EFFECTS OF POSTNATAL EXPERIENCE ON AVOIDANCE, SHOCK SENSITIVITY AND OPEN-FIELD BEHAVIOR OF TWO SELECTIVELY BRED STRAINS OF RATS

by

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THESIS

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ABSTRACT

The effects of postnatal experience on avoidance, shock sensitivity, and open-field behavior were investigated in the Roman high avoidance (RHA/Lu) and the Roman low avoidance (RLA/Lu) selectively bred strains of rats.

The strains were divided into two groups, handled and shocked (HS) and handled and not shocked (HNS), utilizing the split-litter technique. The RHA/Lu strain acquired avoidance learning significantly faster and was more sensitive to electric shock than the RLA/Lu strain. The postnatal experience had a significant effect on avoidance and shock sensitivity in the high-avoidance strain. The females of the RHA/Lu strain had a significantly lower jump threshold, and there was a tendency for the HS group to be heavier. The strain differences in the open-field were not significant and the postnatal experience had only higher order significant interactions. The results were discussed in reference to the direct action hypothesis of postnatal experience.

INTRODUCTION

The area of infantile stimulation or early experience refers to environmental events which act upon the organism during the early developmental period. The developmental period extends from conception to adulthood, and may be divided into three periods during which stimulation can be administered. These three periods are: prenatal, postnatal and post-weaning. During the prenatal period, stimulation is applied to the mother, and the effect may or may not be passed on to the fetus by means of placental circulation. In the postnatal period, the stimulus may be administered to the mother and/or to the infant. Post-weaning stimulation is generally applied to the maturing organism.

As a result of early stimulation, the emotional responses of the target organism may be influenced at some later stage of development when it is confronted with a novel situation assumed to be stressful. Early stimulation can be designed to increase or decrease the animal's emotional reactivity. Generally, when an animal such as rat is confronted with a strange environment or some form of noxious stimulation, it will "freeze." In addition to freezing, the animal may also vocalize, attempt to escape, urinate and defecate. In the context of early experience studies, the emotional animal is one that shows little movement and considerable urination and defecation. The movement of the animal may be measured by its ambulation or by its delay in initiating movement. Defecation is measured by counting the numbers of fecal boli dropped and urination is measured by the occurrence or non-occurrence of the event.

Emotional reactivity can be measured in the open-field. An open-field is a large arena illuminated with bright lights to increase the noxiousness of the situation. In addition, the size and strangeness of the arena is designed to induce the more emotional rats to freeze, defecate and urinate.

There have been equivocal results from prenatal studies on the effects of stimulation applied to the mother before parturition and the action of stress on postnatal behavior of the offspring (Thompson, 1957, Selye, 1952, Gauron, 1966).

There is some agreement that prenatal stress does, by some unknown mechanism, generally modify the later behavior of the young. Noxious stimulation in the form of conditioned "anxiety" was applied to pregnant female rats (Thompson, 1957). It was found that their offspring were more emotional than those of the control mothers when measured in an open-field test and on a timidity test.

There is additional evidence of the importance of the gestational period on postnatal behavior. Several studies have shown that injection of catecholamines into pregnant females have had a deleterious effect on later emotional adjustment of the offspring (Funkenstein, King and Drolette, 1957, Selye, 1952). Ader and Conklin (1963) reduced the emotional reactivity of rat pups by simply handling the pregnant rats three times daily. On the other hand, other investigations (Gauron, 1966, Hockman, 1961) showed different findings than Thompson (1957), Funkenstein, King and Drolette (1957), and Selye (1952). Gauron (1966) shocked complete litters of rats during infancy while a comparable number of litters were not shocked. The females were paired at adulthood and after birth all the offspring were cross fostered to different mothers. All offspring were tested at 70 days of age in an open-field. Gauron's data revealed that shocking the mother in infancy was not a crucial variable in adult behavior of the offspring.

Thompson's (1957) study was replicated by Hockman (1961) using Long-Evans hooded rats. His results indicated that open-field activity and defecation measures only partially supported the hypothesis that prenatal stress affected the emotional behavior of the offspring.

Manipulating pregnant rats by means of electric shock, handling, or injections was thought to arouse a state of "anxiety," the intensity and duration of which is unknown. Although there has been increased understanding of the physiological counterparts of psychological stress, it is unclear whether stress is due to hormones, waste products, or other factors influencing the behavior of the offspring. It is believed that these counterparts are transmitted by means of the maternal-fetal blood exchange system.

The second period during which stimulation can be administered to subjects is the postnatal. Postnatal experience refers to any consistent extraneous stimulation that is applied to the young organism during the preweaning developmental period. This treatment may be applied to the organism at any period from birth to weaning, the latter occurring at approximately 21 to 30 days. Postnatal experience has taken on the form of sensory deprivation, (Wolf, 1943), handling (Levine, 1956), exposure to environmental complexity (Denenberg and Morton, 1962), electric shock (Gauron, 1964a), social rearing (Denenberg and Grota, 1964), hormone treatment (Gray, Levine and Broadhurst, 1965), immersion in water (Gauron, 1965), early separation from the mother (Ader and Friedman, 1965), mechanical rotation and hypothermia (Young, 1965), heat (Haltmeyer, Denenberg, Thatcher and Zarrow, 1966) and drug injection (Young and Klepinger, 1966).

Other investigations of postnatal experience have measured variables such as avoidance learning (Denenberg and Karas, 1960; Levine, 1956), gastric erosion (Ader, 1962), problems solving in an underwater-maze (Karas and Denenberg, 1961; Gauron, 1965), and heart rate (Snowdown, Bell and Henderson, 1964).

The beneficial effects of stimulation during the post-weaning period has been demonstrated by Donaldson, (1924). Animals which were given good care, maintenance and gentling, had an earlier onset of puberty, had litters earlier and lived longer than unstimulated control animals. It was hypothesized (Bernstein, 1957) that the relationship between the experimenter and his experimental animals enhances learning in the gentled animals.

Rosen (1958) investigated the effects of gentling on social dominance in a food competition situation. Rotated pairs of rats were used, every gentled rat paired with every control rat. The results indicated that, in all trials, the gentled animals were dominant over the controls. Becker and Flaherty (1966) using non-rotated pairs of male rats, in which an experimental animal was permanently paired with a control animal across all competition trials, have reported that the gentled animals were dominant only on the first trial.

Weininger (1953) sought to determine the effects of gentling on the rat's ability to withstand later stress. The control animals, on a regimen of food and water deprivation, had enlarged adrenal glands and many small bleeding points in the stomach and duodenum. No gentled animals died or suffered any permanent damage during the course of the experiment.

Wolf (1943) studied the effects of restricting sensory-input in a single sense modality. Instead of severing nerve-tracts and thus doing permanent damage, the receptor mechanism was simply blocked off and then unblocked after a given period of time. One group of rats was deprived of vision at 12 to 25 days of age and another of hearing at 10 to 25 days of age, whereas controls were not disturbed. It should be noted that the animals' sensory modalities become functional within the time spans cited.

A food competition situation was arranged to test the adults. A visual or auditory starting signal was used for each pair of rats; one of each pair had to be visually deprived and the other auditorily deprived. When a visual signal was used for the animals to start running toward the goal box, 62% of the animals that had been visually deprived in infancy lost in the competition. With an auditory signal, 61% of those who had been deprived of vision (but with hearing intact) in infancy won.

