The Effects of Intrauterine Shock on the Emotionality of the Offspring in the Albino Rat

Mary B. Mehrer

THE EFFECTS OF INTRAUTERINE SHOCK ON THE EMOTIONALITY OF THE OFFSPRING IN THE ALBINO RAT

by

Mary B. Mehrer

Bachelor of Arts, University of North Dakota, 1970

A Thesis

Submitted to the Graduate Faculty

of the

University of North Dakota

in partial fulfillment of the requirements

for the degree of

Master of Arts

Grand Forks, North Dakota

August
1973

This thesis submitted by Mary B. Mehrer in partial fulfillment of the requirements for the Degree of Master of Arts from the University of North Dakota is hereby approved by the Faculty Advisory Committee under whom the work has been done.

John B. Carman
(Chairman)

R H Kolstoe

Paul H Wright

A William Johnson
Dean of the Graduate School

Permission

Title THE EFFECTS OF INTRAUTERINE SHOCK ON THE EMOTIONALITY OF THE OFFSPRING IN THE ALBINO RAT

Department Psychology

Degree Master of Arts

In presenting this thesis in partial fulfillment of the requirements for a graduate degree from the University of North Dakota, I agree that the Library of this University shall make it freely available for inspection. I further agree that permission for extensive copying for scholarly purposes may be granted by the professor who supervised my thesis work or, in his absence, by the Chairman of the Department or the Dean of the Graduate School. It is understood that any copying or publication or other use of this thesis or part thereof for financial gain shall not be allowed without my written permission. It is also understood that due recognition shall be given to me and to the University of North Dakota in any scholarly use which may be made of any material in my thesis.

Signature Mary McAvers

Date Aug. 1, 1973

ACKNOWLEDGMENTS

I wish to express my appreciation to the members of my committee, Dr. R. H. Kolstoe and Dr. P. W. Wright, for their suggestions and aid in writing this paper. I also wish to thank Barb McDonald and Brenda Wiseman for their assistance in collecting the data. Their work was invaluable and greatly appreciated. Most of all, I wish to thank my chairman, Dr. John B. Carman. Without his encouragement, guidance, and technical knowledge, the project could not have been completed.

TABLE OF CONTENTS

	Page
ACKNOWLEDGMENTS	iv
LIST OF TABLES	vi
LIST OF FIGURES	vii
ABSTRACT	viii
Chapter	
I. INTRODUCTION	1
II. METHOD	18
Subjects Apparatus Procedure	
III. RESULTS	24
Test A: Open-Field Test Test B: Avoidance Acquisition	
IV. DISCUSSION	48
APPENDIX. Raw Data and Statistical Comparisons	53
REFERENCES	64

LIST OF TABLES

Table | Page

1. Mean Number of Squares Entered for the Combined Three Days of Open-Field Testing by Control, Group I, and Group II Offspring 30

2. Mean Number of Avoidances and Intertrial Responses (ITRs) for Three Days (75 Trials) for Control, Group I, and Group II Subjects 38

3. t-Test Comparisons for the Open-Field Test 54

4. t-Test Comparisons for Avoidance During Avoidance Acquisition in a Two-Way Shuttlebox 55

5. t-Test Comparisons for Intertrial Responses (ITRs) During Avoidance Acquisition in a Two-Way Shuttlebox 56

6. Raw Data for Control Offspring for Three Days of Open-Field Testing 58

7. Raw Data for Group I Offspring for Three Days of Open-Field Testing 59

8. Raw Data for Group II Offspring for Three Days of Open-Field Testing 60

9. Raw Data for Control Offspring for Three Days of Avoidance Acquisition 61

10. Raw Data for Group I Offspring for Three Days of Avoidance Acquisition 62

11. Raw Data for Group II Offspring for Three Days of Avoidance Acquisition 63

LIST OF FIGURES

Figure Page

1. Comparison of the Mean Number of Squares Entered by Males and Females in the Open-Field Test 26

2. Mean Number of Squares Entered by Females in the Open-Field Test 29

3. Mean Number of Squares Entered by Males in the Open-Field Test 32

4. Comparison of the Mean Number of Avoidances Made by the Subjects in Each Group Across Three Days of Avoidance Acquisition 35

5. Comparison of the Mean Number of Total Avoidances (for 75 trials) by Males and Females in Each Group . . 37

6. Comparison of the Mean Number of Intertrial Responses Made by Each Group Across Three Days of Avoidance Acquisition 40

7. Comparison of the Mean Number of Total Intertrial Responses by Males and Females in Each Group 43

8. Mean Number of Intertrial Responses Made by Males Across Three Days of Avoidance Acquisition 45

9. Mean Number of Intertrial Responses Made by Females Across Three Days of Avoidance Acquisition 47

ABSTRACT

Recent research with animals indicates that stress applied during pregnancy can influence the emotionality of the offspring (Thompson, 1957; Fazzaro, 1971). The present study was designed to investigate the effects of escapable versus inescapable electric shock, administered during pregnancy, on the behavior of the offspring.

Female Sprague-Dawley albino rats were mated and placed into three groups. Group I females were given daily sessions of twenty-five, escapable, 0.6mA shocks from Day 10 through Day 16 of pregnancy. Group II females were given the same amount of inescapable shock. Control subjects were placed in the shock apparatus for an equivalent amount of time but shock was never administered.

The offspring were tested for ambulation in an open-field for three consecutive days at 60-80 days of age. They were also tested for avoidance acquisition in a two-way shuttlebox for three consecutive days at 66-93 days of age. The primary data for the latter test consisted of number of avoidances and number of intertrial responses (ITRs). The overall results suggest that the Group II (N=30) offspring were less emotional than either the Group I (N=25) or Control (N=22) offspring. This was inferred from their superior performance in the avoidance acquisition test (also increased ITRs) and their increased activity in the open-field. The Group I offspring were intermediate between the Group II and Control _Ss_ in shuttlebox performance and open-field activity.

CHAPTER I

INTRODUCTION

Evidence from a variety of animals indicates that events occurring early in life have a profound influence on later behavior (Thompson and Schaefer, 1961). Recent findings suggest that the influence may be extended to the prenatal environment (Thompson, 1957).

Sontag (1941) reported that with humans various types of stress applied to a female during the course of pregnancy can affect the structural development of the offspring. Stressor agents such as nutritional deficiencies, x-irradiation, toxins, drugs, disease, anoxia, and various chemical and hormonal compounds can cause offspring abnormalities such as cleft palate, blindness, deafness, cranial malformations, absence of limbs, and many other defects (Fraser, Fainstat, and Kalter, 1953; Sontag, 1941; Warkany and Nelson, 1940).

If stressor agents applied during pregnancy can influence the structure of the developing fetus, it seems likely that such factors could also affect the organism's behavioral development and later adjustment. Sontag suggested this in his 1941 article and stated that:

> . . . such factors as the drugs women use during pregnancy, their nutrition, endocrine status, emotional life and activity level during gestation may contribute to the shaping of physical status, behavior patterns, and postnatal progress of the children they bear (Sontag, 1941, p. 1002).

The hypothesis that prenatal stress may affect the behavior of the offspring is currently receiving a great deal of attention and the effects of both physical stress and psychological stress (anxiety) are being investigated.

Thompson (1957) was one of the first to investigate the effects of prenatal maternal anxiety on the emotional behavior of the offspring. Female Long-Evans hooded rats were given intense shock preceded by a buzzer. They were then taught to avoid the shock. These subjects and an equal number of nonshocked control animals were then mated. When pregnant, the experimental animals were placed in the shock box and three times daily throughout pregnancy presented with the buzzer but not allowed to make the avoidance response. Shock was never given during this time. The presentation of the buzzer, which previously had signaled forthcoming shock, and the blocking of the response which had previously allowed the animal to avoid the shock presumably elicited "anxiety" in the pregnant subjects.

