x——x handled ♂
o——o handled ♀
x– – –x non-handled ♂
o– – –o non-handled ♀

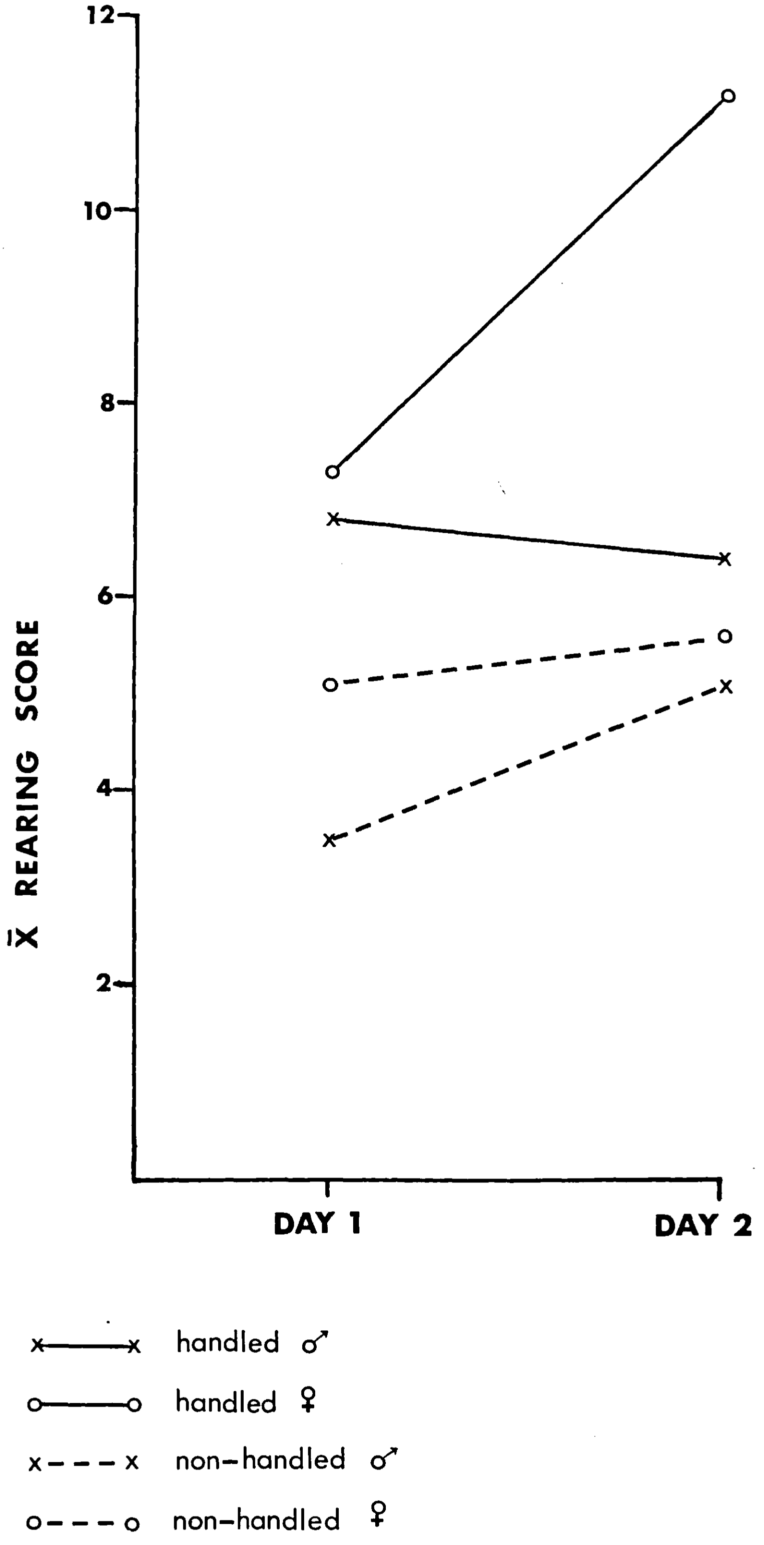
SOURCE	df	SS	VE	F	P
Handling	1	7.20	7.20	0.38	N.S.
Sex	1	451.25	451.25	23.65	< .001
H x S	1	68.45	68.45	3.59	N.S.
Subj. within groups	36	686.90	19.08		
Total	39	1213.80			
Trials	1	125.00	125.00	19.38	< .001
S x T	1	4.05	4.05	0.63	N.S.
H x T	1	0.80	0.80	0.12	N.S.
S x H x T	1	42.05	42.05	6.52	< .025
Trials x Subj. within groups	36	232.30	6.45		
Total	79	1618.00			

TABLE 3

Analysis of "sections entered' measure of Y-maze performance.

FIG. 4

Y-maze performance before and after habituation: 'rearing' measure.


12
10
8
6
4
2
X̄ REARING SCORE
DAY 1
DAY 2
x——x handled ♂
o——o handled ♀
x – – – x non-handled ♂
o – – – o non-handled ♀

SOURCE	df	SS	VE	F	P
Handling	1	192.20	192.20	22.37	< .001
Sex	1	68.45	68.45	7.97	< .01
H x S	1	12.80	12.80	1.49	N.S.
Subj. within groups	36	309.30	8.59		
Total	39	582.75			
Trials	1	39.20	39.20	8.25	< .01
T x S	1	12.80	12.80	2.69	N.S.
T x H	1	2.45	2.45	0.52	N.S.
T x S x H	1	36.45	36.45	7.67	< .01
Trials x Subj. within groups	36	171.10	4.75		
Total	79	844.75			

TABLE 4

Analysis of 'rearing' measure of Y-maze performance.

PLATE 7

Exterior view of Y-maze with indication of scale.

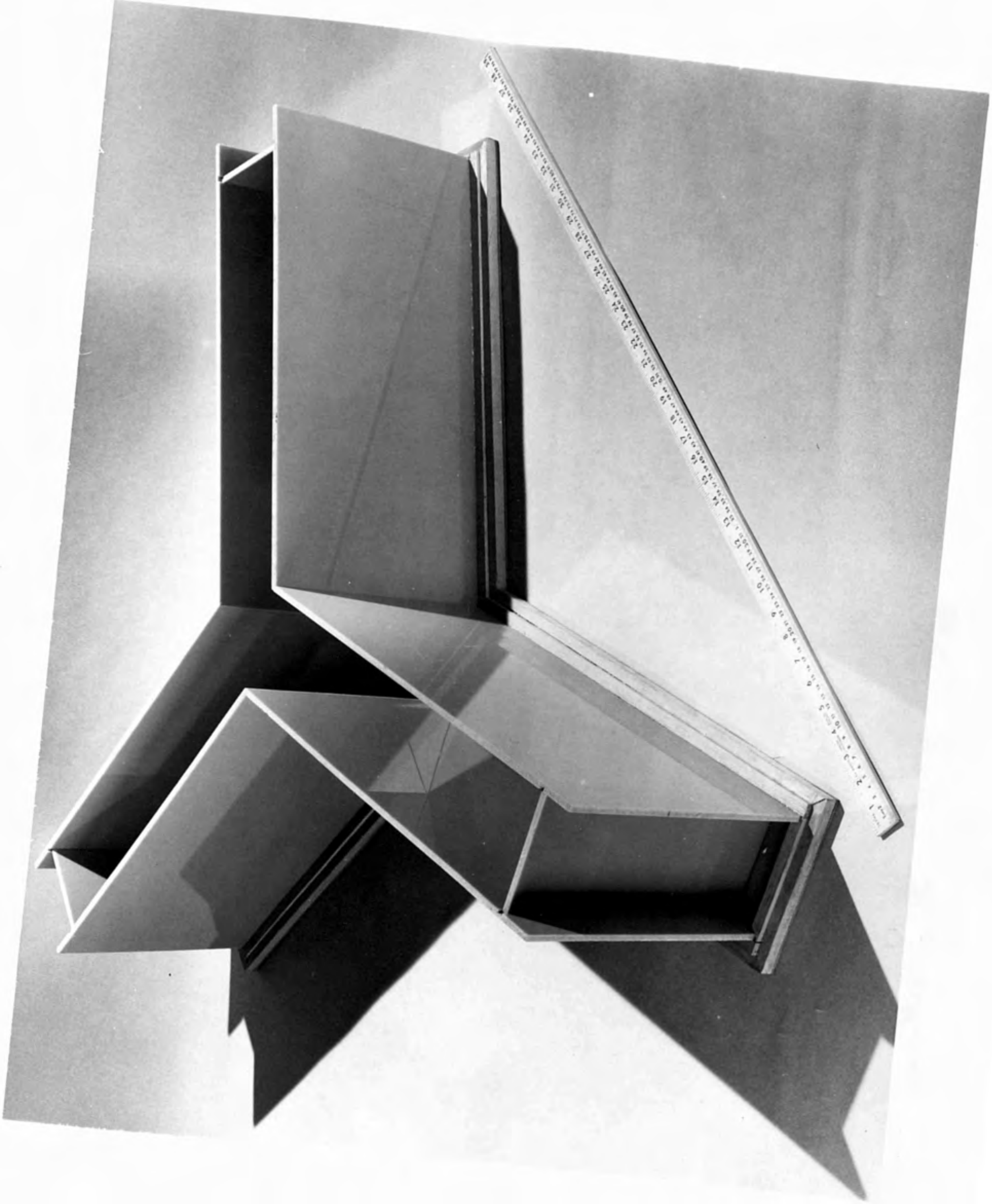
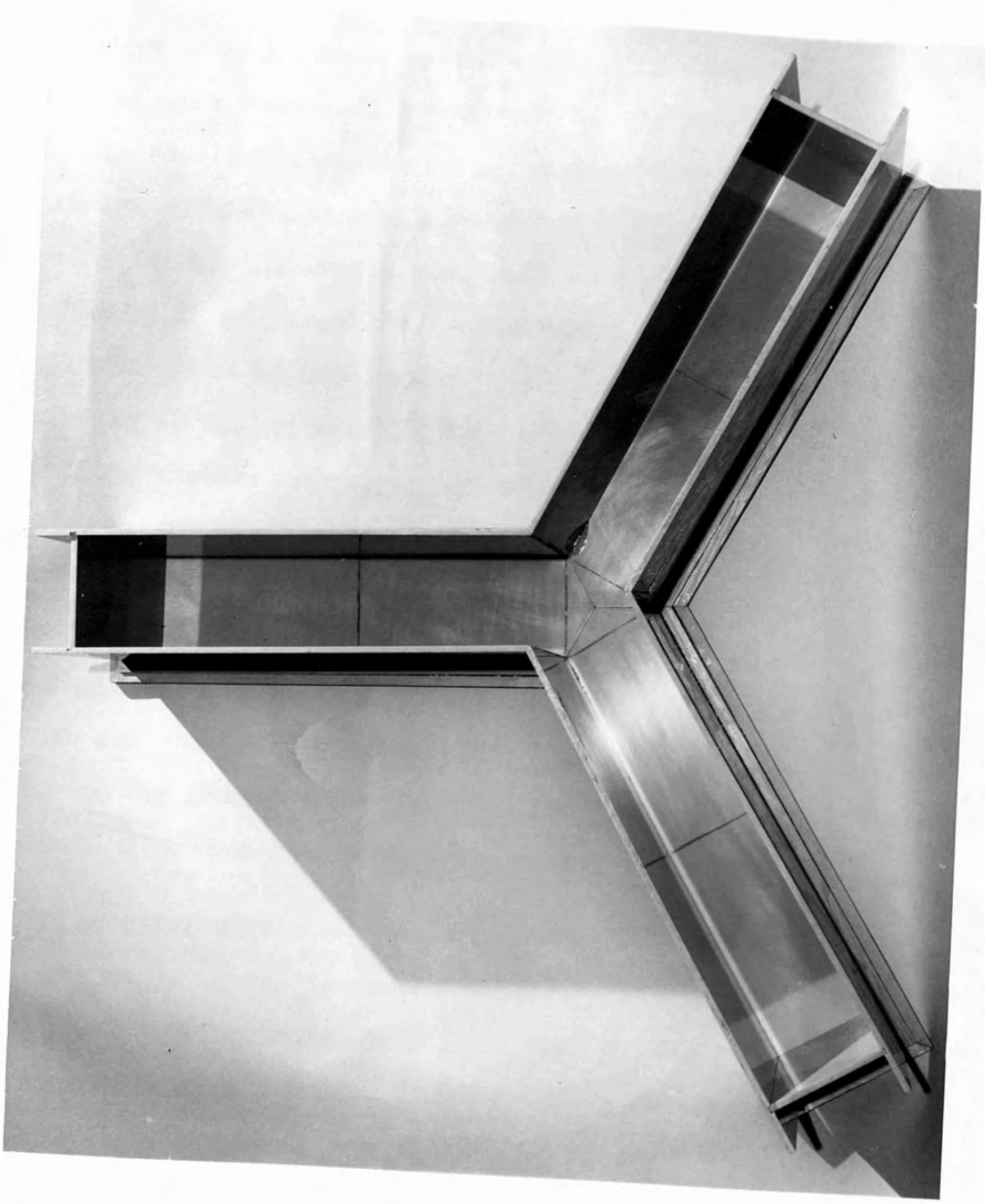


PLATE 8

Interior of Y-maze showing division into sections.



EXPERIMENT 4 : Response to Novel Stimulus (Berlyne Box)

Introduction

The problems involved in the study of locomotor exploration have been well summarised by Berlyne (1960, ch. 5). Briefly, the main difficulties are as follows: firstly, although locomotor activity almost certainly involved a component of exploration, particularly in an unfamiliar environment, it is almost impossible to state at any given moment that exploration is taking place. Secondly, it is by no means clear whether an animal which moves rapidly through the experimental apparatus is engaging in more or less exploration than one which spends most of the available time in the same place; and thirdly, it is logically difficult to distinguish between approach and avoidance tendencies in such a situation, insofar as the animal must be moving away from one set of stimuli in order to approach the next.