Early visual restriction was compared to normal rearing in the dog with the result that the restricted animals could not respond adaptively and intelligently to noxious stimuli (Melzack and Scott, 1957, Thompson and Heron, 1954).

Infant stimulation studies are not limited to rats, but cover mice, monkeys, chimpanzees, cats and dogs. These investigations have studied the effects of maternal deprivation, partial social deprivation and sensory restriction. Mason (1960) and Harlow (1962) concluded that the "well-controlled" laboratory setting deprives the animals of the experiences that are necessary for animals to develop their full capacities. Hayes and Hayes (1951) raised a chimpanzee in their home from birth until it was three years old. Its performance on various learning problems was compared to that of three year old children and a three year old laboratory-reared chimpanzee. The children and the home-reared chimpanzee performed equally well, whereas the laboratory-reared chimpanzee solved only one of six problems.

Wilson, Warren and Abbott (1965) showed that cats handled as kittens more readily approached strange toys and humans and required more trials to learn the avoidance response than kittens that were not so treated. In addition, animals exposed to an enriched environment made significantly fewer errors on the Hebb-Williams maze problems and were more active initially in the open field.

Studies have shown that an organized pattern of intromission and ejaculation in monkeys (Mason, 1960) and guinea pigs (Valenstein, Riss and Young, 1955) is dependent upon social experience with their peers during development. Kagan and Beach (1953) demonstrated that social interaction in rats seemed to have a detrimental effect. Thus, rats raised in isolation after weaning had a higher copulation rate than those reared in a large cage with females.

Valenstein and Young (1955) have shown that in contrast to the rat, social isolation in the guinea pig has a debilitating effect on its sexual behavior. Socially reared guinea pigs engaged in more sexual behavior in adulthood than animals reared in isolation.

The early infantile studies discussed above suggest that one must be cautious in assuming that the effects of early experiences generalize across different animals. There is also a series of investigations indicating that the effects of early stimulation are dependent upon a complex interaction of the strain of the animal, the treatment and the dependent measures utilized.

Levine and Broadhurst (1963) experimented with

Maudsley reactive and non-reactive strains, which are selectively bred for emotional reactivity in open-field. As adults, these animals were tested for emotionality and escape-avoidance conditioning. The score from the open-field showed that infantile stimulation was related to a significant decrease in emotionality indexes which was attributed to a change in the capacity of the organism to respond to stress. The reactive strain was significantly poorer than the non-reactive in avoidance conditioning. However, the manipulation did not change the avoidance performance of either of the strains.

Handling has been one of the most widely used techniques for influencing the emotional reactivity of the rat in studies of early experience. Typically, handling involves removing the pups from the nest cage and placing them in the same type of container in which they remain untouched for periods of two to three minutes and then returned to the nest. Generally, this treatment is administered once daily. The schedule of handling can, however, vary as a function of the purpose of the experiment.

The effect of handling in infancy on later emotional reactivity, however, has been debated. Several experiments (Denenberg, Morton, Kline, and Grota, 1962, Denenberg and Smith, 1963) have shown that handled animals are generally less emotional than the non-handled control animals. It has been hypothesized by Levine (1956) and Denenberg (1959) that early handling is a traumatic event in the life of the young organism and this treatment increases its adaptability to stress in adulthood. Levine (1956) has further suggested that treatments employed in infantile stimulation studies are generally "noxious" or "stressful" in some way and this stress in infancy serves to "immunize" the organism against excessive reactions to stress in adulthood.

In contrast to the positions of Levine (1956) and Denenberg (1959), Bovard (1958) maintains that early stress reduces resistance to later stress. Bovard's contention is that an organism is given only a certain amount of resistance energy to stress, and any loss of resistance in infantile period reduces the animal's ability to handle a stressor in adulthood.

Despite the incompatible positions of Bovard (1958), Levine (1956), and Denenberg (1959), it has been demonstrated that handling in infancy decreases the emotional reactivity of an adult rat. Levine, Chevalier, and Korchin (1956) compared three groups of rats: shock group, a non-shocked group and a control group. The control group remained undisturbed in the nest cage, and received no stimulation except for regular maintenance. The non-shocked group showed a slightly better avoidance learning than the shocked group, while the control group, which received no stimulation, was significantly poorer than the others in avoidance learning. Instead of running and jumping in response to shock, the control group exhibited a marked tendency to freeze and defecate. These responses are incompatible with efficient avoidance learning.

Using three groups of rats: a shocked group, a handled group, and a control group, animals left undisturbed in the nest cage, and neither handled nor shocked, Denenberg and Smith (1963) showed that the non-handled control group was less active in open-field and had a higher defecation rate than the two groups throughout the age ranges studied. Denenberg, Carlson, and Stephens (1962) showed that 1 to 2 day old rats that were shocked emerged into the open field from a container more quickly and were more active than the animals of the non-shocked or control groups.

Electric shock applied in infancy has much the same effect as handling in that it reduces emotional reactivity to later stress. Electric shock has been widely used as an experimental variable because the experimenter is able to exercise precise control over the intensity and duration of its application.

Baron, Brookshire, and Littman (1957) found that exposure to escapable shock in infancy improved learning in rats on avoidance conditioning in adulthood, whereas Gauron (1964a), combining escapable and inescapable shock with two different strain of rats, reported that the strains of the animals and the type of stimulation influenced the animal's avoidance behavior.

It has been reported that early infantile stimulation interacts in a complex fashion with the endocrine system of the organism thus enabling it to better adapt to later stress. Levine, Alpert, and Lewis (1958) reported that the presence or absence of handling during the first 15 days of life had a significant effect on the age at which adrenal ascorbic acid depletion occurred. The handled animals showed significant depletion as early as 12 days, whereas this did not occur in the non-handled animals until 16 days of age. Schaefer, Wingarten, and Towne (1962) proposed that temperature change is a basic variable leading to earlier maturation of the organism and earlier ascorbic acid depletion in the handled animals. Schaefer, et al. (1962) based their conclusions on the observations that hairless neonates have to be removed from the warm nest to the container during the handling experience. Levine and Alpert (1959) reported that infantile stimulation ensures a faster maturation of the central nervous system as indicated by a higher cholesterol content in the brain. Consequently faster maturation of the nervous system implicated faster neuroendocrine integration in young developing organisms. In addition faster adaptive reaction to changes in the environment are immediate through nervous and endocrine systems.

In order to consider the effects of early experience on later behavior one must be concerned with the temporal aspects of the onset of such stimulation. The concept of critical period underlies this concern with age. The critical period hypothesis assumes specific periods in ontogeny during which the organism is particularly sensitive to certain types of stimulation which shape and mold its subsequent behavior (Levine, 1962).

The concept of critical periods has been frequently investigated. Scott (1945) observed that lambs removed from the mother during the first 10 days of life and reared with humans were later unable to make adequate social adjustments to the flock. These inabilities to become associated with the flock endured for several years. Scott, Fredericson, and Fuller (1951) investigated the problem of critical period in the socialization of dogs. The developmental sequences of the puppy was divided into distinct periods: the noenatal period, the transition period, the socialization period, and the juvenile period. During the 10 day neonatal period the principal activities of the puppy are nursing, defecation and urination. Since the animals are essentially blind and deaf, the assumption was made that they were isolated from visual and auditory stimulation. The transition period lasts from 10 days of age and terminates at 3 weeks. It is characterized by the development of perceptual-motor capacities in which the puppy is now vulnerable to environmental changes. The period of socialization, lasting to 10 weeks, is actually a critical period during which socialization occurs. There then ensues a juvenile period which lasts from weaning at 10 weeks to sexual maturity.