The offspring were cross-fostered to control for possible postnatal influence. Cross-fostering involved giving some newborn infants from experimental mothers to nonshocked control mothers, other experimental mothers, or leaving them with their own mothers. Offspring from nonshocked control mothers were likewise raised by their own mothers, experimental mothers, or other control mothers.

To assess the permanence of any effects found, tests of emotionality were given the offspring at 30-40 and 130-140 days of age. One test consisted of recording the amount and latency of activity in an open-field for ten minutes on three consecutive days. Another test recorded latency to leave the home cage and latency to reach food after 24 hours of food deprivation.

The results indicated that while cross-fostering had no effect, the prenatal treatment did. Prenatally manipulated animals were significantly less active and had longer latencies in the open-field than did the control offspring. This finding held true for both the early (30-40 days) and late (130-140 days) tests, but the difference was less dramatic in the later test. Experimental offspring also had significantly longer cage-emergence and time-to-reach-food latencies than did the control offspring on both the early and late tests. Thompson interpreted these results to mean increased emotionality in those subjects whose mothers had been subjected to anxiety during pregnancy.

Interpreting low activity in an open-field situation as an indication of emotionality or fearfulness is congruent with previous findings by Hall and Broadhurst reported by Hall (1941) and Grey (1971). Both Hall and later Broadhurst used a selective breeding procedure to assess the hereditary aspects of fearfulness. Rats which scored high on measures of fearfulness (mainly high defecation scores in an open-field situation) were intermated as were rats which scored low. This procedure was repeated for subsequent generations until separate strains of rats were obtained. When tested in the open-field, the Nonemotional rats ambulated much more than did the Emotional animals. This finding is in agreement with studies indicating that fear inhibits exploratory behavior (Montgomery and Monkman, 1955; Hayes, 1960).

A further attempt to validate the open-field ambulation scores as an index of emotionality was undertaken by Thompson, Watson, and Charlesworth (1962). Open-field activity scores of 40 rats were recorded for three days. The subjects were then divided into two groups matched for activity level. One group was given three daily shock sessions (presumed to increase fear) for two weeks, and the other group was left in their home cage. Upon retesting in the open-field, the nonshocked rats' activity level remained the same while the activity level of the shocked group declined significantly. These results would appear to confirm the hypothesis that lowered activity in an open-field situation is indicative of emotionality or fearfulness.

This interpretation of the relationship between fear and activity level has also received support from a later investigation by Whimbey and Denenberg (1967). In a factor-analytic study they found that ambulation scores in the open-field were positively correlated with exploration and negatively correlated with fear.

Satinder (1968) also investigated intercorrelations between the measures of open-field and escape-avoidance behavior. He found that open-field measures including defecation, ambulation, unination, rearing, and grooming correlated well with each other. The same was true for escape-avoidance measures of avoidances, escapes, no-escapes, avoidance latency, escape latency, and intertrial crossings. However, there were very few significant correlations between the measures of open-field and escape-avoidance.

Latency to leave the home cage, often called an emergence test, has also been used to measure emotionality. Anderson (1938) measured defecation in both an open-field situation and while the animals were forced to wade in water. He then compared these scores with emergence latencies and found that rats which had the shortest emergence latencies defecated less (indicating less fear).

In general, open-field ambulation scores, defecation scores, cage-emergence latencies, and latency to reach food in a runaway have been the most frequently used measures of fearfulness. Previous studies using these measures have reported consistent results, thereby supporting the hypothesis that these measures are, in fact, indices of emotionality.

In order to attribute any change in offspring emotionality to the prenatal maternal manipulations, one must control for other possible variables that could contribute to the change. Among these variables are premating and postnatal factors. The study by Thompson (1957) indicating that prenatal treatment affected the emotionality of the offspring has been criticized by Kaplan (1957) for the absence of premating controls. Kaplan pointed out that the treatment (shock) given the experimental mothers before they were mated could have caused systematic changes and that these changes and not the treatment during pregnancy (anxiety) could have been the causal factor in the offsprings' increased emotionality. This hypothesis, that premating treatment and not prenatal treatment was the important variable, was investigated in a later study by Thompson, Watson, and Charlesworth (1962). Female Sprague-Dawley albino rats were given three shock sessions a day for ten days prior to mating. They were not manipulated during pregnancy. Offspring were cross-fostered at birth and tested in an open-field at 40-60 days and in a timidity runway at 60-80 days of age. The results indicate that stress given prior to conception had little effect on the offspring. However, some evidence was obtained that stressed mothers rear their young differently than nonstressed mothers. The young reared by stressed mothers were more emotional than those reared by nonstressed mothers. However, since there was no stress applied <u>during</u> pregnancy it is not known how the premating and cross-fostering interaction combines with prenatal treatment.

A study by Joffe (1969) also investigated the hypothesis that premating stress could influence offspring emotionality. Maudsley rats were placed in three groups: one group was treated according to Thompson's procedure (i.e., subjected to anxiety during pregnancy); one group, the "premating control" group, was given shock avoidance training before pregnancy, but not treated during pregnancy; a third (Control) group was not manipulated. All offspring were fostered to untreated Non-emotional mothers and the offspring of the latter were fostered to mothers of each of the three groups.

An avoidance conditioning task and open-field ambulation scores were used to assess treatment effects. The offspring of experimental mothers stressed during pregnancy performed significantly better on the avoidance task than did those of control mothers. Offspring of the "premating control" group did not differ from the Control offspring indicating that treatment during pregnancy was the important variable. No significant difference was found between the experimental and control groups on the open-field test.

These and the results of the Thompson et al. (1962) study indicate that prenatal treatment per se can influence offspring emotionality. Joffe's (1969) results also indicate that postnatal treatment (type of postnatal mother) can confound prenatal treatment. Offspring of the untreated Non-emotional mothers which were cross-fostered to mothers which had received either the "premating" treatment or the "stress during pregnancy" treatment were significantly poorer at avoidance learning than those which had untreated foster mothers.

Attempting to isolate and manipulate a single variable such as the effect of prenatal stress on offspring emotionality has proven exceedingly difficult. One needs to be certain that it is the prenatal treatment *per se* and not the fact that the treated mothers are, perhaps as a consequence of the treatment, more emotional and subsequently rear their offspring differently than nontreated mothers. Most researchers use cross-fostering to control for this variable. However, cross-fostering is, in and of itself, a mild form of stress, and it could confound the prenatal treatment by either accentuating or negating its effect. The following study investigated this possibility.

In an attempt to replicate Thompson's 1957 study, Hockman (1961) subjected female Long-Evans hooded rats to anxiety-producing stress three times daily throughout gestation. The litters were cross-fostered in such a manner that experimental young were raised by either their own mothers, control mothers, or other experimental mothers. Control offspring were cross-fostered in a similar manner.

Ambulation and defecation scores in an open-field at 30-45 days and 180-210 days were used to assess emotionality. While the results were not clearcut, they indicated that only experimental offspring which were cross-fostered were more emotional (less active) than controls. This finding was true only for the early test (30-45 days) since there was no significant difference between groups when the animals were mature. Experimental offspring raised by their own mothers did not differ from appropriate controls.

Hockman's results may be interpreted to mean that the prenatal treatment alone was not sufficient to affect the offspring but must be supplemented by the postnatal treatment of cross-fostering. However, nonstressed control offspring that were reared by stressed mothers did not differ from those reared by nonstressed control mothers. In other words, stressed mothers did not alter the emotionality of nonprenatally manipulated offspring which they reared.