These difficulties can be overcome to some extent by closer study of the locomotor activity itself. It can be shown, for example, that rats tend to traverse that part of a maze occupied least recently (Montgomery, 1951, 1952), which indicates that their locomotor responses are ordered rather than random; and there is also some evidence that those animals which move rapidly through a maze also score higher on other measures, such as alternations and rearing up, which appear to indicate exploratory behaviour (Wells et al., 1969). These authors have also shown that the use of an operant situation may prove a more sensitive indicator of exploratory behaviour than would a locomotor measure; in this case, the performance of a group of animals in a baseline condition may be compared with performance when a given stimulus situation is made contingent upon an operant response.

This approach is in accord with Berlyne's (1960) conclusion that " ... it seems preferable ... to resort to a method in which the animal's exploration of one particular stimulus object can be measured separately". Experiments using this kind of technique, in which the number of approaches and/or the amount of time spent in contact with a stimulus object have been recorded, include those by Berlyne (1950, 1955) and Darchen (1952, 1954). It seems likely, therefore, that a measure involving approach to an investigation of an unfamiliar stimulus object would prove to be both capable of distinguishing between the behaviour of handled and non-handled animals, and of permitting the conclusion that any such differences could be attributed to something more specific than changes in the level of general locomotor activity.

Method

Subjects were 36 hooded rats, 18 male and 18 female, bred in the Department of Psychology from MRC stock. Half the animals (equal numbers of each sex) had been subjected to a handling procedure between birth and weaning, as described in the General Methodology section.

Testing was carried out when Ss reached the age of approximately 90 days in a modified version of the 'Berlyne box' (Berlyne, 1955). This was a rectangular box, of similar dimensions to the home cage, constructed entirely of white Perspex with a removeable lid of the same substance.* A stimulus card measuring 55 x 55mm and consisting of two black and two white vertical bars of equal size was visible at the narrow end of a funnel-shaped alcove within the box. A beam of light across the mouth of the alcove triggered a photocell on the opposite side; any breaking of this contact registered on a Rustrak recorder housed some distance from the apparatus. Illumination was provided by a 60w bulb suspended centrally approximately 160mm above the translucent lid of the box.

Ss were given 5 trials, each of 3 mins. duration, with an inter-trial interval of approximately $2\frac{1}{2}$ hours. On each trial the number of occasions on which the animal

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*I am indebted to the Department of Psychology, University of Hull, and in particular to Dr. D.I. Williams, for the loan of this apparatus.

entered the alcove containing the stimulus was recorded as described above, and defecation scores were also noted. Between trials, the apparatus was cleaned with an odour-destroying disinfectant.

Results and Discussion

An analysis of variance was carried out on the scores, and the results are shown in Table 5. No significant effects due to the main variables of Handling or Sex were found, but the effect of Trials was significant beyond the .001 level and there was a significant Sex x Trials interaction. Fig. 5 illustrates a general decrease in responding over trials for all groups. There were no other significant interactions, and no significant differences between groups were found with respect to the defecation scores ($X^2 = 6.5$; df = 4; N.S.)

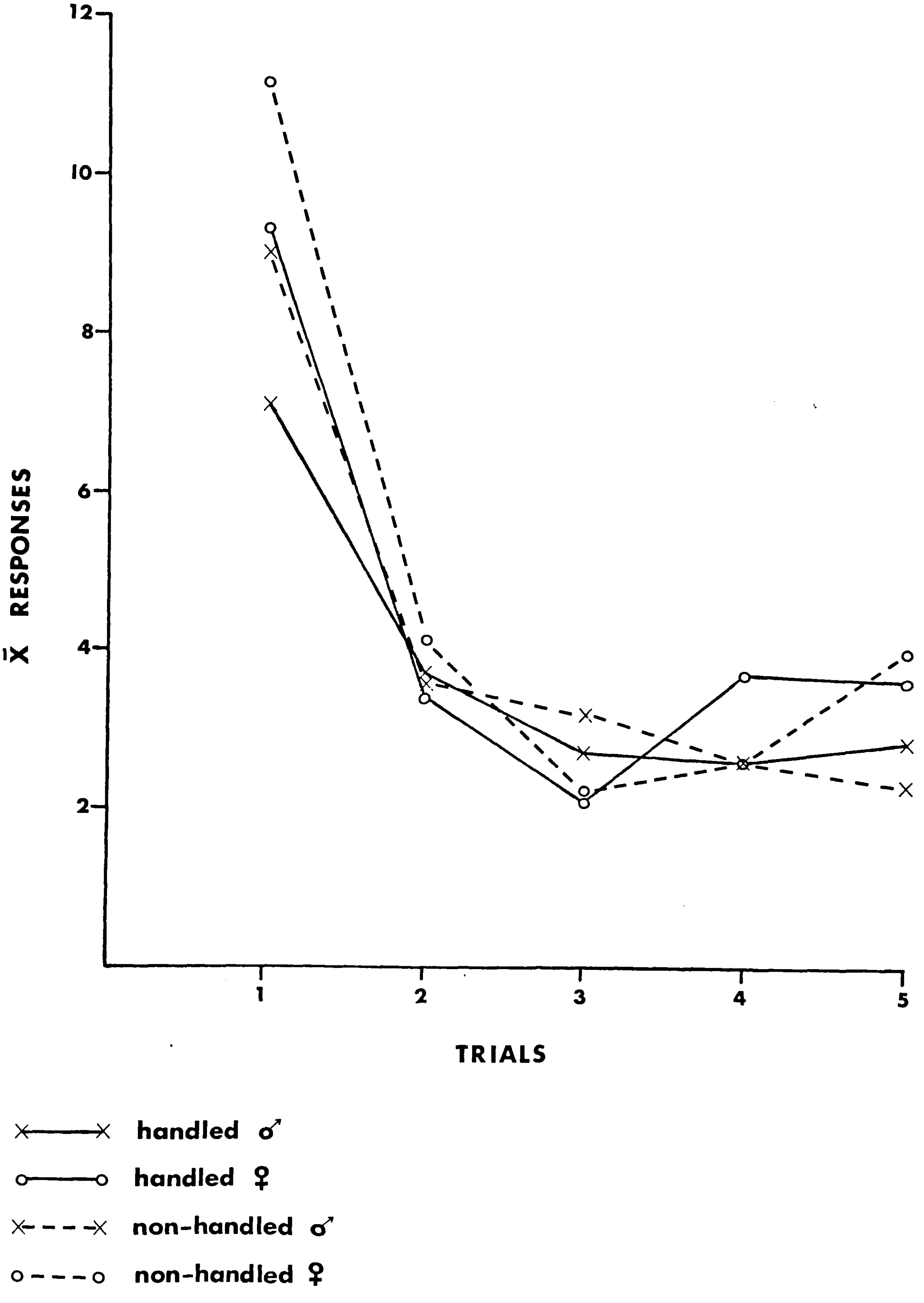
It is therefore apparent that either the handling procedure was ineffective in producing differences between the experimental groups, or that the measures used here were not sufficiently sensitive in revealing any such differences. An attempt was made to clarify the situation by testing each animal for 3 mins. in an open field apparatus, but no significant differences were found between the groups on either activity or defecation measures. This is in contrast to results reported by other workers, who have found this situation capable of discriminating both between reactive and non-reactive strains (Broadhurst & Eysenck, 1964) and between handled and non-handled animals (Denenberg, Karas, Rosenberg & Schell, 1968). However, there are two possible objections here; firstly, differences between groups may be minimal on the first day of testing, at least in the open field (Whimbey & Denenberg, 1967), in which case further testing would have been necessary here; or, alternatively, since the open field test was carried out after testing in the Berlyne box, it could always be argued that any potential differences might have been eliminated by the handling and other experimental procedures undergone by all subjects.

Before concluding, however, that the handling procedure was ineffective in this instance, it is worth considering the experimental situation itself in more detail. There are several problems here. In the first place, the measure used may not have been sampling behaviour which would characterise differences between handled and non-handled animals, especially if the time spent entering the alcove represented only a small component of the animals' total behaviour. This argument, however, must be treated with caution, as it could always be used where no significant differences between groups were found. Secondly, the lack of differences seems unlikely in view of the large body of literature which has reported such differences (although the present author has been consistently unable to differentiate between groups in terms of defecation scores alone, as is borne out by other experiments in this series). Thirdly, since animals were reared in translucent white cages, differences between the home environment and the testing situation may have been slight. This argument, however, loses some force in view of the results obtained using other home-cage procedures (c.f. Expts. 1 and 2).

Finally, there is some evidence from a subsequent experiment (No. 6) that a two-dimensional visual stimulus of the kind employed here is inadequate in engaging the attention of this particular species, whereas stimulus objects of a different nature may be capable of doing so (Expt. 5).

FIG. 5

Responses to a visual stimulus in the Berlyne box over successive trials.


12
10
8
6
4
2
X̄ RESPONSES
1
2
3
4
5
TRIALS
handled ♂
handled ♀
non-handled ♂
non-handled ♀

SOURCE	df	SS	VE	F	P
Handling	1	6.05	6.05	0.68	N.S.
Sex	1	19.34	19.34	2.16	N.S.
H x S	1	0.01	0.01	0.00	N.S.
Subj. within groups	32	286.66	8.96		
Total	35	312.06			
Trials	4	1091.52	272.88	61.74	< .001
S x T	4	43.63	10.91	2.47*	< .05
H x T	4	28.70	7.18	1.62	N.S.
S x H x T	4	5.97	1.49	0.34	N.S.
Trials x Subj. within groups	128	565.78	4.42		
Total	179	2047.66			

* The quadratic trend component of this interaction is significant ($F = 8.18$, df = 1,128, $p < .01$).

TABLE 5

Analysis of responses to a visual stimulus in the Berlyne box.

EXPERIMENT 5 : Response to Novel Objects

Introduction

Although it has been demonstrated (Expt. 4) that a modified Berlyne box containing a visual stimulus is not a situation which will distinguish between the behaviour of handled and of non-handled animals, it is possible that an earlier technique developed by Berlyne and others (Berlyne, 1950, 1955; Barchen, 1952, 1954) might prove more suitable, bearing in mind the sensory capacities of the rat. Previous experiments in this laboratory had suggested that not only could the investigatory behaviour of handled and non-handled animals be distinguished in this way, but that such differences might still be obtained when a drastically simplified procedure was employed (Lawlor & Masoliver, pers. comm.).

The technique is to some extent similar to that used in the previous experiment, in that it requires that a stimulus object should be presented and the amount of contact made by S recorded; but the major differences between this and the Berlyne box are that in this case a free-standing three-dimensional object, rather than a two-dimensional one, is used, and that the situation allows for manipulation and other contacts with the object rather than visual inspection alone.

It is therefore hypothesized that this situation will elicit behavioural differences between the experimental groups which can be described as investigatory in nature, and also that some information will be obtained with respect to the behaviour of the two groups over successive trials.

Method

Ss were 40 hooded rats, 20 male and 20 female, of which half had been handled during infancy and half left undisturbed as previously described. All animals were tested when they reached the age of approximately 90 days.

The testing apparatus consisted of a metal-sided box measuring 0.4m in length, 0.265m in width and 0.23m in height, with a floor covered by black plastic material and a lid of clear Perspex (Plate 9). A total of 6 minutes' testing time for each animal was subdivided as follows:

a) Adaptation. Each S was removed from the home cage and placed in the empty box for a period of 2 minutes. The behaviour of the animals was observed during this time, but no formal measures were taken.

b) Object 1. Immediately following the previous phase, the box was opened and two small wooden cubes measuring 0.02m along each side were placed in the end of the box

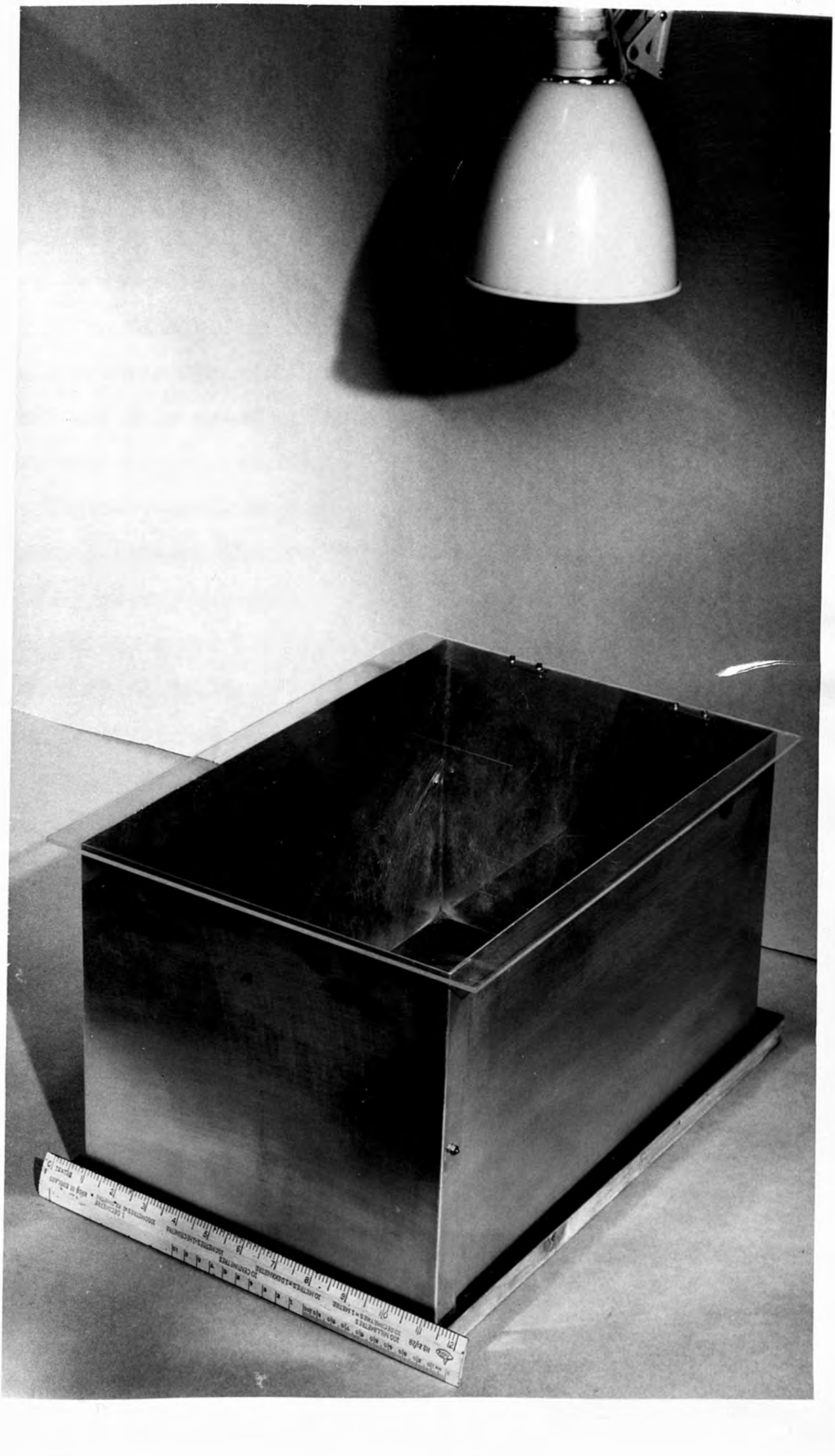
nearest to E, approximately 0.08m from each wall and with a similar space between them; the lid of the box was then closed. The following measures were taken during the succeeding two minutes:
i) latency of approach to either cube, in seconds;
ii) amount of time during the 2-min. test period spent by S oriented towards and in contact with either cube. 'Contact' was defined as either immediate proximity of S's nose, together with rhythmic movements of the vibrissae, or as touching or manipulation of the objects with forepaws or teeth.

c) Object 2. For the final 2 minutes, procedure was as described in section (b) above, except that a cardboard ring 0.04m in diameter and 0.02m high was placed between the two cubes, and the latency and 'time in contact' measures were taken with respect to the ring only.