Scott (1958) investigated the critical period hypothesis with reference to socialization. Scott's findings generally indicate that disturbance of the social environment (i.e., removal from the litter, isolation, etc.) during critical periods for socialization is associated with considerable destruction in the social capacity of the organism. An additional finding is that no experience during the neonatal period of the dog's development appeared to have any permanent effect on subsequent socialization behavior.

Scott (1962) has suggested three major types of critical period phenomena: the formation of basic social relationships, optimal periods for learning, and infantile stimulation.

The critical period hypothesis has been interpreted in at least two different ways. One is that the same stimulation at different ages has different effects. Thus it can scarcely be questioned that age is an important parameter. The second interpretation is that there are certain limited time periods in development during which a particular class of stimuli will have particularly profound effects and that the same stimulation before and after this interval will have little, if any, effect upon the developing organism (Denenberg, 1964).

In order to experimentally examine the critical period hypothesis several experimental groups are required with each group receiving the same stimulation at a different age and a control group which received no special stimulation. If differences emerge between some experimental groups and the control group, it may be construed as evidence to support the critical period hypothesis. Although the age at which a subject is stimulated is an important parameter, the experiments investigating critical periods in infancy in rats and mice provide little evidence for the hypothesis that stimulation has to occur during certain specified time intervals to affect the organism's adult behavior (Denenberg, 1964).

Denenberg and Karas (1960, 1961) experiments indicated that rats handled within the first 10 days of life were superior in body weight, avoidance learning and survival capability to those handled during the second 10 days. Further, both handled groups were superior to subjects which have been handled for 20 days in infancy.

In general, the avoidance learning research supports the critical period hypothesis. However, Denenberg and Bell's (1960) mouse study suggest that the failure to modify avoidance learning by handling (days 1-5) was because the stimulation induced was not sufficiently intense to affect the subjects.

Research investigating stimulation between birth and weaning using the mouse and rat has established that the critical period hypothesis does not fully explain the finding. Where the data are consistent with the hypothesis, further study indicated that the critical period is a complex function of stimulus intensity. Research using the rat and mouse suggests there may be as many critical periods as there are combinations of independent variable parameters and dependent variable measures (Denenberg, 1964).

The basic mechanisms involved in early experience studies have been conceptualized by Russell (1971). According to his position there are four basic mechanisms involved in the study of the effect of postnatal experience. These four mechanisms are: (1) direct action, (2) cooling, (3) maternal behavior, and (4) stress. The "direct action hypothesis" proposes that the independent variable in the infantile treatment studies is tactile stimulation in addition to the stimulation provided by the mother. The additional stimulation received by the pups affect their physiological systems and may be responsible for mediating changes in adult behavior. The "cooling hypothesis" refers to lowering the animal's body temperature using a variety of methods. The "maternal behavior hypothesis" involves removing the mother from the nest. The amount of tactile stimulation received by the pups is reduced and the body temperature is lowered. Further, the animals are deprived of specific patterns of maternal care. The "stress hypothesis" refers to the noxious stimuli received by the experimental animals. There is, however, no objective way to determine what is and what is not stressful to the young organism. But it is extremely doubtful that shocking or other stress that is applied to the animal could be considered non-stressful. To test an animal's emotional reactivity, the shock threshold can be measured by systematically increasing the shock intensity

(May, 1967) or by using the method of constant stimuli (Guilford, 1954). The subject's response to shock stimuli are classified as "flinch" "jump" and "no response" (Kimble, 1955). "Flinch" is recorded when the animal makes an abrupt startle-like movement without removing more than one paw from the grid. "Jump" is recorded if two or more paws are removed from the grid in response to the shock stimulus, and "no response" is recorded when the animal makes no startle response to a shock stimulus.

The research review presented above suggests that early infantile or postnatal experiences effect later animal behavior (Levine, 1956, Denenberg, 1964). However, an underlying assumption in almost all the postnatal experiments is that the effect of postnatal experiences on later behavior is generalized and non-specific. There is a growing awareness that there is a complex relationship between early experience and the animals' later behavior. Thus, early stimulation interacts in a complex manner with the animals' endocrine system. Also, the investigations of the critical period hypothesis suggest that the later effects of postnatal experience is related to the time at which the stimulation was administered in infancy.

There is recent evidence (Russell, 1971) that the impact of postnatal experience is most effective if there is similarity between early experiences and later environmental stress. For example, the effects of post-natal experience are likely to be more effective on later behavior if there are certain definite similarities between electric shock in infancy and electric shock in adulthood (Russell, 1971).

Another factor influencing the outcome of early stimulation is the strain of the animal. The two strains used in this study were developed originally by Bignami (1965). These strains are the outcome of bidirectional selection for speed of acquisition and retention of a conditioned avoidance response (CAR) developed in a standard type escape-avoidance conditioning apparatus, i.e., Miller-Mowrer shuttle box (Broadhurst and Bignami, 1965). These two strains, the Roman high avoidance (RHA) and Roman low avoidance (RLA), have been used in a number of studies in avoidance learning and open-field behavior (Broadhurst and Bignami, 1965; Fulker, Wilcock and Broadhurst, 1972; Imada, 1972; Wilcock and Broadhurst, 1967); drugs (Gregory, 1967, Holland and Gupta, 1966, 1967a,b; Jordan and Satinder, 1971; Satinder, 1972). Generally, the RHA strain has shown a very high degree of avoidance learning over a 5 day training period whereas the RLA has shown very little learning over the same period. However, under the effect of a CNS stimulant drug the RLA showed an increase in the rate of avoidance learning which tend to lessen the difference between the strains (Satinder, 1971). Further details of the strains are provided by Satinder (1971).

There are only two studies investigating the relationship between early stimulation in selectively bred strains (Levine and Broadhurst, 1963; and Fulker, Wilcock, and Broadhurst, 1972). Levine and Broadhurst (1963) utilized Maudsley reactive and nonreactive strains selected for emotional defecation. These strains were subjected to controlled infantile stimulation by manipulation. Test of open-field emotionality and escape-avoidance conditioning showed that infantile stimulation caused a significant decrease in adult emotionality indices. Fulker's et al study was published after the completion of the present research study. These studies suggest that the use of bidirectionally selectively bred strains serves as a control over the animals' genetic make-up. Further, it is suggested that there is a complex interaction between the type of early stimulation, the particular strain's susceptibility to that stimuli and the animals' later response to that environmental stimuli.

It is important to note that previous studies did not utilize a precise match between factors studied and those performance factors for which the animals were bred. Specifically, there is no current study investigating the effect of shock on later behavior of strains of animals selectively bred for shock avoidance.

The present study attempts to investigate the specific influence of an early experience upon a similar stimuli administered in adulthood. The study of the match between early and later experiences is investigated in conjunction with the strains that are selectively bred for shock avoidance learning. Specifically, this study examines the effects of postnatal electric shock on adult avoidance conditioning, shock sensitivity, and open-field behavior in two strains of rats selectively bred for avoidance conditioning.