Another study which investigated the effect of prenatal maternal anxiety on the emotionality of the offspring concluded that prenatal stress increased offspring emotionality irrespective of postnatal treatment (Ader and Belfer, 1962). This study followed the usual procedure of teaching female Long-Evans rats an avoidance response and preventing that response when the warning stimulus was presented during pregnancy. Offspring emotionality was assessed by open-field and cage-emergence tests at 30-40 days of age and again at 135 days of age. Prenatally manipulated animals were significantly less active (more emotional) than controls in the open-field when tested at 30-40 days. No difference was obtained at 135 days. No significant difference was found between experimental and control offspring on the emergence-from-cage test. In this study, cross-fostering appeared to have no effect.

In general, the previous studies suggest that prenatal maternal anxiety increases the emotionality of the offspring. Other variables such as premating stress or postnatal treatment may interact with prenatal stress. However, the postnatal treatment (cross-fostering) appears to either accentuate the effect of the prenatal treatment or have no effect at all. While the premating treatment may affect the mothers, it does not appear to affect the emotionality of the offspring.

Contrary to the findings that prenatal maternal anxiety increases offspring emotionality, several studies have concluded that prenatal stress decreases the emotionality of the offspring (Thompson, Watson, and Charlesworth, 1962, Hutchings and Gibbon, 1970; Fazzaro, 1971; Fulkerson, 1971). Using a procedure similar to that discussed in the previous studies, Thompson et al. (1962) attempted to replicate and extend the findings of their earlier experiment. Sprague-Dawley females were used in this experiment whereas Long-Evans hooded rats were used in their first study. The presentation and type of anxiety was similar to that used before. Offspring were tested in an open-field sitation under normal conditions and under stress conditions in which they were shocked immediately prior to testing. They were also tested in a timidity runway and in a water maze (under normal and stressed conditions).

The data from the various measures were consistent with each other and indicated that offspring of anxious mothers (experimental offspring) were less emotional than control offspring. The experimental offspring were more active, had shorter latencies, and defecated less in the open-field under both normal and stressed conditions than controls. The experimental offspring also had shorter latencies in the initial segment of the timidity runway. The results of the water maze test were in congruence with the other measures of emotionality. The experimental subjects performed more poorly (in terms of time per trial and errors per trial) than controls under normal conditions. However, under stress the experimental offspring had significantly fewer errors than the control offspring. Compared to the nonstressed condition, there was a decrease in errors committed by the experimental subjects and an increase committed by the controls.

Thompson and his associates believe that the experimental offsprings' poorer performance under normal conditions is indicative of lower emotionality. If fear motivates performance in the water as is believed (Broadhurst, 1957), then the experimental animals (Es), having less fear, should do worse than the control animals (Cs). The following explanation for the reversed performance under stress is offered by Thompson et al.

> It is a little puzzling why stress should improve the performance of Es much more than that of Cs. Perhaps the explanation lies in this: Es have less fear drive to begin with. Hence, the addition of a stress condition to the water-maze is enough to facilitate their performance but not to disrupt it. On the other hand, Cs start from a higher basic level of emotionality. The addition of stress is then sufficient to disrupt their performance (Thompson et al., 1962, p. 16).

The basic assumption that there is an inverted U-shaped function depicting the effect of emotionality on behavior has been well defended Freeman, 1940; Courts, 1942; Hebb, 1955). In other words, the effect of emotionality on behavior is facilitative up to a point and then, as it increases, is disruptive. If this is the case, then the innate level of offspring emotionality is an important factor in determining the results. To the extent that this emotionality is determined by prenatal stress, the amount and type of stress may be crucial variables.

> In behavioral terms, we might suppose that an excessive or continual flow of maternal hormones somehow sensitizes or, on the other hand, adapts the growing organism to stress conditions, but we can only guess how this actually works physiologically. . . .
>
> During the prenatal period and up to a certain age neonatally, the organism must acquire a certain reaction norm to environmental stimulation. The norm must result from a combination of the genotype with which the organism is born, and the environmental circumstances to which it is subjected. Presumably, genotype supplies a range of strength of possible reactions. Out of this available range, a certain portion is,

> in a sense, selected by environmental pressures. If stimulation has been high and varied, then presumably the responsiveness of the organism to situations later on will tend to be strong also. On the other hand, if stimulation has beeen excessive, the individual will probably be underreactive later on, and if the stimulation has been rather weak or moderate, then probably responsiveness will be intermediate (Thompson et al., 1962, p. 23).

Several studies have been conducted using various stressor agents of differing strengths during pregnancy. One study investigated the effect of injections of adrenalin during the second trimester of pregnancy on the emotionality of the offspring (Thompson et al., 1962). Open-field tests and the water maze test, under both normal and stressed conditions, and the timidity runway test under normal conditions were used to assess offspring emotionality. In general, the results indicated that prenatal maternal adrenalin injections increased the emotionality of the offspring and improved their performance in the water-maze.

Magnitude of stress has been investigated by Hutchings and Gibbon (1970). Female Sprague-Dawley rats were given one of two treatments during either the second or third week of gestation. The mild treatment consisted of "handling" the animals (holding, weighing, and transporting them to an experimental room). The females in the more intense treatment group, termed the Escape group, were given daily sessions of signaled shock (1.0 mA) which they could terminate, but not avoid, by pressing a lever.

Offspring were tested at 25-28 days of age in an open-field for four minutes. A loud noise was sounded after two minutes and level of emotionality was inferred from the amount of time the animal spent in a crouching position after the sound presentation.

The study concluded that offspring from both the Escape and Handled groups were less emotional (crouched significantly less) than the control offspring. No difference in emotionality was found between the Escape and Handled offspring. Trimester of treatment administration had no significant effect. Hutchings and Gibbon believe these results indicate that the severity of maternal treatment may not be an important variable in determining the direction of offspring emotionality. In speculating on what aspect of the treatment could be responsible for the observed effects, they suggest that simply removing pregnant females from their home cages at a time when maternal instincts orient them toward remaining near their familiar territory could be the important stress variable.

Hutchings and Gibbon also point out that the strain of rat could be an important variable. Studies using Long-Evans hooded rats to assess the influence of prenatal maternal anxiety on offspring behavior typically found "increased" emotionality (Thompson, 1957; Hockman, 1961; Ader and Belfer, 1962) while studing using Sprague-Dawley albino rats found "decreased" emotionality (Thompson, et al., 1962; Ader and Conklin, 1963; Hutchings and Gibbon, 1970; Fulkerson, 1971).

Other forms of prenatal maternal stress that have been investigated include audiogenic seizure (Thompson and Sontag, 1956), electroconvulsive seizures (Anderson, 1968), x-irradiation (Furchtgott and Echols, 1958), administration of sodium bromide (Hamilton, 1945), and injections of reserpine, iproniazid, 5-hydroxytryptohane, and the benzyl analogue of serotonin (Werboff, Gottlieb, Havlena, and Word, 1961).

Thompson and Sontag (1956) subjected albino females to audiogenic seizures during pregnancy. Offspring were tested for general activity and water maze performance. The offspring of stressed mothers did not differ in activity level from control offspring, but they were significantly slower in learning the water maze. Thompson and Sontag suggest that the learning deficit may be a function of disorganization of behavior under stress.

An experiment employing maternal x-irradiation as a stressor agent also found learning deficits in the offspring (Furchtgott, Echols, and Openshaw, 1958). Prenatal x-irradiation also appears to produce hyperemotionality in the offspring as assessed by tilting-cage activity, open-field ambulation, and cage emergence scores (Furchtgott and Echols, 1958).

On the other hand, offspring from albino mothers which had received various dosages of sodium bromide during gestation were less emotional than controls and more susceptible to audiogenic seizures (Hamilton, 1945). These results are in agreement with those obtained by Martin and Hall (1941) indicating a relationship between non-emotional rats and susceptibility to seizure.

Further evidence that prenatal administration of certain drugs may cause behavioral changes in the offspring has been supplied by Werboff et al. (1961). Pregnant albino rats were given daily injections of reserpine, iproniazid, 5 HTP (5-hydroxytryptohane), BAS (the benzyl analogue of serotonin) or water throughout the second trimester of pregnancy. These drugs have been found to influence the level of serotonin which is thought to be an important chemical in mental function and in mental illness (Page, 1958).