Each animal was given 4 trials under these conditions, with an inter-trial interval of approximately 24 hours. The apparatus and stimulus objects were washed between trials with an odour-destroying disinfectant, or (in the case of the cardboard rings) replaced when necessary.

PLATE 9

Box used in test of response to novel objects.



Results and Discussion

An analysis of variance was carried out on each measure (Tables 6 to 9) and the major effects are illustrated in Figs. 6 to 9. It is apparent that in all cases there is a highly significant difference between the handled and non-handled groups, with the handled animals approaching the novel objects more quickly and also spending more time in contact with them. Contrary to the findings of some workers (e.g. Hughes, 1968), however, there is no significant difference between the scores for males and females in either group, and it is tempting to speculate that sex differences are likely to be most appparent where the measure of exploratory behaviour employed has a strong 'activity' component, as opposed to the 'investigatory' aspect which is stressed here. (See also Wells et al., 1969).

The four measures taken are also fairly consistent in that all except one (namely 'time investigating Object 1', on which the Handling factor alone was significant) show both a significant effect of Trials and also a significant Handling x Trials interaction, with no other significant main effects or interactions. The significant effect of Trials must, however, be regarded in the light of the Handling x Trials interaction, which reveals that the non-handled group showed both a reduced latency and an increase in time spent investigating the objects as the trials progressed. The handled group, on the other hand, spent approximately the same amount of time in investigation on each trial; but the latency scores for this group are probably suffering from a ceiling effect attributable to the fact that many Ss tended to be investigating the objects even before they had been correctly positioned in the box. Latency scores were therefore extremely low, and showed little change over trials.

There is little doubt that this test can effectively distinguish between handled and non-handled animals, and that although a locomotor component cannot be entirely excluded, it is at least reduced to a minimum as compared with open field and maze situations. Although differences between handled and non-handled animals may be found in these circumstances, they are often along the dimension of 'emotionality' (Denenberg, 1962, 1964), as defined in terms of defecation or urination in the test situation. These scores were recorded in the present study, but although there was a general tendency for scores to decrease over successive trials, no significant differences between the groups were found ($\chi^2_r = 3.33$, $p = 0.389$). It is possible that strain differences may account for this discrepancy; if not, any theory attempting to explain the differences between handled and non-handled animals in terms of emotionality must construct a definition of this term which takes no account of the usual criteria.

The results of this experiment seem to imply that, under certain conditions, non-handled animals can 'adapt' to an unfamiliar stimulus situation over time so that their performance finally approaches that of the handled group. (It should be noted, however, that the performance curves for the two groups do not in fact intersect, and it is by no means clear whether the non-handled group would ever have manifested the range of behaviours referred to below). This finding raises some important points of discussion.

In the first place, it is often assumed by workers in this field (e.g. discussion in Ambrose, 1969, p. 38-41) that, under laboratory conditions, the non-handled group are in some sense 'deprived' in comparison with the handled animals, and that handling or other forms of stimulation during infancy have some compensatory effect whereby the recipients are restored to a near-normal condition. However, although there is little evidence in the literature by way of direct comparison, the non-handled rat seems behaviourally closer to the supposedly non-deprived wild rat (c.f. Barnett, 1958). This leaves open the question of whether the handled rat, in its confidence and willingness to explore new situations, is in any real sense 'better adapted', or whether it has been thus considered merely because of its suitability for laboratory procedures.

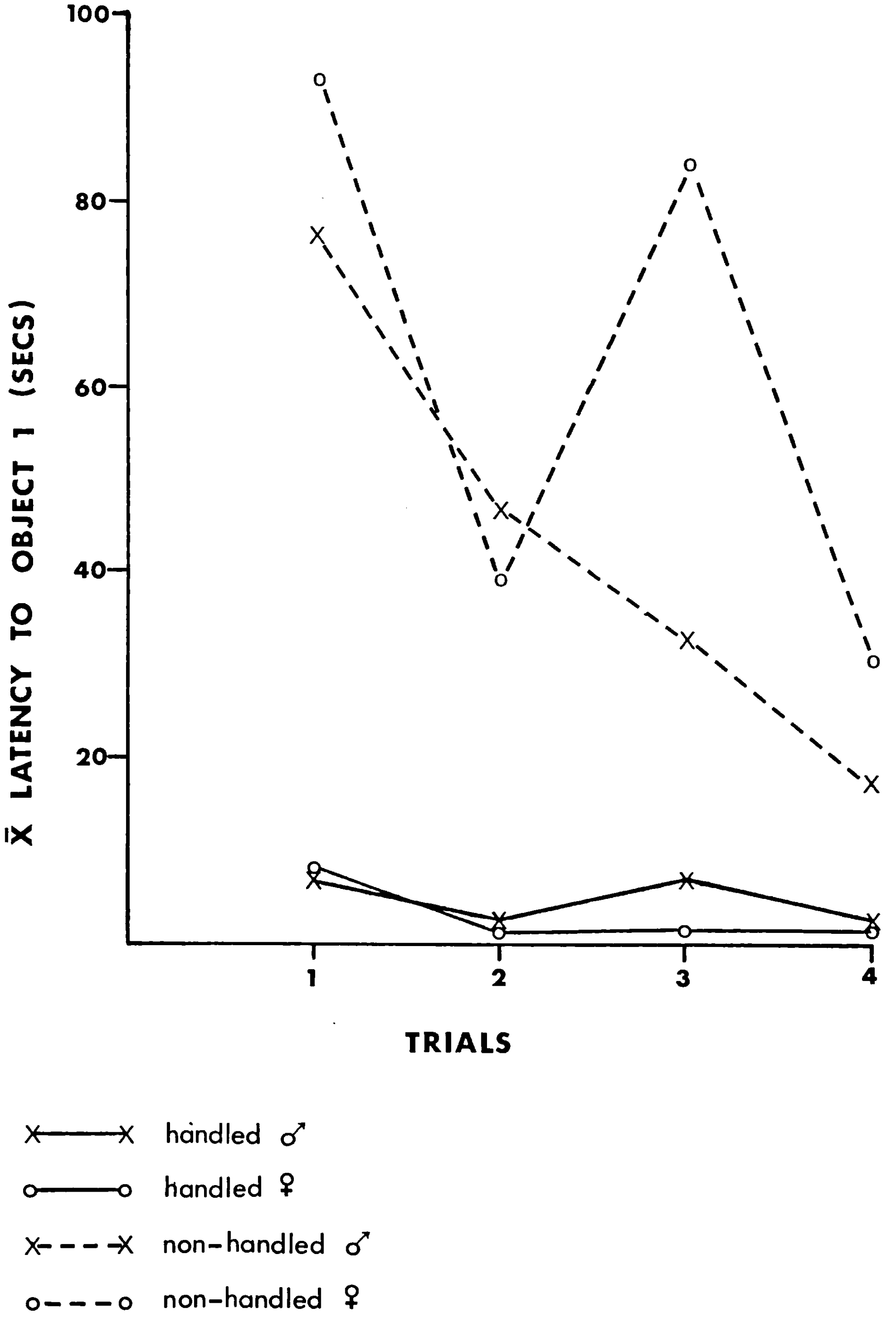
A second point of interest is that the handled rats in this situation showed a much wider range of responses to the test objects than did the non-handled animals. Although this is not demonstrated directly by the data presented (which shows only quantitative rather than qualitative information), the accompanying photographs (Plates 10 to 11) illustrate the point to some extent. It is also confirmed by a second observer (MML) who was present during most of the testing in this experiment. While the non-handled animal typically 'freezes' in a corner or against a wall of the apparatus (at least in the initial trials), at the same time showing a marked orientation response to the objects (Plates 10a, 10b), the handled animal employs a variety of procedures ranging through sniffing, biting, carrying in the teeth, chewing, manipulation with the front paws (and, in one case, kicking with a hind paw), scent marking, pushing with the nose, rolling the cardboard ring, and moving about the apparatus with the ring encircling the nose. Some of these activities are depicted in Plates 11a to 11e. The contrast between the behaviour of the two groups is strongly reminiscent of the distinction drawn by Hutt (in Jewell & Loizos, 1966) between exploratory behaviour and play in children, the former characterised by the phrase, "What does this object do?" and the latter by, "What can I do with this object?" This parallel cannot be drawn too closely, of course, particularly since the conditions of the present experiment make no provision for exploratory behaviour which may depend on distance receptors alone, nor for any distinction between play and exploration; but it is perhaps worth bearing in mind that play behaviour in the higher mammals can rarely be elicited unless the organism has made itself familiar with its immediate surroundings, presumably in order to reduce their fear-evoking properties (c.f. Harlow & Zimmermann, 1958).

Finally, it should be stressed that although the behaviour of handled and non-handled animals was in general readily distinguishable as soon as the test objects were placed in the apparatus, there was no perceptible differences between the groups in the adaptation period. Unfortunately, no provision had been made for recording behaviour at this stage, since it had not been intended to form part of the testing procedure; but once again both observers were agreed in being unable to detect any major differences between experimental and control animals when these were first placed in the apparatus. This is in contrast to other studies, for example those employing various forms of Y-maze, where the groups are usually distinguishable even when the experiment is nominally run 'blind'. It is possible that the similarity of dimensions between the home cage and the test apparatus acted in this case to reduce initial fear responses, which were shown only by the non-handled group when the novel objects were introduced.

These observations, however, are subsidiary to the main result of the experiment, which has shown conclusively that early handling can produce an effect upon investigatory behaviour rather than locomotor activity or emotionality alone; and that, over the period studied, handled animals show little change in their comparatively high level of investigatory behaviour, whereas non-handled animals tend to show an increase from an initial comparatively low level. The sex differences characteristic of most locomotor measures were not, however, obtained.

FIG. 6

Latency scores to presentation of first novel object (wooden cubes) over successive trials.


100
80
60
40
20
X̄ LATENCY TO OBJECT 1 (SECS)
1
2
3
4
TRIALS
X——X handled ♂
o——o handled ♀
X- - -X non-handled ♂
o- - -o non-handled ♀

SOURCE	df	SS	VE	F	P
Handling	1	95111.26	95111.26	82.41	< .001
Sex	1	2830.81	2830.81	2.45	N.S.
H x S	1	3831.81	3831.81	3.32	N.S.
Subj. within groups	36	41549.96	1154.17		
Total	39	144323.84			
Trials	3	23763.32	7921.11	8.12	< .001
T x S	3	3831.82	1277.27	1.31	N.S.
T x H	3	16232.77	5410.92	5.54*	< .001
T x S x H	3	5109.12	1703.04	1.74	N.S.
Trials x Subj. within groups	108	105406.72	975.99		
Total	159	298667.59			