METHOD

General Experimental Design

Sixty-two experimentally naive rats RHA/Lu (N=30) and RLA/Lu (N=32) of 20th generation (S_{20}) of the respective strains were given a selection test on a two-way avoidance condition at 100 days of age. From these groups, three pairs of RHA/Lu, and three pairs of RLA/Lu were selected and bred to provide the subjects for this investigation.

Twenty-four hours after birth each litter of pups was divided in two equally matched groups according to body weight and sex. The split-litter technique was used to lessen the genetic variability between litters since the test behaviors of the animals may be influenced by genetic factors (Henderson, 1968). Then all the pups belonging to both groups were taken away from the mother and carried to the experimental room. The animals of one group were placed, individually, on a stainless steel grid and shocked continuously for 3 minutes and designated as handled and shocked (HS). The animals of the other group were also placed individually on the same stainless steel grid for 3 minutes but they were not shocked. They were designated as handled and not shocked (HNS). A non-handled non-shocked (NHNS) group was not used as it is almost impossible not to handle the animals in the split-litter technique. As suggested by Russell (1971), the HS and HNS groups were used to control for the maternal behavior hypothesis, the cooling hypothesis, and the stress hypothesis. A control group (NHNS) does not allow for the control of these three important variables.

The early experience treatment was repeated once every 24 hours for 15 days continuously. The animals were placed on three bars of a shock box. The bars were .5 in. apart and were connected to a shock generator, and shock intensities of 100μa and 200μa were calibrated with an oscilloscope. A shock intensity of 100μa was administered for the first four days and increased to 200μa for the remaining 11 days. All pups were returned to the mother at the same time at the end of the daily treatment. The experimenter then observed both HS and HNS groups for one-half hour. Maternal behavior such as litter gathering and feeding was considered.

For purposes of identification the HS group was marked with a dye on the right rear leg, and the HNS group on the left rear leg.

After 15 days of treatment the animals were left undisturbed except for daily maintenance. They were weaned at 28 days of age and maintained in the laboratory in separate cages according to strain, sex and treatment.

The laboratory temperature was thermostatically controlled with the range 72 ± 2° F. with a humidity level of 40%. A 12 hour light-dark cycle was in effect. Food and water were available ad lib.

Experiment 1

The purpose of this experiment was to investigate the effects of postnatal experience in terms of handling and shocking on the two-way avoidance conditioning.

Subjects

At the age of 85 days, 51 rats, 27 from the RHA/Lu, S_{21} (14 HS, and 13 HNS) and 24 RLA/Lu, S_{21} (11 HS and 13 HNS) were given a two-way avoidance conditioning test using a shuttle-box.

Apparatus

The apparatus was essentially that of Satinder (1971). Basically it was an automated shuttle-box measuring 18 in. x 7 1/2 in. x 7 1/2 in. with no barriers. The box was pivoted on its short axis in the center so that when the animal crossed from one side to the other side the box tilted slightly and activated a microswitch. Only a small shift of the animal's weight across the axis was needed. The conditioned stimulus, a tone, was delivered through 3 1/2 in. speakers, one each in the center of the two opposite ends of the box. The unconditioned stimulus, an electric shock was presented through the grid floor with neon bulbs arranged to maintain a constant voltage drop between adjacent grids. The shuttle-box was enclosed in a sound insulated ventilated chest.

A digital computer with a single timing device accurate to ± .05 sec. was programmed to control the following: the number of trials, the intertrial interval, the duration and the intensity of conditioned and unconditioned stimuli.

It also recorded and displayed the number of trials completed, the number of avoidance responses made, the accumulated avoidance-response and escape-response latencies and the frequency of intertrial crossings.

Procedure

Each animal was tested in an avoidance conditioning situation using the shuttle-box apparatus. For the first 2 days each animal was given 10 minutes for familiarization with the apparatus.

From day 3 to 7, each animal was placed in the apparatus, and given 1 minute, and one practice trial to adapt to the apparatus. This score was not counted towards the daily score. After the practice trial the apparatus was set for 10 trials for the day. When the trials were over the animal was returned to its home cage.

The avoidance conditioning procedure consisted of a conditioned stimulus of 22/kc sec. tone for 5 sec. at 82.5 db. of intensity against a background masking noise of 62.5 db; (sound intensities were averages at the floor level above the standard reference level of .0002µ bar measured by General Radio Sound level meter type 1551-C). This was followed by an unconditioned stimulus of electric shock for 5 sec. It should be noted that in the event that an animal crossed from one side of the shuttle-box to the other during CS delivery, the CS would be terminated and no shock delivered. It was also decided that the animals' movement to the opposite side during UCS delivery would result in UCS termination. The shock generator was set for a pulse duration of 10 m sec. with a peak pulse amplitude of 9 x 10^3 V. and a peak pulse current of 3 x 10^{-3} amp. The pulse repeated at the rate of 55/sec. The intertrial interval was variable from 45 to 55 sec. with an average of 50 sec. (Satinder, 1971).

On each day of the experiment each animal was weighed and carried to the experimental room in a plastic cage.

Experiment 2

This experiment investigated the effects of postnatal experience in terms of handling and shocking on electric shock sensitivity. Since electric shock was utilized in the postnatal experience, it was considered desirable to investigate if the subjects' sensitivity to electric shock was affected in adulthood.

This is the second of three experiments in which the same subjects were used. Ideally, there should have been three independent experiments using three different sets of experimentally naive subjects. There is no doubt that the experience of Experiment 1 could have had a confounding effect on later experimental behavior. However, as different behaviors were tested in all three experiments, the confounding effect was considered minimal.

Subjects

Thirty-two animals at the age of 140 days were randomly selected from the subjects of Experiment 1. The animals were equally matched for strain, treatment (HS and HNS) and sex.

Apparatus

The apparatus consisted of a Plexiglas box 10 3/4 in. x 8 3/4 in. x 8 in. with a grid floor through which shocks of various intensities could be delivered at variable time intervals. The grid was of stainless steel rods 1/2 in. apart and 1/8 in. diameter. The grid was electrified by a step-up transformer with a center-tapped secondary through a small auto-transformer from an A.C. power source. The secondary voltage rating of the transformer was 250-0-250 V., and the output 41 volts/amps.

The shock voltage was delivered to each of the individual grids through a 450,000 ohms resistor (non-inductive) so that each animal has its own limiting resistance. Assuming that the animal contributed an additional 47,000 ohms, the total resistance was 497,000 ohms. This provided a convenient basis for determining the intensity of the shock received by the animal, which was delivered through a rheostat and monitored on an oscilloscope. The time interval and presentation of the shock stimuli were automatically controlled. The apparatus was similar to the one described by Gibbins, Kalant, LeBlanc, and Clark (1971).

Procedure

Each animal was weighed and given 10 trials for each of the 11 electric shock intensities, i.e., .0, .1, .2, .3, .4, .5, .6, .7, .8, .9, and 1.0 ma. On each trial, the order of the 11 shock intensities was presented randomly. Each animal was observed by two observers who recorded the following responses on each of the 110 trials: No Response when the animal did not show any reaction to the shock stimulus. Flinch when the animal displayed a mild startle response by lifting only one paw to the shock stimulus. Jump when the animal displayed a startle response by jumping or lifting more than one paw in response to the shock stimulus.