Although there were no uniform effects on the offspring, the results indicate that experimental offspring were more active and more emotional than the controls. Offspring from mothers which had been administered any of the drugs were also more susceptible to audiogenic seizures.

Subjecting pregnant rats to electroconvulsive shock (ECS) during the second or third trimester of pregnancy produced no significant effect on offspring behavior (Anderson, 1968). An open-field test, water runway test, water maze preference test, single alternation water maze, and a water submersion test revealed no significant difference between prenatally stressed and control animals. Anderson suggested that, due to the retrograde amnesic properties of ECS, the maternal stress response was only acute and may not have been intense enough or long enough to influence the fetus.

Fazzaro (1971) stressed pregnant females with electric shock during the third trimester of pregnancy and examined offspring emotionality by an avoidance conditioning task and an appetitive conditioning task (running speed toward a food reward). He found that offspring of shocked mothers were less emotional as indicated by superior avoidance conditioning and faster running speeds.

In general, there is currently a great deal of evidence demonstrating the effects of prenatal maternal stress on the behavior of the offspring. Whether the stress is physical or emotional appears to be an important variable.

How maternal anxiety per se affects the emotionality of the offspring has not been established. However, it has been demonstrated that such hormones as cortisone, adrenalin, and adrenocorticotropic hormone injected into a pregnant female affect the fetus via the maternal-fetus blood system (Jones, Lloyd, and Wyatt, 1953). It has also been shown that strong emotions such as fear, anxiety, and anger alter the discharge of the adrenocortical system (Grey, 1971). It would therefore seem probable that such factors as maternal anxiety affect the emotionality of the offspring through endrocrine changes which affect the fetus.

In addition to type of stressor agent, other variables which may be important include: strain of animal; intensity of stressor; time of stress application; postnatal treatment; method of behavioral assessment; and age of the offspring when tests of emotionality are administered. Some of the effects of these variables have been discussed.

That psychological and physiological stress during pregnancy can influence the subsequent behavior of the offspring is of importance when applied at a human level. The etiology of many types of abnormal behavior in humans is not yet fully understood and investigation of the influence of prenatal stress on offspring behavior could increase our understanding in this area. Some research has already revealed a correlation between complications during pregnancy and some deviant behavior in children (Pasamanick, Rogers, and Lilienfeld, 1956). Toxemias and hypertensions of pregnancy appeared to be more highly associated with behavior disorder than were mechanical difficulties. While the results of the Pasamanick et al. study and other evidence derived from correlational studies do not prove the existence of a cause and effect relationship between prenatal stress and abnormal behavior in the offspring, it does suggest that further investigation of this area could be valuable.

The present study attempted to extend the knowledge in this area by using a different variation of prenatal stress. The purpose of this study was to investigate the effect of escapable versus inescapable mild electric shock, administered during pregnancy, on the emotionality of the offspring. Several investigations have indicated that inescapable shock is more aversive (more anxiety producing) than an equal amount of escapable shock (Ragusa, Shemberg, and Rasbury, 1968; Moot, Cebulla, and Crabtree, 1970). Ragusa et al. exposed rats to 23½ hours of either escapable, inescapable, or nonshock conditions. Rats which were subjected to the inescapable shock treatment lost significantly more weight than those in either the escape or nonshock conditions. Ragusa et al. indicate that this finding is consistent with prior research suggesting an inverse relationship between stress and weight gain. The authors believe their data support the hypothesis that the availability of a coping response may partially reduce the effect of shock induced stress.

Moot, Cebulla, and Crabtree (1970) found that rats which were able to terminate shock by making an instrumental escape response developed significantly fewer stomach ulcers than did rats that were unable to escape the shock. The authors suggest that tension (anxiety) is not as great when an organism's behavior enables it to terminate an aversive situation as when its behavior is ineffective and it is, in essence, powerless.

The majority of the studies reviewed which used albino rats as subjects found a decrease in offspring emotionality as a result of prenatal manipulation. The present study also used albino rats and it was expected that the mild electric shock administered during pregnancy would lower the emotionality of the offspring. Any difference in offspring emotionality between subjects whose mothers had received escapable versus inescapable shock could be attributed solely to a difference in maternal anxiety. It was expected that the inescapable shock would generate more maternal anxiety and would produce a heightened "innoculation effect" on the offspring. In other words, offspring of mothers who had received the inescapable shock treatment would be the least emotional, followed by those whose mothers had been given escapable shock, with the control (non-shock) offspring being most emotional.

Open-field activity and avoidance acquisition in a two-way shuttlebox were the methods used to assess offspring emotionality. It was hypothesized that the offspring of the inescapable shock group would be more active in the open-field and would perform better in the avoidance acquisition test. Both of these results would be indicative of lowered emotionality. The offspring of the escapable shock group were expected to be less active than the inescapable shock offspring but more active than control offspring in the open-field. The performance of the escapable shock group offspring in the avoidance acquisition test was also expected to be inferior to that of the inescapable shock offspring but superior to that of the control offspring.

CHAPTER II

METHOD

Subjects

Fifteen naive, female albino rats of the Sprague-Dawley strain, approximately 120-160 days of age, were mated with five males of the same strain. A total of 78 offspring, 36 males and 42 females, served as subjects (Ss).

Apparatus

The avoidance conditioning apparatus consisted of a two-way shuttlebox manufactured by Lehigh Valley Electronics (Model 146-04). All sides of the apparatus were covered with 1 in. black and white horizontal stripes. The shuttlebox was approximately 18 in. long, 8 in. wide, and 8 in. high. A 2 in. high plexiglass barrier, the top of which could be electrified, separated the two compartments. Shock was supplied by a Grayson-Stadler shock generator (Model E6070B). The shuttlebox was completely automated with avoidances, escapes, and intertrial responses recorded on digital counters. A five channel BRS Foringer digital print-out counter (Model PO-901) recorded the latencies of avoidance and escape responses. The shuttlebox was also equipped with two lights, one at each end of the chamber, which served as the conditioned stimulus (CS). The experimental room was kept completely dark during the experimental sessions.

The open-field apparatus consisted of a wooden box 2 1/2 ft. long, 2 1/2 ft. wide, and 2 ft. high. All sides were painted white. The floor of the box was divided into twenty-five 6 in. squares. These squares were white with black borders.

Procedure

The procedure can be divided into two parts. The first concerns the treatment of the mothers and the second deals with the testing of the offspring.

Maternal Treatment

Thirty females, housed four or five to a cage, were mated with one of five males. Eight to ten hours later, the males were removed and all females were examined for pregnancy by the slide technique described by Nicholas (1949). Presence of sperm was taken as evidence that the female was pregnant and the time of this determination was treated as Day 1 of pregnancy. Nonpregnant animals were replaced in their cages and mated again at a later period.

Females classified as pregnant were assigned to one of three groups: Control, Group I (escapable shock treatment), or Group II (inescapable shock treatment). Approximately half of the Control *Ss* were run concurrently with Group I and half with Group II. Animals were unsystematically assigned to either the Control Group or Group I until there were five animals in Group I and two animals in the Control group. This assignment was required because the Group I animals were given an escapable shock treatment (of variable duration as it was under the *S*'s control) which necessitated their being run before Group II so that the groups could be equated for duration of shock received. Upon the completion of the treatment administered to Group I (described below), additional animals which became pregnant were assigned to either Group II or the Control group such that there were five Ss in Group II and three in the Control group (these plus the two Ss previously assigned totaled five Control group Ss).

Four females were discarded from the experiment; one Control animal developed a middle ear infection, one Group I animal developed a badly swollen back leg, and two subjects (one Control and one from Group I) never littered (undetected false pregnancies). The first female to become pregnant after an animal was discarded from a group was assigned to replace it.