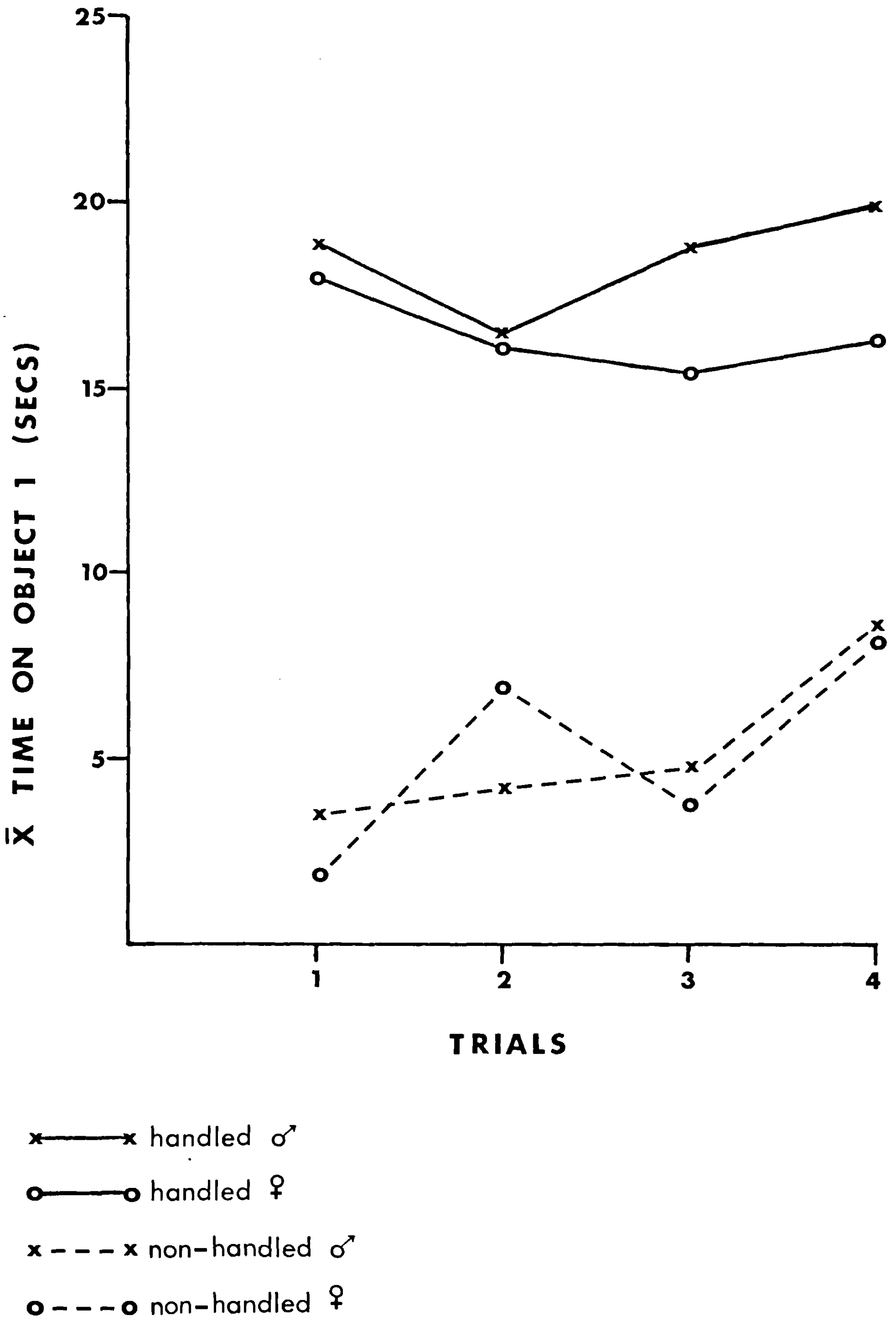
* The linear and cubic trend components of this interaction are significant (F = 11.86, df = 3,108, p < .001; and F = 4.73, df = 3,108, p < .05 respectively).

TABLE 6

Analysis of latency scores to Object I.

FIG. 7

Amount of time spent investigating first novel object (wooden cubes) over successive trials.


25
20
15
10
5
X̄ TIME ON OBJECT 1 (SECS)
1
2
3
4
TRIALS
x——x handled ♂
o——o handled ♀
x - - - x non-handled ♂
o - - - o non-handled ♀

SOURCE	df	SS	VE	F	P
Handling	1	6039.31	6039.31	113.65	< .001
Sex	1	51.76	51.76	0.97	N.S.
H x S	1	37.06	37.06	0.70	N.S.
Subjects within groups	36	1913.11	53.14		
Total	39	8041.24			
Trials	3	189.87	63.29	2.24	N.S.
S x T	3	73.22	24.41	0.86	N.S.
H x T	3	202.07	67.36	2.38	N.S.
S x H x T	3	27.82	9.27	0.33	N.S.
Trials x Subj. within groups	108	3053.77	28.28		
Total	159	11587.99			

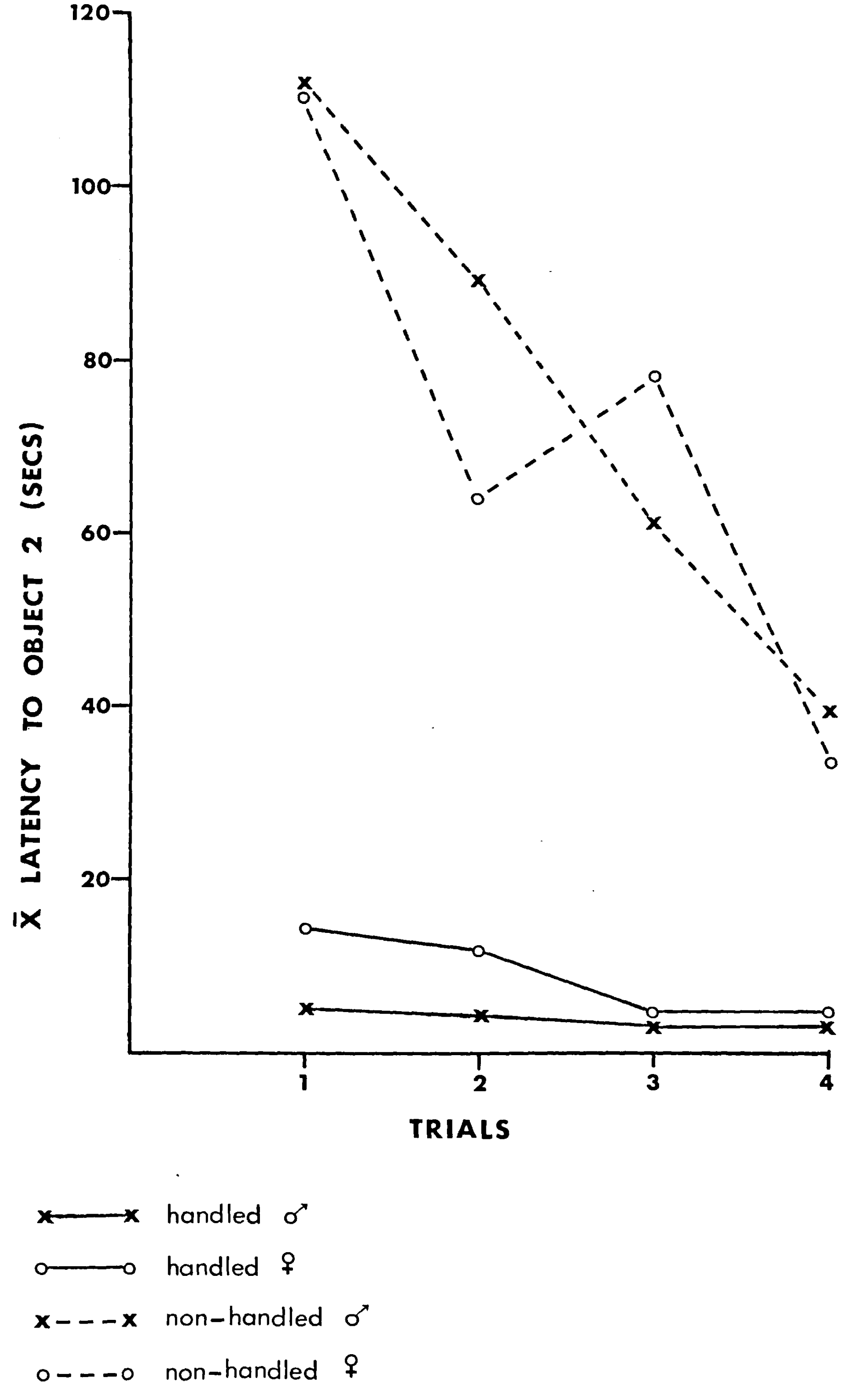
TABLE 7

Analysis of time spent investigating

Object I.

FIG. 8

Latency scores to presentation of second novel object (cardboard ring) over successive trials.


X̄ LATENCY TO OBJECT 2 (SECS)
120
100
80
60
40
20
1
2
3
4
TRIALS
x——x handled ♂
o——o handled ♀
x---x non-handled ♂
o---o non-handled ♀

SOURCE	df	SS	VE	F	P
Handling	1	180499.23	180499.23	116.83	<.001
Sex	1	7.23	7.23	0.00	N.S.
H x S	1	756.90	756.90	0.49	N.S.
Subj. within groups	36	55621.24	1545.03		
Total	39	236884.60			
Trials	3	33350.15	11116.72	13.43	<.001
T x S	3	1710.43	570.14	0.69	N.S.
T x H	3	24083.13	8027.71	9.70*	<.001
T x S x H	3	2959.45	986.48	1.19	N.S.
Trials x Subj. within groups	108	89375.34	827.55		
Total	159	388363.10			

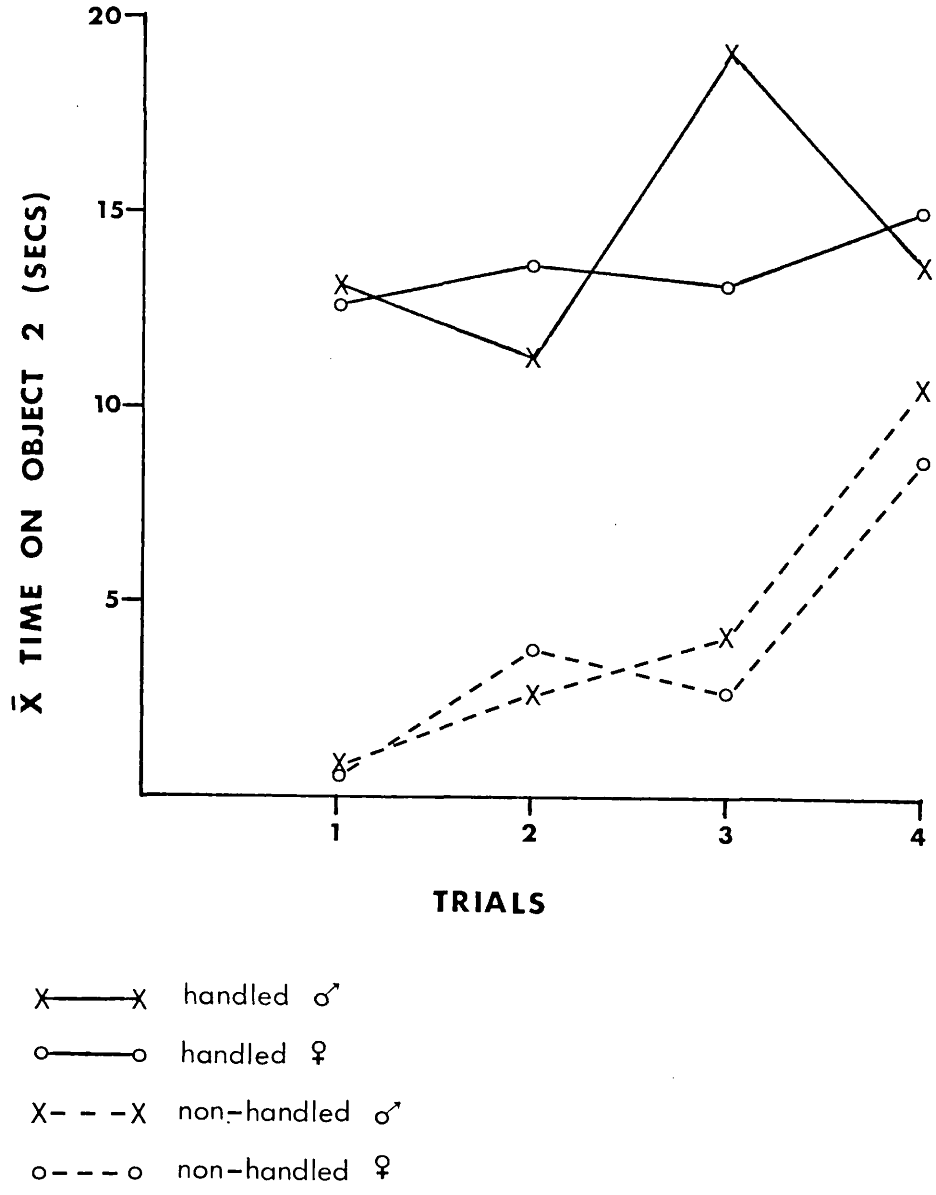
* The linear trend component of this interaction is significant (F = 26.82, df = 3,108, p < .001)

TABLE 8

Analysis of latency scores to Object II

FIG. 9

Amount of time spent investigating second novel object (cardboard ring) over successive trials.


20
15
10
5
X̄ TIME ON OBJECT 2 (SECS)
1
2
3
4
TRIALS
X——X handled ♂
o——o handled ♀
X- - -X non-handled ♂
o- - -o non-handled ♀

SOURCE	df	SS	VE	F	P
Handling	1	3822.03	3822.03	64.30	< .001
Sex	1	21.03	21.03	0.35	N.S.
H x S	1	0.40	0.40	0.01	N.S.
Subj. within groups	36	2139.94	59.44		
Total	39	5983.40			
Trials	3	606.65	202.22	4.14	< .01
T x S	3	155.53	51.84	1.06	N.S.
T x H	3	394.73	131.58	2.69*	< .05
T x S x H	3	79.45	26.48	0.54	N.S.
Trials x Subj. within groups	108	5276.64	48.86		
Total	159	12496.40			

* None of the trend components of this interaction reaches significance.

TABLE 9

Analysis of time spent investigating Object II.

PLATES 10a, 10b

Characteristic responses of non-handled rats to novel objects.

Plate 10a.

Orientation to wooden cubes

Plate 10b.

Orientation to cardboard ring

PLATES 11a, 11b, 11c, 11d, 11e

Characteristic responses of handled rats to novel objects.