A double blind technique was used. Three experimenters were involved with the first experimenter administering the shock while the other two served as independent observers. The two independent observers recorded the responses of the animals but did not know which shock intensity was being presented, nor did they know the strain or treatment group of the animal.

Experiment 3

The purpose of this experiment was to test the animals from both strains and treatment groups in the open-field situation, in order to measure emotional reactivity.

Subjects

The same animals from Experiment 2 were utilized. These animals were 250 days of age.

Apparatus

The open-field apparatus was 36 inches square with sixteen 9 in. square sections marked on the floor. It was made of plywood and white Arborite and the walls were 18 in. high. The front wall was a sliding door of transparent Plexiglas which served as an observation screen as well as a door for cleaning the arena. The arena was lighted by four 36 in. fluorescent lights at the height of 36 in. from the floor level and illuminated the arena at

230 foot candles (ftc). A white noise generator was used to produce 65 db. of masking noise (sound intensity was average at the floor level above the standard reference level of .0002μ bar measured by General Radio sound-level meter type 1551-C). In the center of the wall on the right of the observation screen was attached a start-box measuring 9 in. x 9 in. x 6 in. The start-box was separated from the arena by a clear plastic sliding partition.

Procedure

Each day each animal was weighed and taken to the experimental room in a plastic cage. All the animals were tested in the open-field apparatus on four successive days at approximately the same time of the day. The animal was placed in the start-box with the door to the arena closed. Both illumination and sound stimuli were turned on, and at the same time the door of the start-box to enter the arena was lifted. The time the animal took to emerge from the start-box into the arena was recorded. Emerging behavior occurred when the hind legs of the animal crossed into the first square of the arena. Recordings were also made during the 5 min. trials of the total number of sections crossed, number of inner four sections crossed, number of fecal boli, presence or absence of urination, and frequencies of rearing and grooming.

RESULTS AND DISCUSSION

Experiment 1

The response measures of the avoidances, avoidance latencies and escape latencies were evaluated by analysis of variance. Differences with associated probabilities of less than .01 were considered significant. A conservative significance level was used in this experiment as all experimental animals were bred for the acquisition of avoidance responses.

Figure 1 indicates that the HS groups of both strains had higher rates of avoidance response. In the RHA/Lu strain the HS group learned the avoidance response at a significantly faster rate than the respective HNS group ($F = 15.54$, $df = 1/25$, $p < .005$). Both RHA/Lu groups showed a significant learning over the five days of training ($F = 14.71$, $df = 4/11$, $p < .001$). In the RHA/Lu strain, however, there was no significant difference between the HS and HNS groups and no significant learning appeared to have occurred over 5 days of training. The avoidance performance of the RHA/Lu strain was significantly higher than that of the RLA/Lu strain

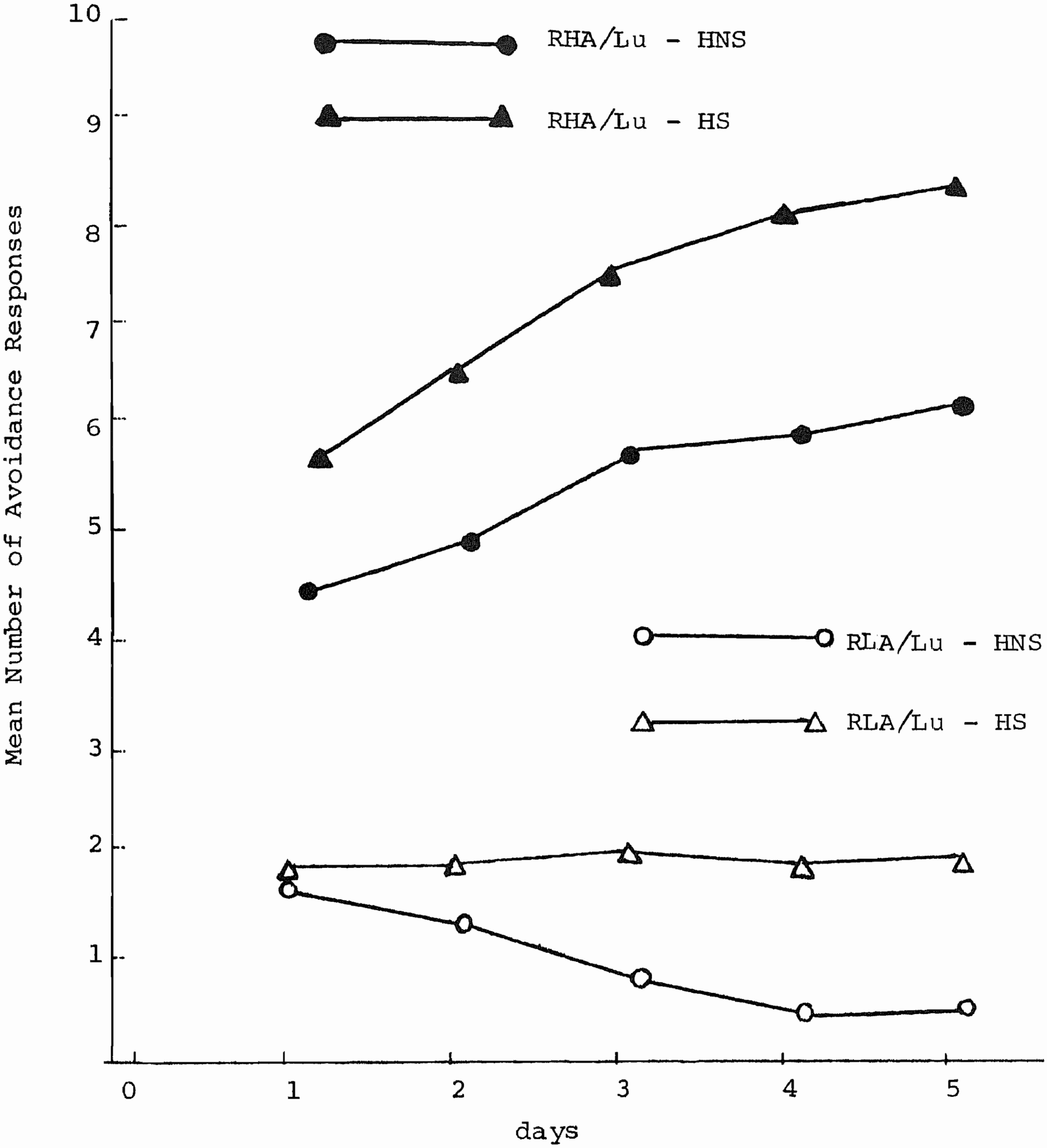

Fig. 1.--Mean number of avoidance responses of the RHA/Lu and the RLA/Lu strains according to HNS and HS treatment groups.

($p < .001$).

Both Figures 2 and 3 show that the HS groups of both strains took less time to avoid and escape than the respective HNS groups. In the RHA/Lu strain, the differences between the HS and HNS groups were significant for both avoidance ($F = 9.78$, $df = 1/25$, $p < .005$) and escape ($p < .005$) latencies. There were no significant differences between HS and HNS groups of the RLA/Lu strain for either of the latency measures. Significant differences were observed between strains for both avoidance-response ($F = 112.49$, $df = 1/47$, $p < .001$) and escape response ($p < .001$) latencies. The present results are consistent with the findings of Levine (1956), Baron, Brookshire, and Littman (1957), Levine and Wetezel (1963), and Gauron (1964b), in which infantile manipulation produced a significantly higher rate of avoidance acquisition. These findings and the present results support the notion that early infantile stimulation enhances later avoidance conditioning.