All animals were housed individually from Day 1 of pregnancy and were given free access to food (Purina Rat Chow) and water. Daily records were kept of each pregnant female's weight and if an animal had not shown an appreciable gain by Day 9, she was classified as a false pregnancy and was discarded. Two subjects were discarded for this reason.

The experimental treatment described below was administered from Day 10 through Day 16 of pregnancy.

Group I (escapable shock group):--Each S was placed in the shuttlebox once daily and give 25 exposures to a 0.6 mA electric shock which she could terminate by jumping over the 2 in. barrier that separated the compartments. Shocks were programmed to occur 60 seconds after the termination of the preceding shock. The average duration of shock received was one second.

Group II (inescapable shock group):--The Ss in this treatment group were each placed in the shuttlebox once a day and given 25, 0.6 mA electric shocks of one second duration which they could not escape. An aluminum barrier the height and width of the shuttlebox was placed in the center, thus preventing the animal from crossing from one side to the other and terminating shock. One shock was administered every 60 seconds.

Control group:--Each S was placed in the shuttlebox for approximately 25 minutes a day from Day 10 through Day 16 of pregnancy. No shock was ever administered to this group.

On Day 18 of pregnancy, each female was placed in a circular wooden nesting box approximately 18 in. in diameter and 6 in. high. Each box was supplied with adequate wood chips and straw for nesting material. All animals littered on Day 22 or 23. The young remained with their mothers in the nesting box until they were 14-16 days old. They and their mothers were then transferred to stainless steel cages approximately 17 in. long, 17 in. wide, and 20 in. high. The young were separated from their mothers at 28-33 days of age. Offspring were sexed at 40-50 days and four or five members of the same sex (from the same litter) were placed in group cages.

The design of the present study did not include the cross-fostering of offspring. While cross-fostering may be desirable, the literature indicates that, in general, cross-fostering either accentuates the effect of the prenatal treatment or has no effect at all (Thompson, 1957; Hockman, 1961; Ader and Belfer, 1962).

Testing of Offspring

Test A:--Offspring were tested in the open-field when they were 60-80 days old. Each animal was transported to the testing room and placed in the center square of the open-field box. A record was kept of the total number of squares entered in a three minute period. This procedure was carried out on three consecutive days. The floor of the box was cleaned with a liquid cleaner (Clorox's 409) and water and air freshner (Johnson's Sun Country) was sprayed into the box after each animal was removed.

Test B:--Beginning three to ten days following the open-field testing, Ss were tested for acquisition to avoidance in a two-way shuttlebox. Each S was placed in the shuttlebox in a darkened room for one session a day on three consecutive days. Each session consisted of 25 trials. A trial began with the presentation of the CS, a 15 watt light on the same side of the chamber as the S. The avoidance interval was five seconds (beginning with the CS presentation). During this period the S could jump over the center barrier thus avoiding shock and terminating the trial. If the S had not responded within the five second avoidance interval, a 0.6 mA electric shock was administered. The animal could escape this shock by crossing the center barrier. If the S failed to make an escape response, within the 15 second escape interval, the CS and shock were terminated. A trial was programmed to start 60 seconds after the termination of the previous trial.

After the first five trials were completed, the center barrier was electrified during the time shock was on. This was done to prevent the animals from balancing on the barrier and thereby escaping or avoiding shock in an unacceptable manner.

The total number of avoidances, escapes, and intertrial responses were recorded for each S during every session. An avoidance was defined as a response (crossing the barrier) which occurred within the five second avoidance interval; an escape was a response which occurred after the avoidance interval and terminated the shock; and an intertrial response was a response (crossing the barrier) which occurred after the termination of a trial and before the onset of the succeeding one.

CHAPTER III

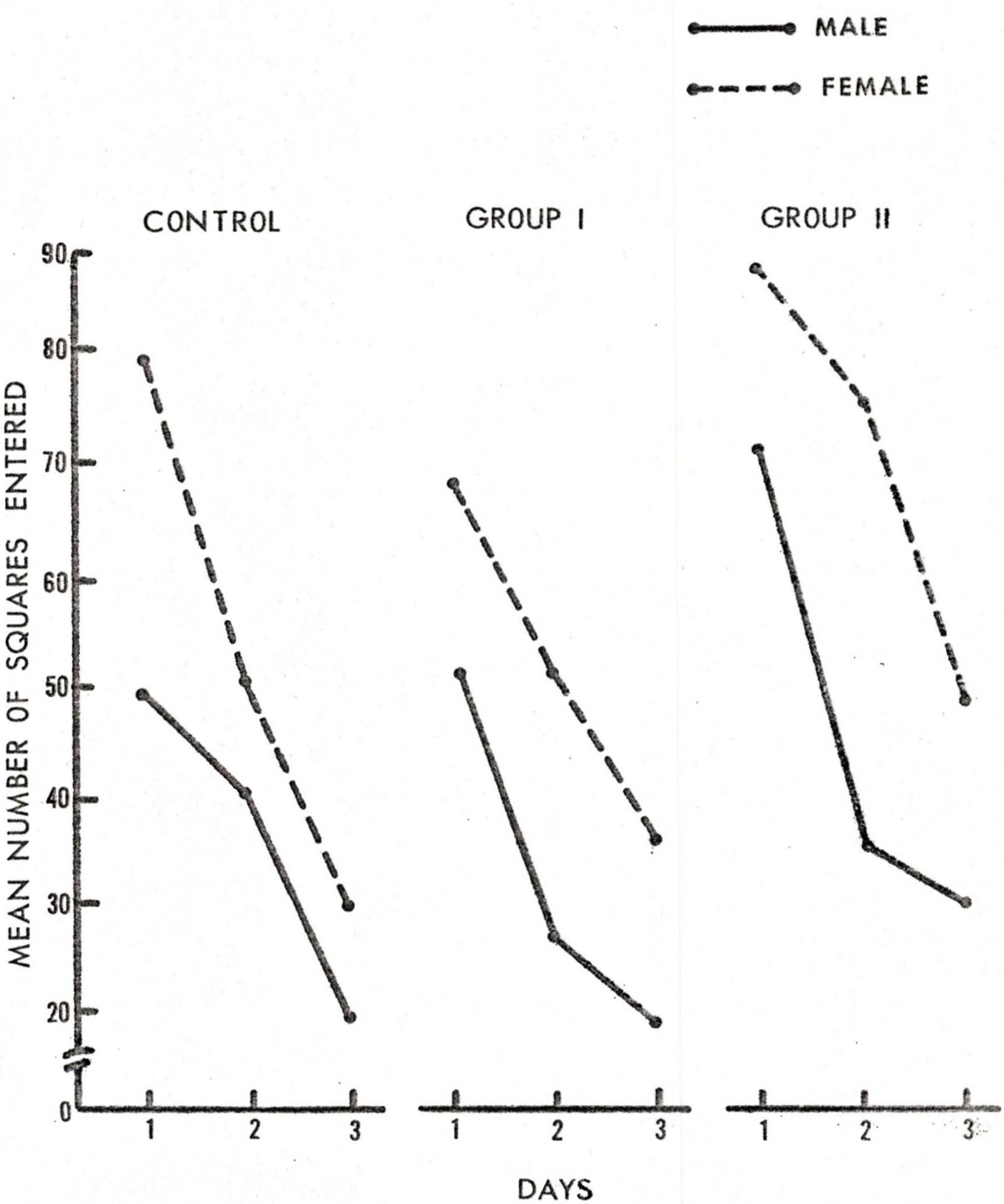
RESULTS

The results are divided into two sections. The first section consists of the open-field data and the second section concerns acquisition to avoidance in a two-way shuttlebox.