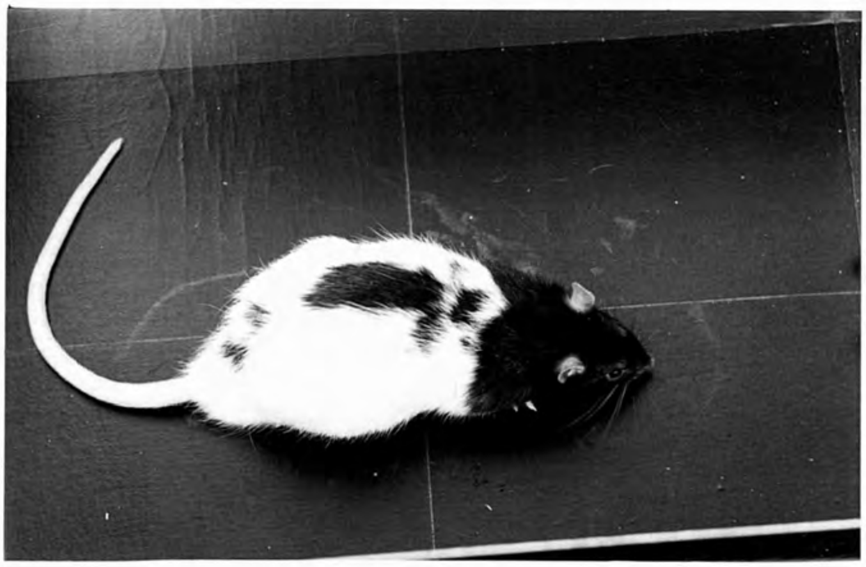


Plate 11a.

Adaptation period (no apparent behavioural differences between handled and non-handled animals).

Plate 11b.

Investigation of wooden cube

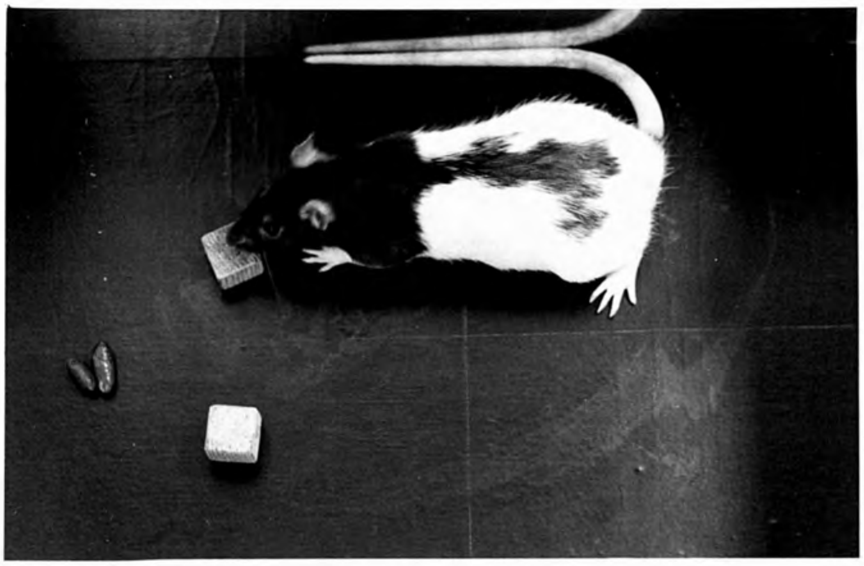


Plate 11c.

Wooden cube carried in mouth

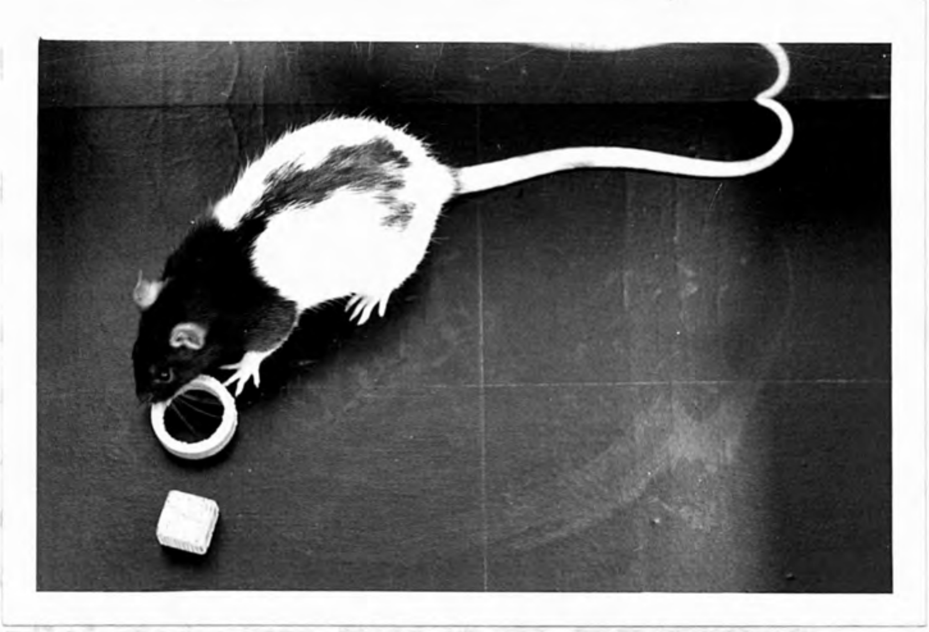


Plate 11d.

Investigation of cardboard ring

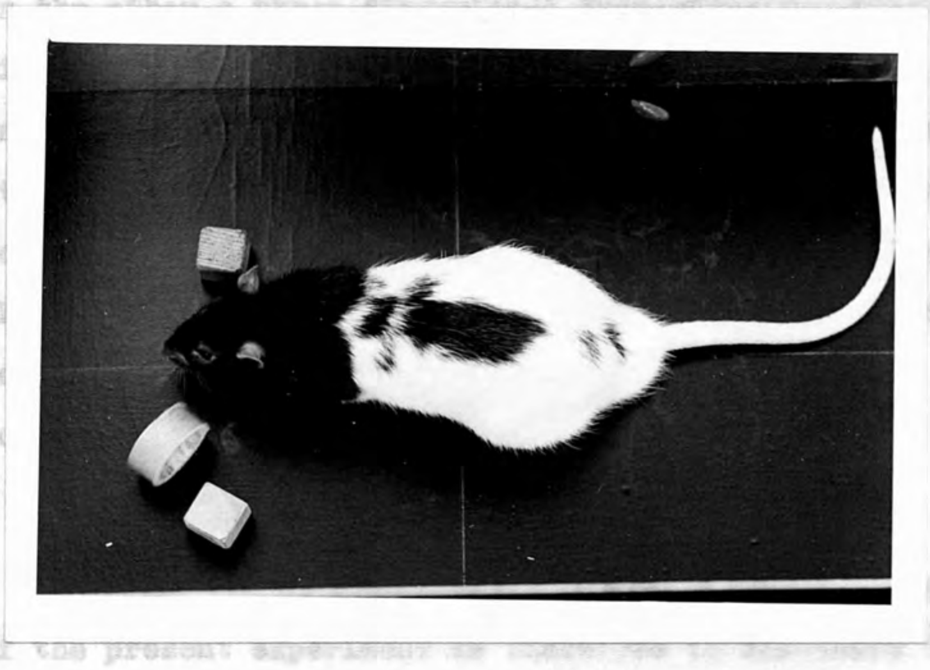


Plate 11e.

Cardboard ring turned on edge and rolled

EXPERIMENT 6 : Response to Vertical Stripes

Introduction

This experiment provides a link between Expt. 4 (Berlyne box) and Expt. 5 (response to novel objects). It will be recalled that in the former case no significant differences between handled and non-handled animals were found, whereas in the latter significant differences between handled and non-handled groups were found on all four measures.

The major difference between the two experimental situations lies in the nature of the stimuli presented (in one case a two-dimensional visual stimulus , and in the other a three-dimensional free-standing object). Since no differences between handled and non-handled animals were observed in response to the two-dimensional stimulus, but marked and highly significant differences were found in response to the three-dimensional object, the effect of the handling procedure cannot adequately be described in terms of a generalised increase in activity or decrease in emotional factors, but leads to a much more rigorously defined behavioural syndrome.

This point is a critical one, and the main purpose of the present experiment is therefore to eliminate the possibility that the difference between the results of Expts. 4 and 5 was due to some experimental artefact arising from slight differences in the nature of the apparatus used or in the handling procedures with differing batches of animals. Unless the possibility of such artefacts can be confidently excluded, the more important conclusions concerning the nature of the differences in response cannot be fully justified.

Method

Six handled and six non-handled hooded rats (3 male and 3 female in each group) were chosen at random from among those animals which had already been found to differ with respect to the handling variable on the test for response to novel objects (Expt. 5). These 12 Ss were now each tested for 3 mins. in the same apparatus as was used in Expt. 5, except that the vertical striped stimulus used in Expt. 4 was fixed to one end wall with black masking tape approximately 50mm. from the floor of the box. The amount of time spent by each S in investigating this stimulus (as defined in Expt. 5) was recorded.

Results and Discussion

The mean times, in secs., spent by each of the four groups in investigating the stimulus were as follows:

	Handled	Non-handled
Male	4.2	4.0
Female	4.C	4.0

There are no significant differences between the groups on this measure. The range of means, or rather the lack of range, indicates that they may be regarded as a kind of baseline measure of the performance of both handled and non-handled groups in a 'neutral' environment, comparable to the scores reported by Wells et al. (1971) for Ss in an operant situation before response-contingent stimulation was introduced. Similarly, both the author and the second observer (MML) were unable to discern any behavioural differences between handled and non-handled animals in terms of pre-test activity in Expt. 5, whereas the groups were immediately distinguishable on the introduction of the test objects.

A typical response to the vertical striped stimulus is illustrated in Plate 12, which may be compared with Plates 11a to 11e.

This experiment also indicates that the Berlyne box experiment (No. 4) was probably not sampling the investigatory behaviour of the animals with respect to a specific stimulus, but was sampling a rather limited form of generalized locomotor activity instead. This interpretation allows us to reconcile the results of the two experiments by reference to the nature of the stimulus situation, as suggested above.

Plate 12.

A typical response to the vertical striped stimulus

III. GENERAL CONCLUSIONS

Taken together, these experiments give a strong indication that early handling may indeed affect cognitive processes such as investigatory behaviour. Although we cannot conclude with certainty that this occurs independently of locomotor activity, there is some evidence in support of this conjecture, and even more to indicate that emotionality (as defined in terms of defecation scores) is not a major underlying factor.

It is striking, however, to note the extent to which differences between handled and non-handled animals appear to be situation-specific (and in fact, the same could be said of differences between the sexes). Thus in a comparatively short series of experiments we have been able to demonstrate highly significant differences between the groups (Expts. 2 and 5), no apparent differences (Expts. 4 and 6), differences which are demonstrable on one measure of behaviour but not on another (Expt. 3) and differences which are manifested only in association with some other factor (Expt. 1). Although we have been able to reconcile these findings through consideration of the specific situations in question, it is perhaps unfortunate that so few negative reports are available in the literature, since these would almost certainly throw further light on the processes involved. However, one of the few studies to compare performance in a variety of testing situations (Smith, 1967), using mice as subjects, has found that there do exist situations where the non-handled group excel - such as an easy rather than a difficult learning task.

It is also unfortunate that, possibly for historical reasons, so much emphasis has been placed on locomotor scores as a measure of behaviour. Whether or not these scores are to be regarded as having any bearing on exploratory behaviour, we have now demonstrated that, in general, the greater the locomotor element in a test situation, the less sensitive the test as a differential measure of behaviour as far as early handling is concerned. This can be concluded both from a comparison of the results from the two home cage emergence studies, and, more importantly, from Expt. 3, in which the handled and non-handled groups can be differentiated clearly on the rearing measure but not on the basis of their locomotor scores. We have already indicated that this accords well with earlier findings by the present author, notwithstanding the fact that the two measures may to some extent be correlated.

Assuming that the handled animals have been subjected to a process which is in some way beneficial (although this is a dubious assumption, as is indicated in the discussion following Expt. 5), we are immediately tempted to ask what kind of 'therapy', if any, would be effective in enabling the non-handled animals to attain the same levels of performance as the handled group. One obvious, if not very helpful, answer is that they should perhaps attempt to be born female rather than male, since the males seem to be much more affected by the presence or absence of the experimental treatments.

The subject of sex differences in exploratory behaviour is a complex one, particularly since few investigators have employed direct comparisons. In some cases only females have been tested (for example, in studies by Montgomery, Halliday or M.H. Sheldon), while other workers - such as Levine and Denenberg - tend to use only males. Among those who have used both sexes are Broadhurst, Hughes and Lester; of these, Broadhurst has been principally concerned with open field activity, a situation in which large sex differences are found but which is not necessarily an ideal measure of exploratory behaviour. Hughes (1968), on the other hand, appears to have demonstrated that sex differences in exploratory behaviour depend to some extent on the measure employed, since he found that females engaged in more 'exploratory activity' (a measure which included sniffing, rearing and walking), but that there was no difference between the sexes in their preference for a novel rather than a familiar environment. It is interesting to note that once again the measure which includes a locomotor component is the one which differentiates the sexes, in view of the findings we have reported in the present series of experiments. Russell (1973b), however, makes the suggestion that " ... there may be a basal difference in the level of such activities rather than, or as well as, a sex difference in the response to novelty." In other words, although the two forms of response may be related, there is no a priori reason for supposing that they must necessarily be.

Similarly, Lester (1967a,b) has shown that sex differences in exploration are liable to interact with other variables such as degree of deprivation, since females were found to explore more when satiated and males to explore more when deprived. This, like the Sex x Handling interaction reported in Expt. 1 of this series, illustrates that even when sex differences are found they cannot be assumed to operate in a straightforward manner. This is, of course, likely to be true of situations other than exploratory behaviour alone; for example, Russell (1973c) reports that "open field defecation ... appears to be a valid emotionality index only in females."

Some of the differences may be accounted for by the fact that male and female rats differ in adrenocorticotrophic hormone (ACTH) secretion, even in the absence of ovaries or gonads (Kitay, 1961;

Levine & Mullins, 1967), and that handled and non-handled rats differ in ACTH secretion when confronted with novel stimuli as adults (Levine, Haltmeyer, Karas & Denenberg, 1967). Levine also states (in Ambrose, 1969, p. 46) that "one of the differences in central nervous system organization between male and female is the differential sensitivity of the target organ, the brain, to similar levels of circulating hormones." Hutchings (1967) has also found that the response to early cold exposure is sex dependent, which may in part account for possible differences between males and females in the response to early handling.