The finding that the HS group of both strains had higher avoidance scores than the respective HNS group contradicts the findings of Levine, Chevalier, and Korchin (1956), Denenberg and Smith (1963), Levine and Broadhurst (1963), Gauron (1964a) in which infantile handling or shocking proved detrimental to the effective acquisition

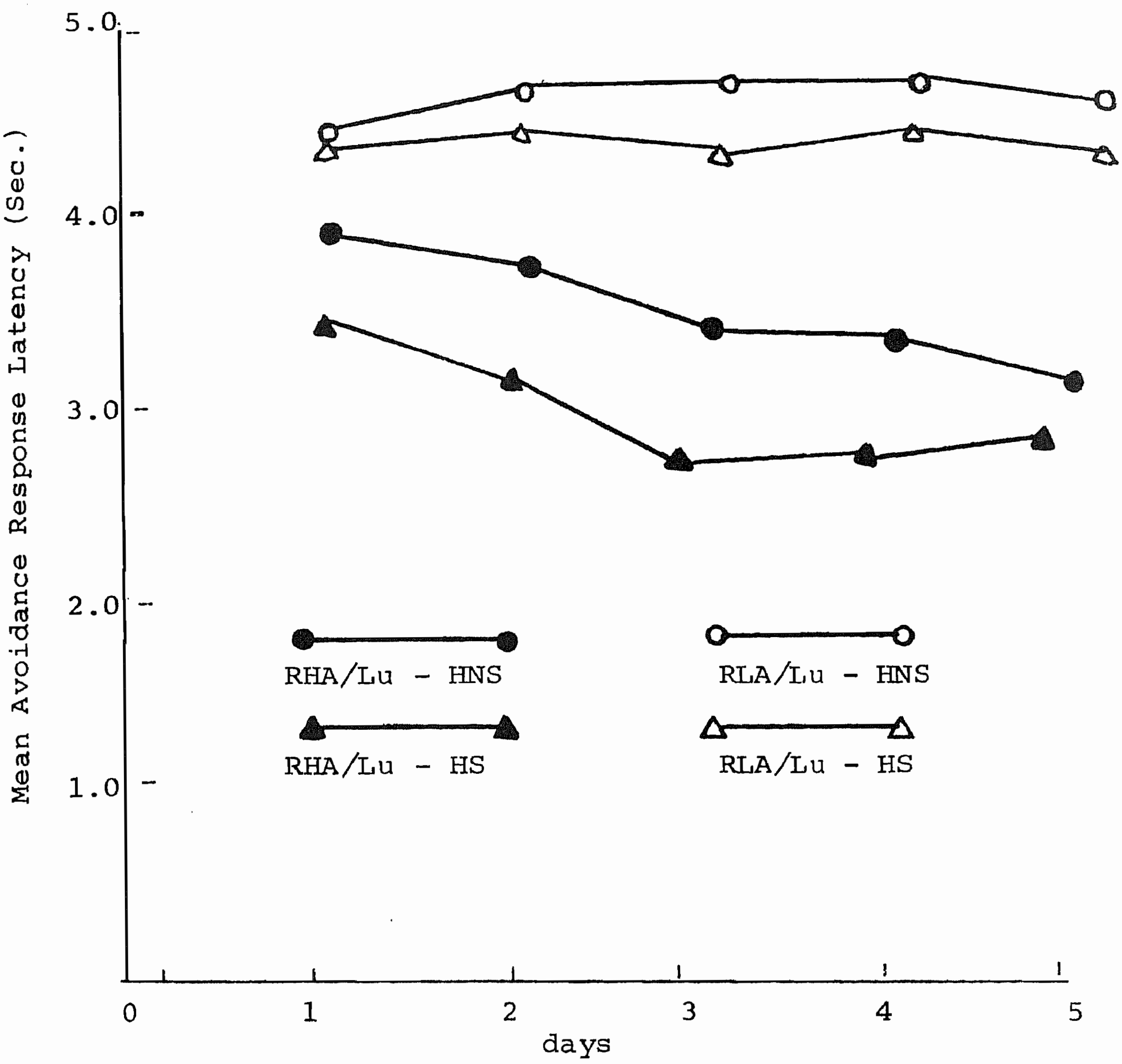

Fig. 2.--Mean avoidance-response latency (sec.) of HNS and HS groups of the RHA/Lu and the RLA/Lu strains.