Test A: Open-Field Test

A total of 78 Ss, 36 males and 42 males, were tested in the open-field. The data from three Ss, one male from each of the treatment groups and one female from the Control group, were discarded because they were judged to be extremely deviant (greater than 2.2 standard deviations from the mean). These and all other raw scores from the open-field test are presented in Tables 6, 7, and 8 in the appendix. The Day 3 data from six Group I females and three Group II females were misplaced and never found subsequently reducing the N size of those two groups. The final data consisted of scores from 21 Control Ss, 18 Group I Ss, and 27 Group II Ss. All statistical analyses were made by a one-tailed t-test (Kolstoe, 1969) unless otherwise indicated. The 0.05 region of rejection was adopted throughout. All comparisons for the open-field data are presented in Table 3 in the appendix.

A comparison of the mean number of squares entered by males and females on Days 1, 2, and 3 is illustrated in Figure 1. The curves clearly show that the females in each group were consistently


MALE
FEMALE
CONTROL
GROUP I
GROUP II
MEAN NUMBER OF SQUARES ENTERED
90
80
70
60
50
40
30
20
0
1
2
3
1
2
3
1
2
3
DAYS

more active than the males on all three days. This difference was found to be significant (p=.004) using the two-tailed binomial test (Kolstoe, 1969). Because there was no overlap between the activity level of males and females in each group, the data from each sex were analyzed separately.

A comparison of the activity level of the females in each group is presented in Figure 2. The curves show the differences in activity between females in the two experimental groups and the Control females. The females in Group II were consistently more active than both the Group I and Control females. This difference was significant for both comparisons ($p < .025$ for Group II and the Controls; $p < .01$ for Group II and Group I). There was no significant difference between the activity level of the Group I and Control females ($p < .35$). All three curves show a consistent decrease in activity across days.

The mean number of squares entered by both males and females in each group for the total three days is presented in Table 1. It should be noted that the females in Group II entered over one third again as many squares as either the males or females in any other group.

The open-field data for males are depicted in Figure 3. The curves show that the Group II Ss were more active than both the Group I and Control Ss on Days 1 and 3. The Control males were slightly more active than the males in the two treatment groups on Day 2. While the difference between the mean number of total squares entered by the Group II and Control males was not significant ($p < .088$), the difference between the Group II and Group I males was significant ($p < .05$). There was no reliable difference in

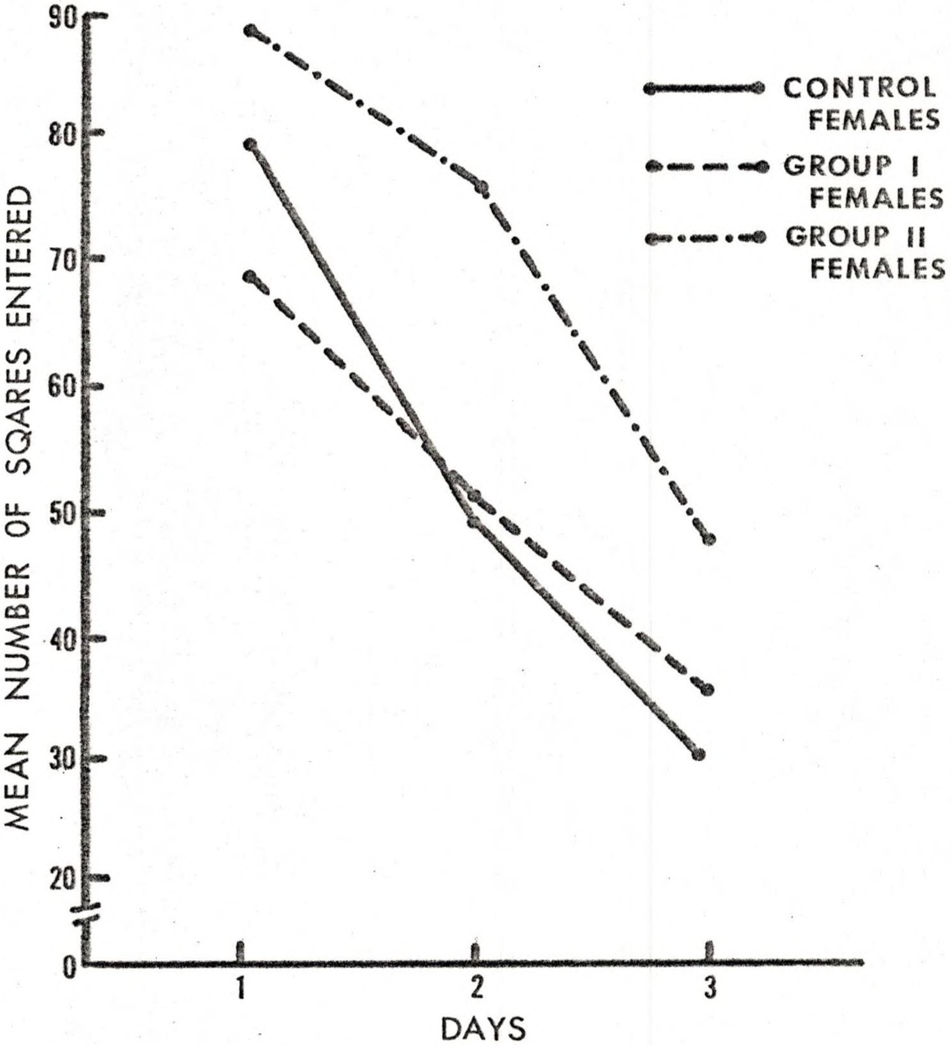

90
80
70
60
50
40
30
20
0
MEAN NUMBER OF SQARES ENTERED
1
2
3
DAYS
CONTROL FEMALES
GROUP I FEMALES
GROUP II FEMALES

TABLE 1

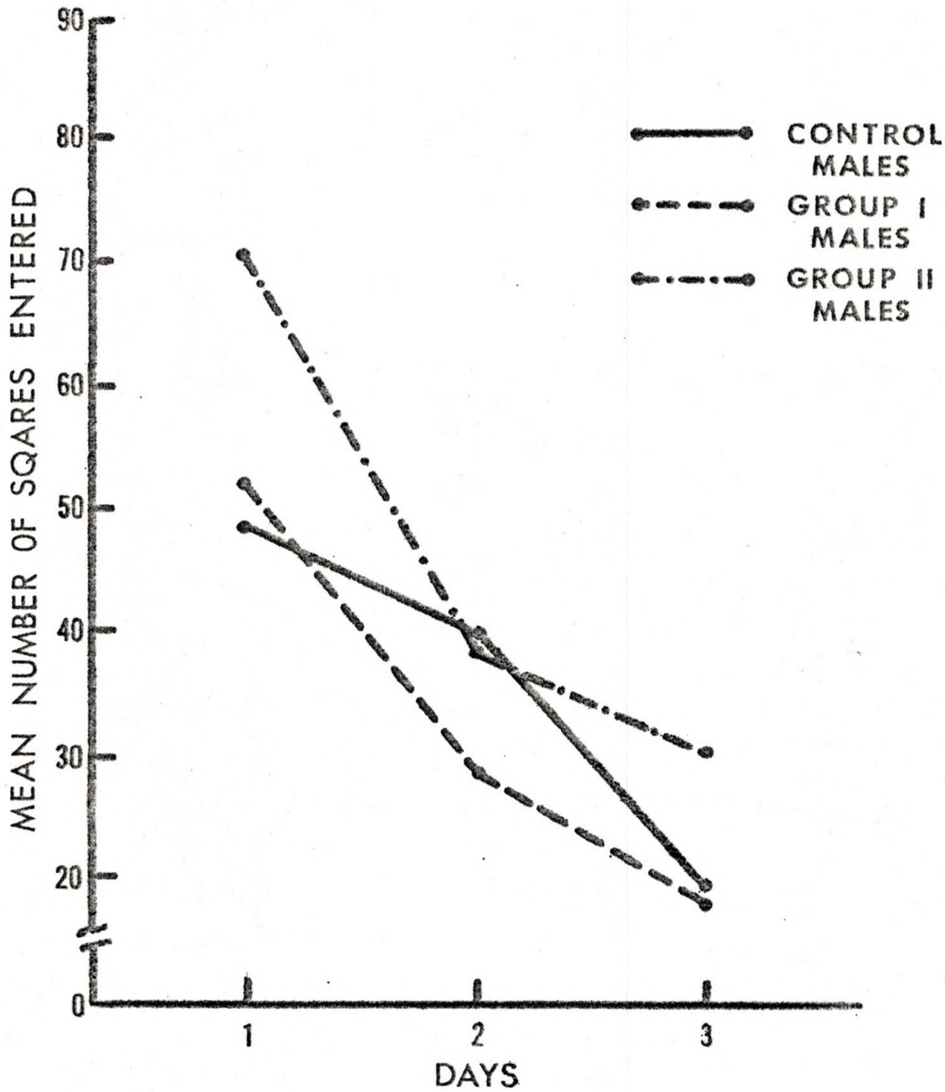
MEAN NUMBER OF SQUARES ENTERED FOR THE COMBINED THREE DAYS OF OPEN-FIELD TESTING BY CONTROL, GROUP I, AND GROUP II OFFSPRING