The difficulty here - always assuming that the ACTH response can be shown to have behavioural correlates - is that although we would be led to expect from this information a Handling x Sex interaction in response to novel stimuli, as we have found on at least one occasion, we are not able to explain why such an interaction does not occur in other experimental situations. Another difficulty is that, since we have found the males to be the group most affected by handling or its absence, the use of females as subjects would create some problems for Levine's argument that the non-handled animals in general respond in an all-or-none manner as a result of early modification of the 'setpoint' (see Ambrose, 1969, p. 49).

If it were methodologically possible, a start might be made by attempting a controlled study which involved handling only one sex within each litter. A great deal of work remains to be done on this topic, and we are compelled to conclude that those workers who confine their studies to one sex only are likely to forego a substantial amount of interesting information in the process.

Returning to our previous topic, however, the prospects for the non-handled animal do not seem to be altogether favourable. We have seen that exposure to an extremely familiar environment (a situation which should supposedly favour the non-handled group) either produces complete cessation of activity in both groups or, on re-test, finds the handled group still in the lead (Expt. 3). In Expt. 1, the situation (for the non-handled males, at any rate) is even less promising, since the performance curve for this group appears to be diverging, rendering it unlikely that their scores will ever be comparable with those of the other groups. The 'novel objects' measures, on the other hand, appear to show an 'improvement' in the scores of both non-handled groups; but as we have already pointed out, the curves for these and the handled animals do not meet at any point. Obviously, it would be interesting to extend the number of trials in future experiments.

There is little evidence on this point, but Sackett (1967), comparing dark and light-reared animals, found that effects of rearing conditions on motor activity were persistent, but that effects on more complex exploratory behaviours were reversible.

From the results of the present experiments, we are tempted to infer that although handled and non-handled animals both have strategies - perhaps equally valid from different points of view - for coping with a new and unfamiliar environment, these strategies may have very little in common. Furthermore, since each new experience to which the two groups are submitted is likely to be assimilated in a different way in interaction with the whole complex of past experiences, there is a cumulative process in operation which ensures that the same situation (from the experimenter's point of view) will in fact be perceived and responded to quite differently by the two groups. If this is so, then in a sense it will never be possible to compensate for the effects of early experience.

This is not to say that there do not exist ways of equalising the performance of the two groups: it is possible that training the non-handled animals in specific situations, 'social therapy' (Denenberg & Morton, 1962), or perhaps sessions of 'remedial handling' might produce the desired effect. Against this, however, must be set the findings that there are differences between the groups even after long familiarisation with the stimulus situation, and that handling later in life is less effective. Nevertheless, it must continually be borne in mind that there are situations (e.g. avoidance learning tasks) in which the non-handled animals excel, and also that we must always be careful to specify in what ways the changes produced in an animal's behaviour are to be regarded as an 'improvement' (Daly, 1973). Finally, before attempting to generalise any conclusions to other species, we may mention that preliminary studies in this laboratory (Lawlor, Weinberg & Wells; unpublished data) using hamsters rather than rats have indicated that various combinations of early handling and enriched environment produce effects which can only be described as adverse in the extreme in this species, not merely on behavioural measures but also in terms of viability.

It is therefore with the greatest caution that we must proceed to consider briefly the possible relevance of these studies to the human species, particularly since it is difficult to conceive of a direct analogue of the handling process which we have been describing in relation to the animal experiments. Nevertheless, several workers have investigated the effects of 'handling' or stroking on the subsequent behaviour of human infants, often using premature or institutionalised babies as subjects, presumably on the grounds that these infants are likely to be at risk from the effects of deprivation of stimulation. One of the earliest of these studies found, however, that the long-term effects of what the authors describe as "attentive care" during months 6-8, over and above the current institutional procedures, could be regarded as negligible, since at 19 months more of the experimental group were observed to vocalise during social tests, but otherwise both groups appeared "friendly and of normal intelligence" (Rheingold & Bayley, 1959).

A study of the effects of early handling (in this case equated with stroking) on premature infants was carried out by Solkoff, Yaffe, Weintraub & Blase (1969). These authors report that the 'handled' infants, which had been stroked for 5 minutes every hour for 10 days, were more active, regained initial birth weight faster, and could be described as physically healthier than controls. There were, however, only 5 subjects in each group. A follow-up at approximately 7 months of age also indicated that a greater amount and variety of stimulation was available to the handled group. If this latter finding can be substantiated, it is particularly interesting in that it seems to imply that stimulation received from the environment is partially regulated by the characteristics of the organism itself, and that these characteristics can be modified at an early stage of development.

White & Castle (1964) and Casler (1965) have also found that varying amounts of early handling can affect such behaviours as 'visual interest' (in the former case) and performance on a variety of items on the Gesell scale (in the latter). Motor functioning, however, was apparently not affected, according to Casler's report.

An interesting paper by Rubenstein (1967) suggests that maternal attentiveness may be an important correlate of the infant's exploratory behaviour; although, as the author points out, it may be that pre-existing characteristics of the infant (perhaps associated with exploration) themselves elicit greater maternal attentiveness. Whatever the mechanism, however, those infants who had experienced a greater amount of variety of stimulation were found to be more responsive to novelty.

One possible mechanism is suggested in a report by Korner & Grobstein (1966), who found that soothing crying babies by the procedure of picking up and putting to the shoulder also tended to induce a state of visual alertness, even within two or three days after birth when this state is not very frequently observed. It is possible that this procedure therefore presents the neonate with more opportunities for learning about the environment, particularly through visual channels; and, by analogy with the previous experiment, the 'attentive' mothers are thus likely to provide their offspring with more opportunities of this kind.

It will be apparent even from these few experiments that, even if exact parallels cannot be drawn, the experimental approach in some of the human studies has been considerably influenced by earlier animal experiments. The so-called 'handling' procedure is perhaps the most striking example of this. It is unfortunate, however, that there is far less constancy of method with respect to type and amount of stimulation, age at which administered, age at time of testing, and so on; and also that there is little evidence regarding long-term effects (although any attempt to match human and rat development in order to find the human equivalent of, say, 90 days of age in the rat would seem to be a rather meaningless exercise in any case).

Nevertheless there does seem to be a little common ground between the two areas of research. For example, the provision of 'extra stimulation' does appear to have some effect in both cases (within limits); there is at least a possibility that the effects are mediated through the behaviour of the mother or principal caretaker; and - again with some reservations - it appears that exploratory behaviour and the response to novelty may be affected by certain forms of early experience. Although Hutt (in Hutt & Hutt, 1973) rightly points out that " ... there is a tacit assumption that concepts like reward, novelty, complexity, have an equivalent valency for all species", and stresses that this assumption is almost certainly unjustified, she goes on to remark that both rats and humans are among those species apparently capable of surviving in a variety of habitats, and that " ... it seems reasonable to suppose that their respective exploratory tendencies have conferred a distinct advantage". If these characteristics are potentially so important in terms of evolution, perhaps we would be justified in concluding that the study of exploratory behaviour in relation to early experience is not such an esoteric activity as it might have appeared at first glance.

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EFFECTS OF INFANTILE STIMULATION AND ENVIRONMENTAL FAMILIARITY ON EXPLORATORY BEHAVIOUR IN THE RAT

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Adult rats, which had either been handled daily between birth and weaning or left undisturbed during this period, were tested (i) in an enclosed Y-maze for 3 min. on five successive days, and (ii) in a dark soundproof box for ½ hr. on six successive days; the box had a single lever, a response to which produced dim light of 1 sec. duration on the final three sessions only. An interaction between the effects of handling and of environmental familiarity was predicted. This was found in the response-contingent light condition, but not in the maze study.

Handling rats between birth and weaning has been shown to have far-reaching effects on the organism's development and on its adult behaviour (e.g. Levine, 1962). Adult exploratory behaviour in particular seems to be influenced by early experience; for example, De Nelsky & Denenberg, using tactile (1967*a*) and visual (1967*b*) stimulation, claimed that as the degree of stimulus variation increased, the exploratory behaviour of handled rats increased, whilst that of non-handled rats was depressed. DeNelsky & Denenberg manipulated stimulus variation by varying the visual and tactile difference between sections of the testing apparatus for separate groups of rats. The two experiments reported here are based on the assumption that another way of producing changes in the amount of stimulus variation is to manipulate the animal's familiarity with its environment. If stimulus variation declines with successive exposures to the environment, then it would be expected to follow from DeNelsky & Denenberg's findings that the exploratory activity of handled and non-handled rats would vary in a different fashion over successive exposures. There should be an interaction between the effects of familiarity and handling.

This is tested in Expt. I by testing handled and non-handled rats on successive days in an enclosed Y-maze.

EXPERIMENT I

Method

Subjects. The subjects were 57 hooded rats (31 male, 26 female) from a colony maintained within the Hull department.

Apparatus. A symmetrical enclosed Y-maze was used, with arms 18 in. long and 4 in. wide, and walls 9 in. high, painted in a flat medium grey. Each arm of the maze had two lines marked across it: one halfway along, and one where it joined the other two arms. These lines divided the maze up into six sections, each 9 in. long, and one triangular section at the junction of the three arms. The maze was placed in a curtained enclosure 4 ft. 6 in. × 4 ft. 6 in. × 4 ft. high, illuminated by a single 100 watt bulb suspended centrally 6 in. from the top. Observation was made through an aperture in one side with the help of an angled mirror which reflected the two most distant arms of the maze.

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Procedure

(*i*) *Handling.* At birth complete litters were randomly allocated to one of two conditions: 'handled' or 'non-handled'; but litters which contained fewer than eight animals, either at birth or by the time they were weaned, were not used. Handled animals were taken singly and at random from the nest, on each of the 20 days between birth and weaning, and placed in order on a plastic tray until all the remaining pups in the litter had been removed. They were then replaced in a similar manner; the operation time for each rat was approximately 30 sec. Non-handled animals remained in normal colony conditions, but were undisturbed during this period. When they reached 21 days, subjects were removed from the breeding cages, weaned, weighed and placed with litter mates in group cages. At approximately 40 days of age, they were ear-punched, re-weighed and caged with like-sexed litter mates of the same group. Throughout the experiment animals were housed in wire-mesh cages, the breeding cages having solid floors.

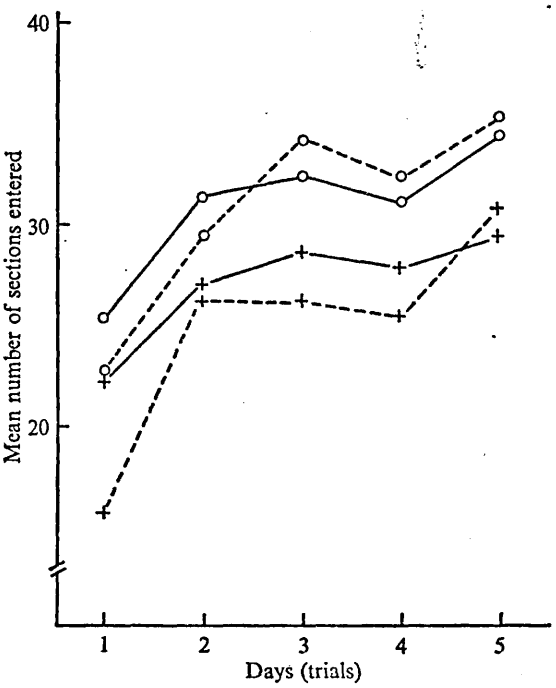

Fig. 1. Expt. I. Mean number of sections entered as a function of sex and infant treatment. +——+, handled male ($n = 17$); O——O, handled female ($n = 11$); +– – –+, non-handled male ($n = 14$); O– – – –O, non-handled female ($n = 15$).

(ii) *Testing.* At 90 ± 2 days each rat was placed in the maze for 3 min. on each of five successive days, being placed initially in one arm of the maze facing the choice point. Measures were taken of the number of sections entered and the order in which they were entered. An entry was scored (*a*) when the head and three of the animal's feet had crossed one of the lines marked halfway along a maze arm, or (*b*) when at the junction of the arms the head and three of the animal's feet had crossed the line at the entrance to a second arm. A measure was also taken of the number of times a subject reared up on its hind legs, having touched the ground with a fore-foot since last rearing up.

Results

A partial analysis of variance of the section entry scores showed significant effects for days ($F = 21{\cdot}8$; d.f. = 4, 1700; $P < 0{\cdot}001$), $\frac{1}{2}$-min. periods within sessions ($F = 147{\cdot}0$; d.f. = 5, 1690; $P < 0{\cdot}001$), litters ($F = 11{\cdot}8$; d.f. = 5, 1690; $P < 0{\cdot}001$), and sex ($F = 37{\cdot}2$; d.f. = 1, 1700; $P < 0{\cdot}001$), but not for treatment; i.e. handled *v.* non-handled ($F < 1$; d.f. = 1, 1700). The only significant interaction was that between litters and sex ($F = 3{\cdot}7$; d.f. = 5, 1690; $P < 0{\cdot}01$).

A measure of alternation was taken and expressed as a percentage of opportunities to alternate. Both groups showed similar behaviour, alternating on about 70 per cent of opportunities on each of the five experimental sessions. Separate sets of rank order correlations for handled and non-handled animals were calculated for the three measures taken of exploratory behaviour: sections entered, alternations, and rearing. All correlations were positive and significant ($P \leqslant 0{\cdot}05$).

Discussion

The handled and non-handled groups cannot be differentiated by any of the measures used. The experimental hypothesis predicts an interaction between the effects of handling and stimulus familiarity. When exploratory activity, in this case measured by sections entered, is plotted against trials, it can be seen from Fig. 1 that the curves do in fact intersect, but this interaction fails to reach significance.

The significant effect found for $\frac{1}{2}$-min. periods can be attributed largely to the sharp decline between the initial period of each trial and subsequent periods. It is usual to find such a rapid intra-session decline (e.g. Montgomery, 1951). The inter-session decline which is sometimes reported (e.g. Halliday, 1967) was not found in this study. The small effect of days was significant, and Fig. 1 suggests increased responding over sessions.