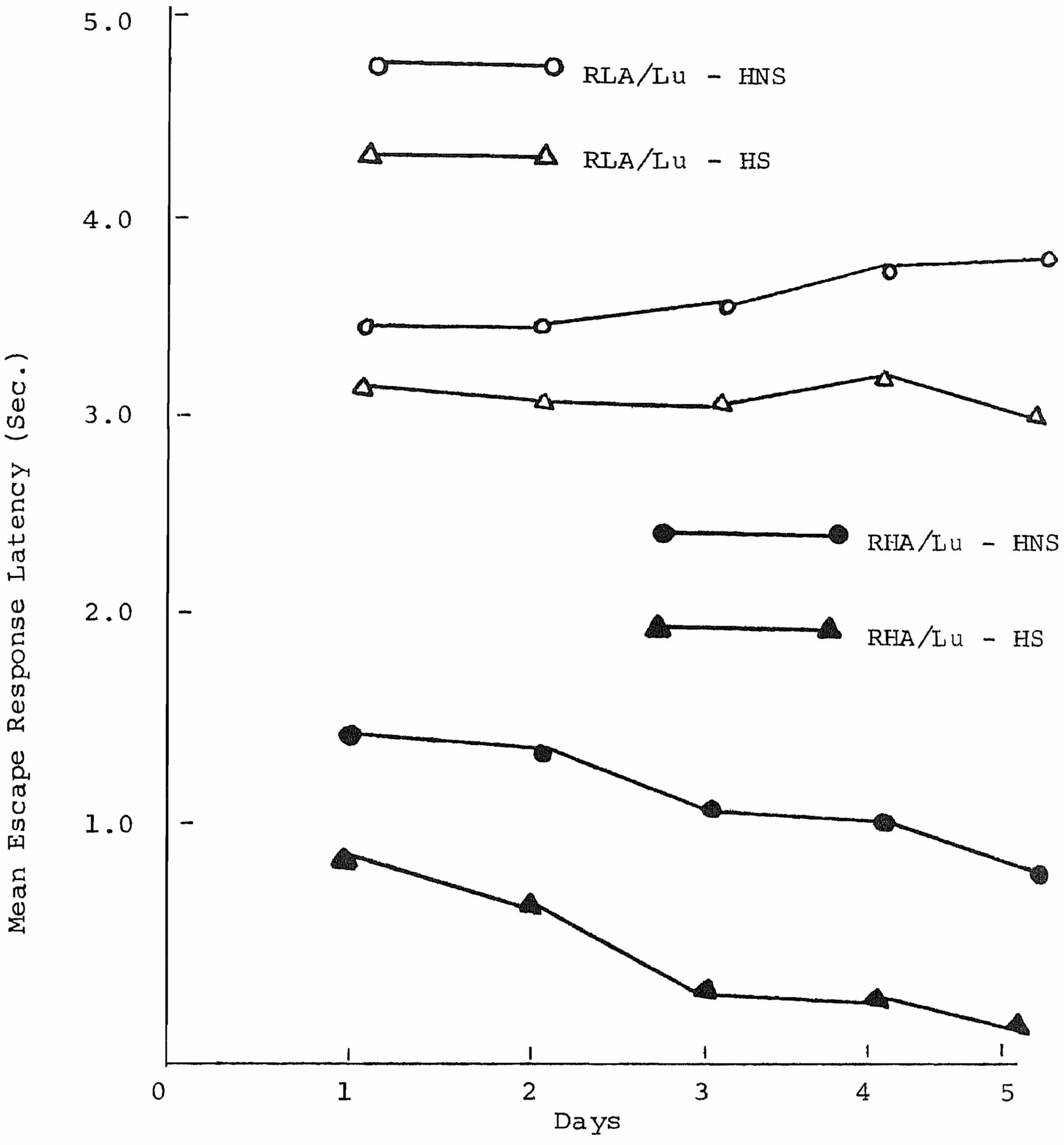

Fig. 3.--Mean escape-response latency (sec.) of HNS and HS groups of the RHA/Lu and the RLA/Lu strains.

avoidance response.

The contradiction between the present findings and other investigations yielding no significant differences in avoidance behavior due to early experiences may be explained in several ways. Part of the difference may be due to methodological differences. In studies where early stimulation was detrimental to adult performance, there was no clear match between infant stimulation and the task requirement for the adult. In Gauron's (1965) study, the infant stimulation was water traumatization while the adult task was open-field testing and avoidance conditioning. In the present experiment, the early stimulus and the later avoidance task involved the same noxious stimulus, and early stimulation was found to enhance later avoidance behavior. Another explanation for divergent finding may be found in the specific methodology employed in the experiments. In the present study, the split-litter technique was used while previous investigation utilized separate litters. The separate litters technique allows for more random error difference between the litters than does the split-litter technique. The reduced error variance may then permit the attainment of the group difference found in the present study.

Experiment 2

Table 1 shows the means of electric shock thresholds for the flinch and jump responses. The threshold was determined by the minumum shock intensity at which the animal responded 50% or more for each given response measure.

Inter-observer reliability based on the observation made on the 32 animals was $\underline{r}$ = .825 for the flinch response and $\underline{r}$ = .927 for the jump response. There were no systematic significant differences between the recordings made by the two observers.

The RHA/Lu strain had a significantly lower flinch threshold ($\underline{F}$ = 43.88, $\underline{df}$ = 1/24, $\underline{p}$ < .001) than the RLA/Lu strain. The HS group of the RHA/Lu strain and the HNS group of the RLA/Lu strain had lower flinch thresholds than the HNS group of the RHA/LU strain and HS group of the RLA/LU strain, respectively. Further, there were no significant differences between the HS and HNS groups of both strains. A further analysis indicated that the females of both strains had significantly lower flinch thresholds than the males ($\underline{p}$ < .01).

The jump threshold (Table 1) of the RHA/Lu strain was significantly lower ($\underline{p}$ < .001) than that of the RLA/Lu strain. The HS group of the RHA/Lu strain had a significantly lower jump threshold ($\underline{F}$ = 5.52, $\underline{df}$ = 1/12,

TABLE 1

MEANS OF ELECTRIC SHOCK THRESHOLDS

Flinch Threshold (Ma.)							
RHA/Lu				RLA/Lu			
.307				.552			
HNS	HS	Females	Males	HNS	HS	Females	Males
.318	.297	.213	.396	.539	.566	.478	.627

Jump Threshold (Ma.)							
RHA/Lu				RLA/Lu			
.807				.996			
HNS	HS	Females	Males	HNS	HS	Females	Males
.872	.741	.691	.922	.996	.997	.992	1.000

p .05) than the HNS group of the RHA/Lu strain. There were no significant differences between the HS and HNS groups of the RLA/Lu. Additional analysis indicated that there was a tendency for the females to have a lower jump threshold than the males of the respective strains. The sex differences, however, were significant only for the RHA/Lu strain ($p < .001$).

There was a trend for the HS groups of both strains to be heavier in body weight than the respective HNS groups. This finding is in line with those of Weininger (1956) and Gauron (1964a). The differences between the HS and HNS groups were significant for the RHA/Lu strain ($p < .05$). The RHA/Lu strain was also heavier than the RLA/Lu strain ($F = 5.34$, $df = 1/24$, $p < .05$).

The results that the HS group of the RHA/Lu strain had low flinch and jump threshold support the findings of May (1967) in which it was reported that the handled animals were more sensitive to differences in electric shock intensity than the non-handled controls. The present findings, however, contrast with the results of Littman, Steven, and Whittier (1964) in which movement (comparable to flinch) threshold for previously shocked animals were significantly higher than those of the control animals, whereas there no differences in squeal (comparable to jump) thresholds.

The discrepancy between this study and Littman et al. (1964) may be related to the different strains used in the two investigations. Whereas significant differences were obtained using the RHA/Lu strain, no such differences were found between the HS and HNS groups of the RLA/Lu strains. Nevertheless, the present results, in relation to the effects of postnatal shock experience on adult shock threshold, suggest that the postnatal experience made the HS animals more sensitive to shock than the HNS animals.

Experiment 3

Table 2 shows the means of the open-field measures and body weight on the first day of open-field testing. No significant differences were found between strains on any measure of open-field behavior. These findings are in keeping with those of Broadhurst and Bignami (1965) in which no significant differences were found between the high-avoidance and low-avoidance strains in open-field behavior. Further, there were no significant differences between the HS and HNS groups on these measures. There was however, a tendency for the HS groups to differ from the HNS group in several measures of open-field behavior. Thus the HS groups of both the RHA/Lu and RLA/Lu strain tended to have shorter latencies to emerge from the

TABLE 2

Means of Open-Field Measures and Body-Weight

Measures	RHA/Lu				RLA/Lu			
	HNS	HS	Females	Males	HNS	HS	Females	Males
			151				136	
Latency to Emerge (sec.)	160	142	62	240	157	114	108	164
			33				27	
Total Number of Sections Crossed	31	35	52	14	26	28	37	16
			1.2				1.0	
Number of Inner Sections Crossed	1.2	1.3	2.0	.5	1.1	.8	1.4	.5
			1.0				.5	
Number of Defecations	1.1	.9	1.5	0.5	.7	.3	.1	.9
			.3				.3	
Presence or Absence of Urination	.2	.3	.4	.2	.2	.4	.1	.5

Continued on page 42

TABLE 2.--Continued

Measures	RHA/Lu				RLA/Lu			
	HNS	HS	Females	Males	HNS	HS	Females	Males
			17				15	
Frequency of Rearing	14	19	27	7	15	15	20	10
			1.3				1.9	
Frequency of Grooming	1.1	1.6	2.2	.5	1.8	2.1	2.5	1.4
			357				335	
Body Weight (gms.)	336	378	278	436	328	341	269	400

start-box. Also, the HS groups crossed a higher number of sections, had higher frequencies of rearing and grooming, lower defecation scores, and were heavier than the HNS groups. The fact that the HS group of both strains tended to be active and defecated less in the open field, is in keeping with the findings of Denenberg and Morton (1962), Denenberg and Whimbey (1963) and Denenberg and Smith (1963) in which handling and/or shocking resulted in higher levels of activity and lower defecation scores in the open field.