	Males			Females		
	Mean	S.D.	N	Mean	S.D.	N
Control	107.88	47.64	9	160.16	62.14	12
Group I	99.50	44.07	10	148.00	47.36	8
Group II	138.93	51.44	15	225.50	72.21	12

activity levels between Group I and Control males ($p > .10$). The curves for all three groups decline consistently across days as did the curves for the females. Referring again to Table 1, it can be seen that the mean number of total squares entered by the Group II males was considerably higher than that for either the Group I or Control males.

Test B: Avoidance Acquisition

The other major data of the experiment concern the acquisition of an avoidance response in a two-way shuttlebox. The experimental design required that all Ss be tested for avoidance acquisition between 66 and 93 days of age. Thirteen Ss surpassed the upper age limit before there was time available to test them and thus, were not tested. Animals which were totally inactive on 10 or more trials, receiving the full 15 seconds of shock, were eliminated from the study. There were three of these animals in each group. The final data consisted of scores from 56 Ss, 30 males and 26 females. The statistical considerations which applied to the open-field data were also adopted for the avoidance acquisition data.

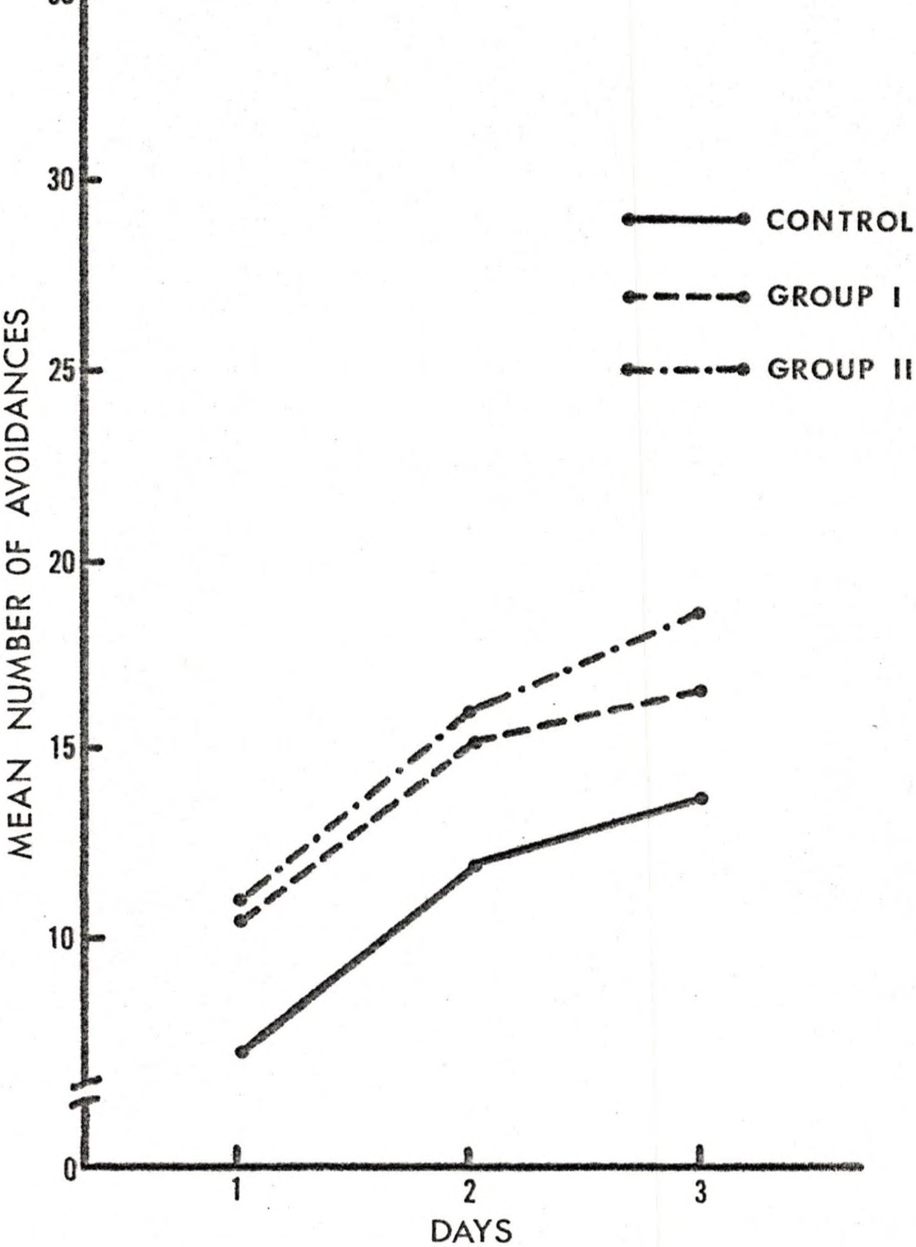


90
80
70
60
50
40
30
20
0
MEAN NUMBER OF SQARES ENTERED
1
2
3
DAYS
CONTROL MALES
GROUP I MALES
GROUP II MALES

In the acquisition to avoidance test, the Ss had only three behavioral options: an S could avoid shock, escape it, or not escape it (thereby receiving 15 seconds of shock). With the majority of the subjects making either escape or avoidance responses on each trial, the escape data are the inverse of the avoidance data and hence are not reported. All statistical comparisons for the avoidance data are presented in Table 4 in the appendix and the raw data are presented in Tables 9, 10, and 11 in the appendix.

The mean number of avoidances made by each group during each session are graphically depicted in Figure 4. None of the curves overlap and all three are similar in form showing a negative acceleration. The Group II Ss' performance was superior to the Control's ($p<.01$). Group I Ss also performed significantly better than the Control Ss ($p<.05$). Although the Group II animals' performance was superior to that of the Group I animals on all three days, the difference between mean total avoidances for these two groups was not significant ($p>.10$).

Figure 5 graphically compares the mean number of total avoidances for the females in each group with the males in each group. The graph indicates that male and female performances were nearly identical for the Control group. Group I males and females were also very similar in their performance as were Group II males and females. Two-tailed t-tests, assessing the difference between males and females in each group, were not significant thus indicating that sex was not a factor in avoidance performance. A summary of the avoidance data is presented in Table 2.