Measurement of sections entered gives but one indication of exploratory behaviour, and one which is likely to reflect the non-exploratory activity of the organism. One of the reasons often given for regarding locomotor activity in mazes as exploratory in nature is that animals alternate their choice of arms at a level significantly above chance (e.g. Montgomery, 1951). It is interesting to note that in the present experiment both section entries and rearing scores correlate highly with alternation and with one another.

The obvious conclusion from this experiment is that the handling procedures were ineffective in producing differences in the animal's adult behaviour. Another possibility is that the maze constituted a more complex environment than was supposed, such that five trials were not sufficient for the animals to become familiar with it; the predictions made would not then apply. The failure to find a drop off in exploration over trials could be interpreted as supporting this contention, for with a complex stimulus situation no decrement over trials may be expected (e.g. Glanzer, 1961).

EXPERIMENT II

A second way of testing the hypothesis that there is an interaction between the effects of infantile handling and stimulus variation manipulated through changes in familiarity is to use a situation where stimulus change is made contingent upon some response. In the present experiment dim light is made contingent upon a bar press. The phenomenon of light reinforcement is well-established (cf. Lockard, 1963), and may provide a useful technique for further defining the effects of early experience.

Method

Subjects. The subjects were those used in Expt. I, with the addition of one male in the handled group which had had only one day's experience in the maze used in Expt. I.

Apparatus. The experimental box, which was contained within a sound-insulated cabinet, measured 10 × 10 × 10 in. It had a metal mesh floor with walls and lid of Perspex; these were black, except for the end wall which was white. In this end wall was a single Perspex bar, 2 in. wide, being 3 in. above the floor and extending 1 in. into the box. Above the bar an area of the wall 8 × 5 in. could be evenly illuminated from behind; the light intensity 3 in. from the end wall and 3 in. above the lever was approximately 1·5 ft. c. Frequency of bar-pressing was recorded on print-out counters set at a 30 sec. rate; a measure of total response duration for each rat in each session was also obtained. Six identical sets of apparatus were used simultaneously.

Procedure. At 100 ± 2 days each rat was placed in the dark experimental box for half an hour on each of six successive days. On the first three (base-line) sessions no light was contingent upon a response, whilst on the final three sessions dim light of one second duration was made contingent upon a bar press.

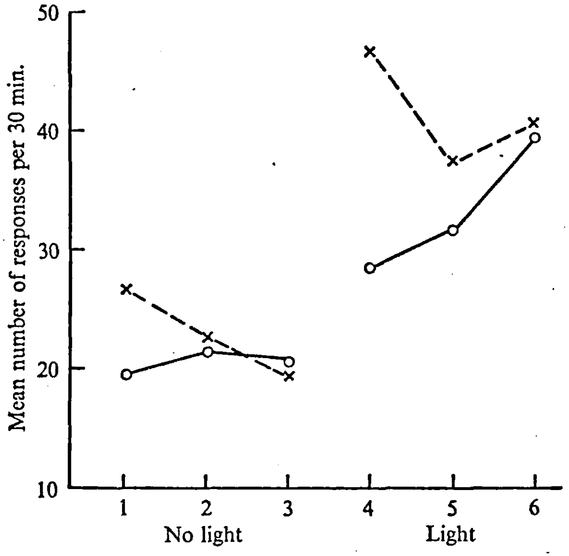

Fig. 2. Expt. II. Mean number of responses per 30 min. as a function of light contingency and infant treatment. ○——○, non-handled; ×----×, handled.

Results

Fig. 2 shows the pattern of responding of the two groups. Separate analyses of variance were carried out on the response scores for the base-line period and for the period with response-contingent light. For the base-line condition none of the main effects (groups or days), or interactions, was significant, and there were no significant differences between the groups on individual days. In the response-contingent light condition the main effects of groups and days were not significant, but the groups × days interaction was ($F = 4{\cdot}35$; d.f. $= 2, 112$; $P < 0{\cdot}025$). The handled and non-handled groups differed significantly only on the first session with response-contingent light ($F = 7{\cdot}5$; d.f. $= 1, 168$; $P < 0{\cdot}01$).

A significant increase in responding from day 3 (no response-contingent light) to day 4 (response-contingent light) was shown both by the handled group ($t = 6{\cdot}596$; d.f. $= 28$; $P < 0{\cdot}001$) and by the non-handled group ($t = 2{\cdot}7$; d.f. 28; $P < 0{\cdot}02$). No significant differences in average response duration were found between the two groups, either over-all or on any experimental session.

There were 11 females in the handled group and 15 in the non-handled group; however, there were no significant differences in the number of responses made by the males and females of each group on any day, both sexes showing the pattern of responding over time that the group data show in Fig. 2.

Discussion

Expt. II can be considered in two parts: the base-line period and the period with response-contingent light. In the base-line period the animal is placed in what is initially an unfamiliar environment and its rate of bar pressing measured. Fig. 2 shows that there was a difference in responding between the groups on the first session, but this was not significant, nor were the differences on the other two days. When light was made contingent upon a response, the behaviour of the two groups can be distinguished. The handled group responded significantly more than the non-handled group on the first session with light; that is to say, the predicted interaction between the effects of familiarity (as represented by successive days of testing) and handling was shown. This interaction parallels the one DeNelsky & Denenberg found between handling and the degree of stimulus variation.

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EFFECTS OF INFANTILE HANDLING ON LIGHT-REINFORCED BEHAVIOUR IN THE RAT

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Abstract. Differences in exploratory behaviour between handled and non-handled animals, although generally accepted, may depend both on the familiarity of the environment and on the nature of the stimulation available. Handled and non-handled rats were therefore tested under three conditions: no light contingent upon a bar-press, steady response-contingent light, and response-contingent flicker. A strong light reinforcement effect was observed; and after adaptation to the apparatus, comparable differences between handled and non-handled animals were found in all conditions, with the handled group responding significantly more. A dual arousal system encompassing both general stimulus input and stimulus change is suggested as a possible explanation of these findings.

It is now generally accepted that handling one group of animals between birth and weaning while leaving a second group undisturbed during this period will tend to produce substantial differences between the two groups on a variety of subsequent measures. According to Levine (1962), for example, the handled group may show earlier maturation, more vigorous growth, higher resistance to stress, and greater tendency to explore a strange environment.

Recent studies have indicated, however, that the responses of the two groups to a given stimulus situation may not be differentiated in an entirely straightforward way. DeNelsky & Denenberg (1967a, b) have claimed that, as the degree of tactual or visual stimulus variation increased, handled rats showed a corresponding increase in exploratory behaviour, whereas non-handled rats tended to explore less. Similarly, Wells et al. (1969) have shown that the behaviour of handled and non-handled rats can be differentiated over time, if a dim light is made contingent upon a response, even when a more conventional test of locomotor activity has failed to distinguish between them.

The present experiment is an extension of this finding, and is based on the assumption that one way of producing changes in the amount of stimulus variation is to manipulate the animal's familiarity with its environment. In particular, it was intended to investigate further the indication that differences between handled and non-handled animals may depend on changes in the nature of the environmental stimulation which is available.

Methods

Subjects

Subjects were eighty-eight black hooded rats, forty-five male and forty-three female, from a colony maintained within the University of Hull department.

Housing

All animals were raised and maintained with free access to food and water under normal laboratory conditions, with a light cycle of 17 hr light and 7 hr darkness. The breeding cages were plastic, and nesting material was provided; at 8 days of age, animals were transferred to wire mesh cages. For the 'handled' group, this was incorporated into the handling procedure; for the 'non-handled' group, the transfer was effected by gently tipping the animals from one cage to another.

Handling Procedure

At birth, complete litters were randomly allocated to one of two conditions: 'handled' or 'non-handled', but litters which contained fewer than eight animals either at birth or by the time they were weaned were not used.

On each of the 20 days between birth and weaning, the cages of the handled animals were removed singly from the rack and placed on a bench. When the mother had been removed from the cage, the pups were taken individually and at random from the nest, and each was placed in a separate compartment of the 'handling apparatus'. This was an open wooden box which contained twelve compartments each measuring 10 cm^3. When all the remaining pups in the litter had been removed, they were then replaced in the same manner; the operation time for each animal was approximately thirty seconds. Non-handled animals remained in normal colony conditions, but were undisturbed during this period.

When they reached 21 days of age, subjects were removed from their cages, weaned, weighed and replaced with litter mates in group cages. At approximately 40 days they were ear-punched, re-weighed and caged with like-sexed litter mates of the same group. During the testing period, all animals were housed individually.

Experimental Apparatus and Procedure

The experimental box, which measured 25 cm^3 had a metal mesh floor with walls and top of black Perspex, with the exception of one end wall which was white. In this wall, 7·5 cm above the floor, was a single Perspex lever which was 5 cm wide and extended 2·5 cm into the box. Above the lever, an area of the wall 20 × 12·5 cm could be evenly illuminated from behind. The light intensity 7·5 cm from the end wall and 7·5 cm above the lever was approximately 1·5 ft-candles.

Frequency of bar-pressing was recorded on print-out counters set at a 30-s rate, and a measure of total response duration for each rat in each session was also obtained. Six identical sets of apparatus were used simultaneously, and each animal given successive trials in the same box. Testing began when subjects were aged 90±4 days.

Each rat was placed in the dark experimental box for half an hour on each of twelve successive days. On the first 3 days, which constituted a measure of baseline performance, no light was contingent upon a response. On the following 6 days, for half the animals in each of the handled and non-handled groups, dim light of 1-s duration was made contingent upon a bar-press, while for the remaining animals there was no change in the condition. On the final 3 days, those animals which had previously experienced steady light contingent upon a bar-press now experienced 1 s of response-contingent light which flickered at the rate of 200 flashes per minute. At the same time, animals which had been under the condition of 'no light' for the previous 9 days were assigned to the condition of response-contingent steady light of 1-s duration for the three remaining days.

Results

As it had been previously established (Wells et al. 1969) that there tends to be no difference in performance between sexes in this particular reinforcement situation, scores for male and female subjects were combined in this analysis.

No significant differences were found between handled and non-handled groups during the first 3 days (the baseline condition), although, as shown in Fig. 1, there is a slight tendency for the handled animals to respond more by the 3rd day. The introduction of response-contingent light on day 4 produced a significant increase in responding when the first 3 days of light are compared with the baseline condition ($F=774{\cdot}1$, $df=1/42$, $P<0{\cdot}001$). A significant difference between handled and non-handled groups was also found over this period (treatments × blocks: $F=37{\cdot}2$, $df=1/42$, $P<0{\cdot}001$); there was, however, no significant interaction between treatments and conditions. From this it may be concluded that handled animals tend to respond more than non-handled whether light is contingent upon a response or not, although this only becomes apparent after some time spent in the baseline condition. However, after several trials (sessions 4 to 9), this effect tends to disappear both for 'no light' and for 'response-contingent light' groups. In other words, although handled animals can be differentiated from non-handled, this difference may be manifested in both experimental (light) and control (no light) conditions, and its magnitude will depend to a large extent on the nature of previous experience in the experimental situation.

The additional stimulation introduced on day 10 was an attempt to manipulate the environment still further by introducing for the controls a change from the 'no light' condition to that of 1 s light onset, and for the experimental group a change from steady light to flickering light. Inspection of Fig. 1 indicates that the effect of introducing response-contingent light on day 10 for the two control groups was to elevate their responding to a level which even surpassed that shown by the two experimental groups which had previously experienced this condition ($F=431{\cdot}9$, $df=1/42$, $P<0{\cdot}001$); this increased light reinforcement effect is typically found following longer familiarization with the no-light condition (Lowe & Williams 1968). In addition, the handled group produced more responses than the non-handled group over this 3-day period with response-contingent light

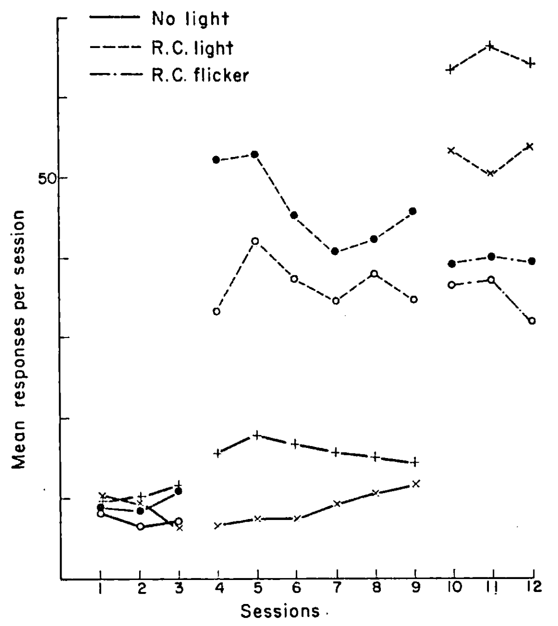

Fig. 1. Mean number of responses per daily 30-min session. ●, Handled experimental; ○, non-handled experimental; +, handled control; ×, non-handled control.

($F=42{\cdot}4$, $df=1/42$, $P<0{\cdot}001$), although in the preceding 3 days of the no-light condition there had been in fact no significant differences between these groups. We therefore have a situation which is comparable to that of the first 6 days of the experiment. In contrast, the two experimental groups which were changed at the same time from the condition of steady light to that of flickering light showed no significant differences in response rate which could be attributed to this change. This is possibly due to the fact that the difference between response-contingent light and response-contingent flicker is relatively minor compared with that between the no-light and response-contingent light conditions.

Response duration scores on initial exposure to response-contingent light tended to follow the same course as the data concerning response rate, in that both handled and non-handled groups showed a significant increase in response duration on day 4 as compared with day 3 (Mann–Whitney U test: $U=82$, $n_1=n_2=22$, $P<0{\cdot}001$ and $U=121$, $n_1=n_2=22$, $P<0{\cdot}01$, respectively), while for the control groups which were not exposed to response-contingent light no such differences were found. However, the data in this case showed such great variability that they cannot be regarded as reliable, and a fuller analysis was therefore not attempted.