There were significant sex differences ($\underline{p} < .01$) for the RHA/Lu strain on several open-field measures. The RHA/Lu males, as compared with the RHA/Lu females, took a longer time to emerge from the start-box, crossed fewer sections, and had lower frequencies of rearing and grooming.

The HS group of the RHA/Lu strain had increasingly shorter latency to emerge from the start-box while the HNS group had an increasingly longer latency. These differences were significant ($\underline{p} < .025$) over a four day testing period. The HS group of the high-avoidance strain crossed more and more whereas the respective group of the low-avoidance strain crossed fewer and fewer sections over 4 days of testing as compared to the corresponding HNS groups, this interaction between treatment groups, strains and days of testing was significant ($F = 6.36$, $df = 3/72$, $p < .005$). There were also significant 3-way interactions between the variables for inner section ($p < .025$), rearing ($p < .005$) and grooming ($p < .05$).

Table 3 shows a correlation matrix based on the scores of all the 32 animals on measures of avoidance, shock-threshold, open-field, and body-weight. An analysis of the significant correlations revealed 2 groups each correlating highly with certain measures and showing a low correlation with others. One cluster of correlations includes measures of the escape-conditioning indices and shock threshold and the other includes primarily the open-field measures. The intercorrelations between the escape-avoidance and open-field response measures are consistent with the findings of Broadhurst and Bignami (1965). Correlations were also calculated for both the strains, treatment groups and sexes. For the high-avoidance strain, the correlations between escape-avoidance and shock thresholds were insignificant while the correlations of shock thresholds with open-field measures were significant. For the low-avoidance strain, however, the correlations between escape-avoidance and shock thresholds were insignificant, and no appreciable significant differences emerged between other variables.

The correlations pertaining to the HNS and HS

TABLE 3

Correlation Matrix of Escape-Avoidance, Shock Threshold and Open-Field Measures

Measures	1	2	3	4	5	6	7	8	9	10	11	12
1. Avoidances												
2. Avoidance Latency	-.98											
3. Escape Latency	-.98	.95										
4. Flinch Threshold	-.61	.61	.62									
5. Jump Threshold	-.58	.62	.58	.78								
6. Defecation	.26	-.31	-.25	-.27	-.59							
7. Urination	-.10	.06	.08	.18	-.14	.53						
8. Latency to Emerge	.04	-.07	-.01	.09	.34	-.39	-.46					
9. Total Sections Crossed	.16	-.14	-.18	-.25	-.40	.34	.31	-.87				
10. Inner Sections Crossed	.15	-.11	-.16	-.19	-.32	.12	.17	-.64	.79			
11. Rearing	.08	-.07	-.11	-.22	-.39	.38	.40	-.88	.97	.74		
12. Grooming	-.10	.10	.06	-.01	-.14	.31	.45	-.85	.77	.59	.80	
13. Body Weight	.06	-.08	-.04	.35	.33	-.15	.11	-.51	-.53	-.41	-.55	-.40

——— $p < .01$ ═══ $p < .05$

treatment groups did not differ in any significant manner from those presented in Table 3.

Analyzing the results according to the animals' sex yielded several significant findings. In males, the intercorrelations of measures of escape-avoidance, body-weight and defecation, along with open-field measures and flinch threshold were all highly significant. In females, the intercorrelations between measures of escape-avoidance, defecation, and urination were significant, while the correlations between body-weight and open-field measures did not reach significance.

The results indicated that there were significant correlations between the two measures of shock threshold and the measures of avoidance conditioning while no such significance was observed between the shock threshold measures and measures of open-field behaviors. The relationship between shock sensitivity and avoidance has recently been investigated by Satinder and Petryshyn (in press). The present results indicated significance in the avoidance behavior (Experiment 1) but not in the shock threshold (Experiment 2). It was realized in retrospect that all 51 animals were utilized in Experiment 1 of which 32 were randomly selected for the second and third Experiments, and in the process of choosing the animals that differentiated the treatment group in Experiment 1 were deleted. This could be one of the reasons for the lack of clear cut results in the shock threshold experiment. Another reason for a lack of clear cut results was that Experiment 1 measured avoidance response, a factor for which the animals were bred, whereas Experiment 2 measured another factor, reactivity.

Russell (1971) suggested that there are 4 possible mechanisms to account for the effects of postnatal experience on adult behavior. The present findings are discussed in the context of the direct action hypothesis, since 3 out of the possible 4 mechanisms were either controlled or manipulated experimentally in this investigation. Thus, cooling, disruption in the maternal care, and subjecting the animals to considerable stress were experimentally manipulated and as a consequence were under the experimenters' control. According to Levine (1962) the effects of postnatal experiences are indicated by the direct action of stimulation impinging upon the young organism. It is assumed that the additional stimulation derived from the postnatal experience serves to modify the physiological systems of the neonate (Levine and Alpert, 1959). However, there are competing viewpoints to explain the above mentioned effects. According to Levine (1956) and Denenberg (1959) stimulation during infancy constitutes a "stress" for the developing organisms and that such early "stress" raises the tolerance of the animal for subsequent stress. This being the case, the HS group should have shown lower rates of avoidance responding and higher shock thresholds. The present results do not support this explanation. The alternative explanation of Bovard (1958) which maintains that early stress reduces resistance to later stress might be more appropriate to explain the present area of avoidance findings and sensitivity to shock. It may appear that the viewpoints of Levine (1956), Denenberg (1959), and Bovard (1958) are irreconcilable. This does not seem to be the case however, since the clinical implications of the early experience research would not permit an exclusive support of one or the other viewpoints. Further, the interaction between genotypes and postnatal experience seem to indicate that one of these theoretical positions is correct under certain conditions (Gauron, 1964a).

The effects of postnatal experience on avoidance, shock threshold and open-field behavior support the position of the specificity of effect. It has been suggested by Russell (1971) that exposure to electric shock postnatally effects only the behaviors involving electric shock, such as shock avoidance and shock threshold but not subsequent open-field behavior.

The present investigation found that early stimulation enhanced the adult's response to that aversive stimulus. These findings indicated that exposure to postnatal electric shock effected only the later behaviors involving the component, i.e., shock-avoidance and shock threshold. Other behaviors (e.g., open-field behaviors) were not effected by early shock exposure. One avenue of future research may involve the more specific effect of early stimulation on adult responses in that realm. It would be of interest, for example, to examine the relative effect of fixed versus variable intensities of early electric shock on adult responses to fixed and variable shock administration. Using the present paradigm, RHA/Lu and RLA/Lu strains would be divided into fixed and variable shock groups for postnatal treatment. The fixed group would receive a constant shock intensity over a 15 day period while the variable group would be exposed to a gradually increasing intensity over the same period. The effect of fixed and variable postnatal shock would then be examined for the fixed and variable avoidance shock in adulthood. This proposed experiment attempts to delineate even further the specific effects of early exposure on later responsiveness within that realm.

Another suggested research project is the use of different strains (e.g., Maudsley reactive and non-reactive) in association with the stimulus for which they were bred. Thus, the present paradigm could be modified to examine the relationship of fixed early handling versus a variable degree of handling for the Maudsley strains. This proposed experiment would examine the effects of specific degrees of early stimulation on strains of animals bred to react to that stimulus. These proposed investigations are suggested to determine if the present effects are generalizable across different situations.

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