Discussion

The results show clearly that handled and non-handled animals respond differentially to response-contingent light, but provide no conclusive evidence that such differences are distinguishable from those produced in the 'no light' condition. A suggestion that this might be so, however, is the difference in responding between the groups, which is produced by the availability of light on day 10, when on the previous 3 days in the no light condition there had been no difference between the groups. The relevant controls are not available here. It could be that handled and non-handled animals differ in their response to environmental change, as seen on day 10, but that the introduction of response contingent light on day 4, did not produce any significant change, as it occurred at a time when the total environment was still novel and exerting an effect in differentiating between the groups.

The main interest in the results lies in the fact that although the differences produced by response contingent light on day 4 was no greater than the difference between the control groups, the total response score for both handled and non-handled groups was elevated in the light onset condition. This would appear to present difficulties for theories which seek to explain the differences in exploratory behaviour that are produced by differential stimulation in infancy.

The pattern of responding of the two control groups is very similar to the pattern of responding shown by similar groups of animals in the open-field. There tends to be very little difference between handled and non-handled animals on initial exposure to this situation, although their pattern of responding can be distinguished on subsequent trials; then, as testing proceeds, the scores of the two groups again become comparable (cf. Denenberg & Whimbey 1967). The kinds of explanation that have been offered of this behaviour (e.g. Denenberg & Whimbey 1967) suppose that it represents an emotional response to a stressful situation. Thus non-handled animals would tend to 'freeze' and move around less in the environment. Alternatively, in terms of some theory of optimum arousal such as that proposed by Leuba (1955) or Fiske & Maddi (1961), non-handled animals could be said to maintain their lower level of arousal with less stimulus input from the environment.

The present finding renders both such formulations implausible, in that, faced with a greater degree of stimulus input when light onset occurs, the non-handled animals respond more than they had done under conditions of no light; whereas, if their initial responding was a measure of emotional response to stress in the situation, they would be expected to continue to 'freeze', or respond less, in the face of increased stimlation. Similarly, if their optimum arousal level was being met in the first situation (that of no light), they would be expected to respond less when lever pressing resulted in greater stimulus input.

Since, therefore, we have found comparable differences between handled and non-handled groups at both levels of stimulus input, the conclusion must be that differences in behaviour do not seem to be a function of the absolute amount of stimulation available.

One way of accounting for this result would be to postulate two arousal systems: one 'general' system governed by absolute stimulus input, and another which monitors specific stimulus change. Optimum arousal levels would therefore not be rigid, but would be set in relation to the absolute level of stimulus input. This would explain why the relative positions of the handled and non-handled groups are maintained under different levels of stimulation. Berlyne (1969) is developing models which could possibly encompass this result. As far as practical strategies are concerned, these findings would suggest that an understanding of differences in exploratory behaviour in relation to emotionality might best be achieved by observing an animal's behaviour in response to gross stimulus change over time, rather than by correlating different aspects of behaviour in a standard environment.

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Differences in home-cage-emergence in the rat in relation to infantile handling[1]

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Adult rats, which had either been handled daily between birth and weaning or left undisturbed during this period, were tested on speed of emergence from the home cage. On opening the cage, handled animals reared sooner than did nonhandled ones, and females sooner than males; the additional time taken to raise the nose above the cage top showed sex differences only.

The time taken for an animal to leave a familiar environment is one index of exploration that has been termed, at various times, a measure of wildness/savageness (e.g., Stone, 1932), emotionality (e.g., Billingslea, 1942), shyness (e.g., Hess, 1953), and timidity (e.g., Bindra & Thompson, 1953). The most familiar environment to the animal is probably the home cage, and measures have been taken simply of the time taken to emerge from it (e.g., Lester, 1967), or of the time taken to come onto a runway (e.g., Bindra & Thompson, 1953) or into an enclosed alley attached to the cage (e.g., Billingslea, 1942). This relatively simple technique has not produced entirely consistent results.

In an early study, Billingslea (1942) showed that emotional animals, as defined in terms of their behavior in Hall's open-field test, took a greater time to enter a tunnel attached to the cage than did less emotional ones. Later studies, however, with rats (Bindra & Thompson, 1953; Hunt & Otis, 1953) and mice (Willingham, 1956) failed to find any relationship between time taken to emerge onto a runway and behavior in the open field. Hunt & Otis (1963), however, went on to report that emergence from home cage was more sensitive in identifying differences between rats differentially stimulated in infancy than was the open-field test. They showed, with male rats, that those "handled" in infancy emerged onto a runway sooner than did "nonhandled" ones, and, in a second experiment, with female rats, that "handled" ones emerged sooner than did "nonhandled" when the cage door was opened. Similarly, Meyers (1965) found that rats "gentled" or receiving "low" electric shock in the immediate postweaning period made more entries into an alley attached to the cage than did "nonhandled" controls; he also reports more entries by females than males. This sex difference is contrary to that found by Lester (1967), who claims that males emerged faster than females. King (1968) also finds sex differences in this situation but gives no indication of their direction. The present study uses the technique of home-cage emergence to examine sex differences and differences produced by infantile stimulation.

SUBJECTS

Seventy-six black hooded rats, 38 male and 38 female, were used.

HANDLING PROCEDURE

At birth, complete litters were allocated randomly to one of the two conditions: "handled" (H) or "nonhandled" (NH), but litters that contained fewer than seven animals at weaning were not used.

On each of the 20 days between birth and weaning, the cages of the handled animals were removed singly from the rack and placed on a bench. When the mother had been removed from the cage, the pups were taken individually and at random from the nest and each placed in a separate compartment of the "handling box." This was an open wooden box that contained 12 compartments, each measuring 8.16 x 8.16 x 8.16 cm. When all the remaining pups in the litter had been removed, they were then replaced in the same manner. The operation time for each animal was approximately 30 sec. Nonhandled animals remained in the normal colony conditions and were undisturbed during this period.

MAINTENANCE

Maternity cages were of plastic with bedding provided. At 21 days of age, Ss were weaned and placed with litter mates in group cages. At approximately 40 days, they were ear-punched, weighed, and caged with like-sexed litter mates of the same group. Five days prior to the experiment reported here, they were housed individually. The cages were wire mesh drawers, 32 cm long, 19 cm wide, and 15 cm deep, divided in the center by a solid metal divider so as to house two rats individually. All animals were raised and maintained with free access to food and water.

PROCEDURE

Rats were tested at 102 ± 4 days. Previous to this study, they had each been used in a study on maze exploration. The cages were not opened during the 5 days prior to the test, food and water being replenished from outside. Each cage was pulled out a distance of 14 cm, and the time noted, by a separate O for each rat in the pair, for the rat to (1) lift both front paws from the cage floor, and (2) rise up so that the nose was above the level of the top of the cage.

RESULTS

The mean time to reach Criterion 1 was: for H females, 3.95 sec; for H males, 15.58 sec; for NH females, 12.66 sec; and for NH males, 25.32 sec. An analysis of the times to reach this criterion showed a significant effect attributable to handling ($F = 59.47$, $df = 1/72$, $p < 0.001$) and sex ($F = 103.1$, $df = 1/72$, $p < 0.001$), and with no significant interaction ($F < 1$). The same differences are significant if the total times taken to reach the second criterion are measured. If, however, the differences between times to reach Criterion 1 and Criterion 2 are analyzed, only the differences attributable to sex are significant ($F = 4.87$, $df = 1/72$, $p < 0.05$), the mean differences being: for H females, 5.4 sec; for H males, 10.0 sec; for NH females, 5.1 sec; and for NH males, 16.5 sec.

DISCUSSION

The direction of the sex difference, females rearing before males, is in agreement with that found by Meyers (1965) but opposite to Lester's (1967) finding. There may be strain differences here, but the results of this study do show the expected relationship to sex differences in other exploratory situations, such as mazes (e.g., Hughes, 1968) or the open field (e.g., Broadhurst & Eysenck, 1964). Similarly, the differences in emergence patterns to the first criterion for H and NH animals parallel those found in open-field behavior (e.g., Levine, 1960) and maze studies (e.g., DeNelsky & Denenberg, 1967).

The fact that the first measure is maximally sensitive to the differences due to infantile stimulation may serve to reconcile some of the previous findings, for those studies (Bindra & Thompson, 1953; Hunt & Otis, 1953) that failed to find a correlation between emotionality and emergence time required the animal to emerge onto an open elevated runway, while those that found a correlation (Billingslea, 1942; Meyers, 1965) used a covered alley, which may have been less stressful. An exception is the study by Hunt & Otis (1963), who found a relationship between infantile treatment and emergence onto an open elevated runway; but here they express the result not in terms of time to emerge but the degree to which an animal emerged in a given time, and, in fact, only 1 out of 19 "restricted" rats did leave the cage. In such a situation, where the animal is required to enter an unfamiliar and exposed environment, there may be a degree of stress that tends to eliminate some possible behavioral differences. If this is so, then a measure that minimizes stress by recording some aspect of behavior within the familiar home cage will provide an even more sensitive estimate of differences attributable to both sex and early handling.

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NOTE

1. This study was carried out at the University of Hull. We are grateful to Miss Julie Hall and to Mrs. Gillian Bailey for their assistance in conducting the experiment.

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Light Reinforcement, Noise and Arousal Level

RATS placed in a dark box will press a bar more often if dim light onset is contingent on this behaviour. Most of the explanations suggested for the reinforcing effect of light onset have been in terms of the absolute characteristics of the stimulation—stimulus change[1] and illumination[2]. But alternatively, the reward value of a stimulus may be a function of its arousal value, which will depend on the initial state of arousal of the organism[3]. The arousal hypothesis is supported by the finding[4] that the reinforcing effect of the light can be modified by the level of auditory stimulation maintained before testing, if the auditory stimulation is assumed to change the basic arousal level of the organism. Administration of drugs affecting arousal level during the test period also influences the rate of bar pressing[4,5]; but in this case direct effects of the drugs on perception cannot be ruled out.

We used continuous auditory stimulation in the light reinforcement situation. The rationale from arousal theory is that there should be a degree of auditory input which would increase arousal level to a point at which behaviour producing minor changes in arousal (for example, a nonreinforced bar press) would remain unaffected, whereas behaviour producing a greater increment in arousal (for example, responding for light onset) would be depressed.

Eighty male hooded rats (strain PVG/C), approximately 100 days old, were used. They were raised and maintained in normal laboratory illumination (light cycle: 17 h on, 7 h off), with free access to food and water. The experimental box was contained within a sound insulated, light proof chest measuring 26 × 26 × 26 cm and was lined in black 'Perspex' except for the end wall which was white. In the white wall was a single bar 5 cm wide, 7.5 cm above the floor, extending 2.5 cm into the box; above this an area of the wall 20 cm × 12 cm could be evenly illuminated from behind. The illumination at a point 7.5 cm above the bar and 7.5 cm from the wall was 16 lx. A 10 cm speaker was fitted in the roof of the box. White noise (20 kc/sec band width) could be relayed through this; the noise level at a point 26 cm from the speaker was 80 dB. re 0.0002 μbar.

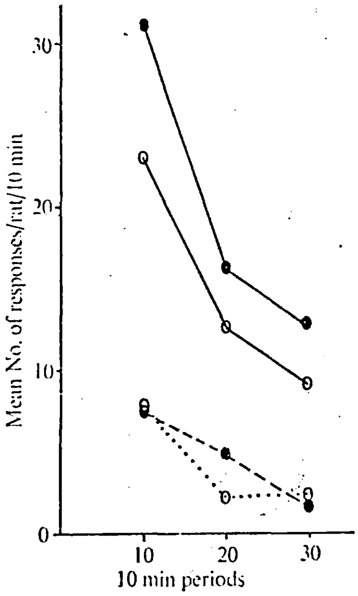

Fig. 1 Mean number of responses per rat per 10 min for groups having either light (RCL) or no light (NL) contingent on a response, under conditions of either continuous noise (N) or no noise (NN). ●——●, NN/RCL; ○—○, NN/NL; ●- - -●, N/RCL; ○. . . .C, N/NL.

Each rat was placed in the dark box, with no white noise, for 30 min, during which a bar press produced no change in illumination. Twenty-four hours later they were returned to the dark boxes for a further 30 min. For half the animals, a bar press produced no change in illumination (NL controls); for the remainder, it produced light onset and the light remained on for as long as the bar was depressed (RCL). Half the rats in each group had white noise (N) relayed through the speakers; for the other half there was no noise (NN). The four groups were matched on the basis of responses made in the first test period.

An analysis of variance on response frequencies in the second experimental session showed a significant effect of noise ($F=7.67$, d.f. 1/84, $P<0.01$) in depressing overall response rate, and significantly greater responding with RCL than with NL ($F=77.48$, d.f. 1/84, $P<0.001$). There was also a significant interaction between NL : RCL conditions and NN : N conditions ($F=6.02$, d.f. 1/84, $P<0.05$). This could be attributed to the greater differences between N/RCL and NN/RCL groups (mean response rates of 29.3 and 44.3

respectively). than between N/NL and NN/NL groups (11.1 and 12.0 respectively). An analysis of variance on mean response durations showed no significant effect due to noise ($F < 1$) and no significant interaction between noise conditions and light onset ($F < 1$); mean response durations were longer with RCL (1.53 s) than NL controls (1.22 s), but this difference failed to reach an acceptable level of significance ($F = 3.84$, d.f. 1/84, $P > 0.05$).

The result is in accord with the prediction from arousal theory, in that responding for light was depressed in the noise condition whereas there was no difference in responding in the control groups. The depression in responding was maintained throughout the 30 min experimental period; the NN/RCL group responded 27%, 23% and 29% more than the N/RCL group respectively in each 10 min period (Fig. 1). The particular noise level used was chosen after a series of pilot studies, where it was found that noise levels louder (85 dB) than those used here produced a marked depression of responding in both NL and RCL groups, while lower noise levels (70 dB) produced no effect on responding in either condition. One possibility is that loud noise may reduce the sensory effect of light as a result of an attentional mechanism, thus making light onset a less effective reinforcer. Our data, however, are certainly consistent with an interpretation of light reinforcement in terms of arousal, and create considerable difficulties for preference theory and the simple stimulus change position.

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