35
30
25
20
15
10
0
MEAN NUMBER OF AVOIDANCES
CONTROL
GROUP I
GROUP II
1
2
3
DAYS

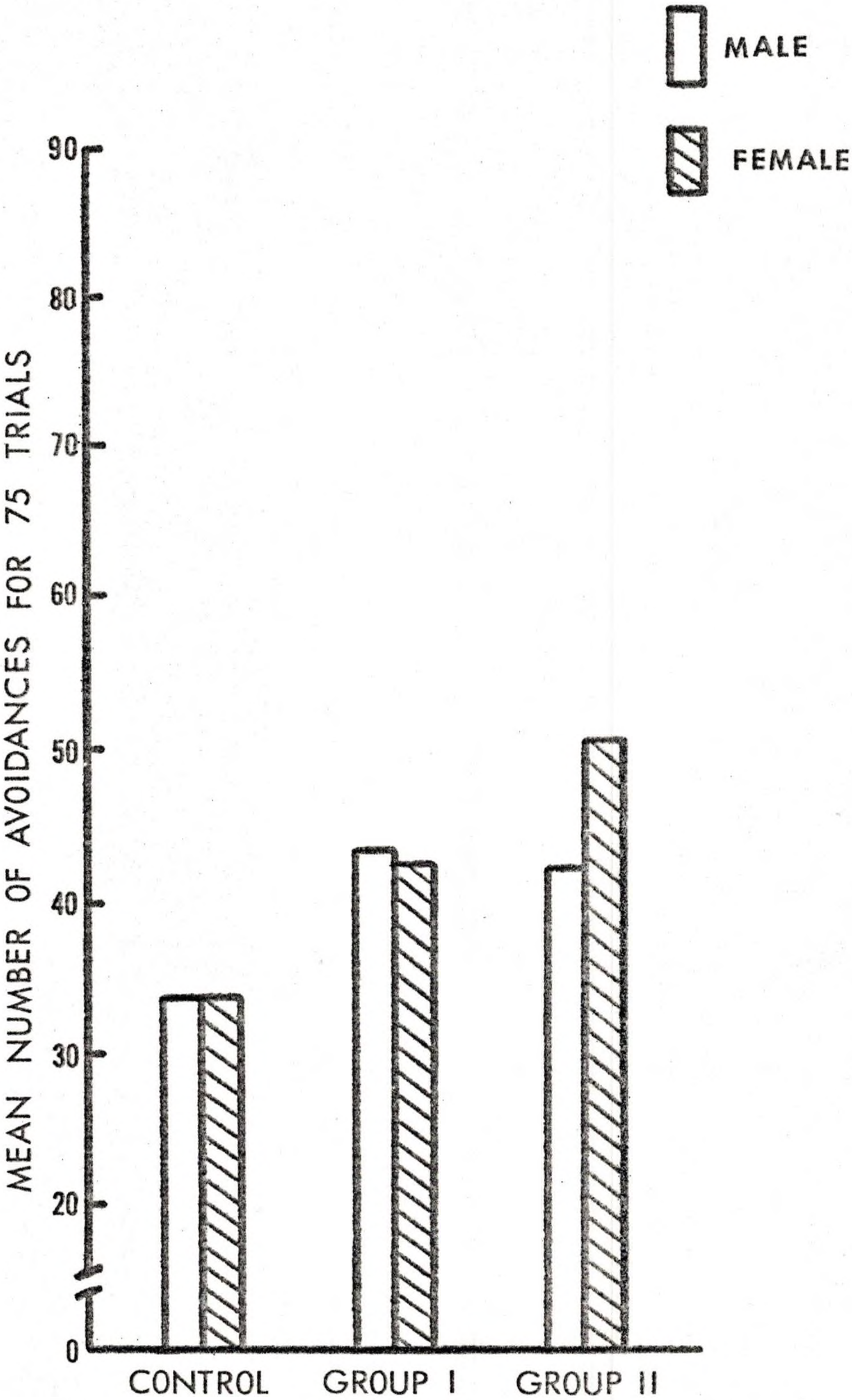

MALE
FEMALE
MEAN NUMBER OF AVOIDANCES FOR 75 TRIALS
90
80
70
60
50
40
30
20
0
CONTROL
GROUP I
GROUP II

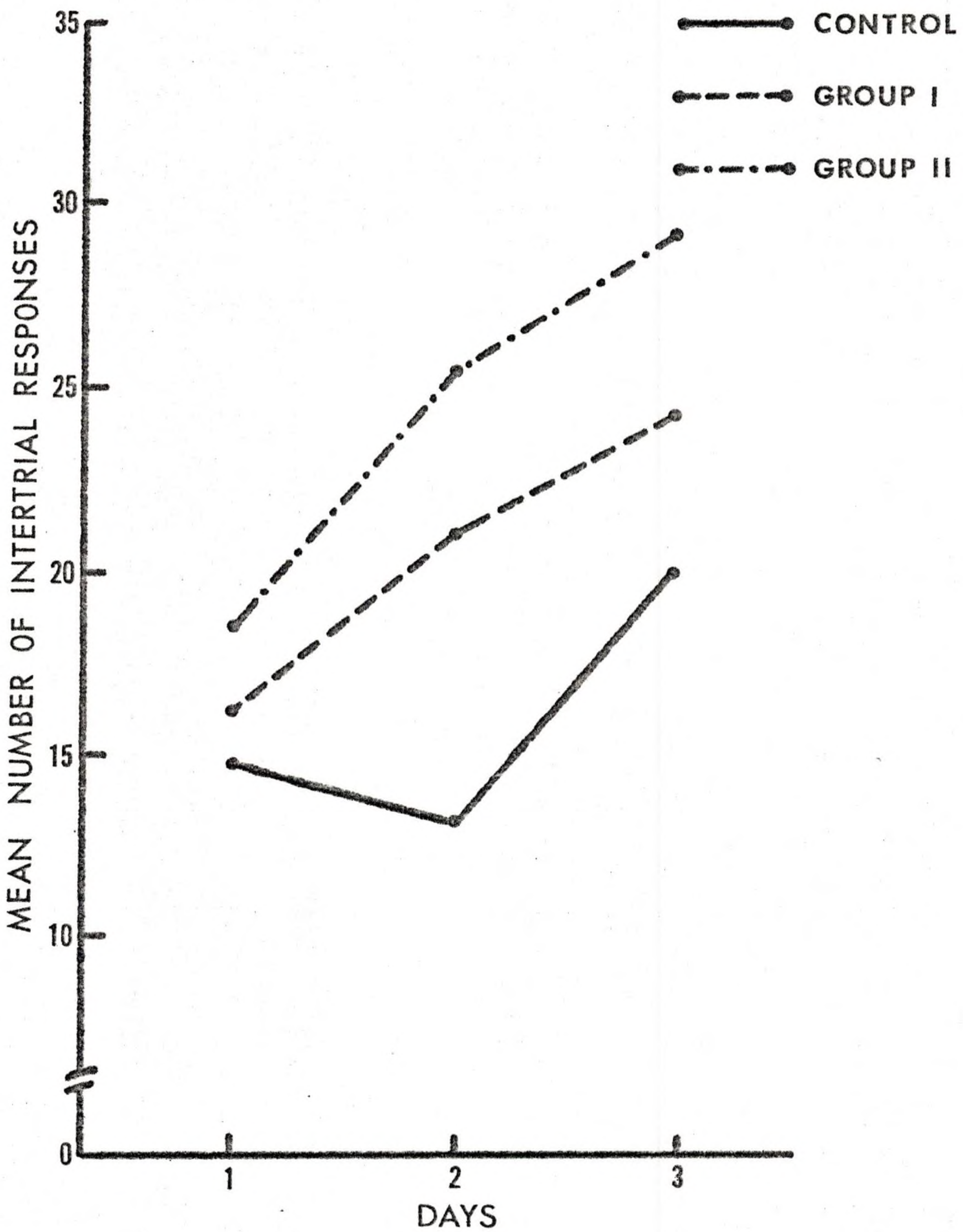
TABLE 2

MEAN NUMBER OF AVOIDANCES AND INTERTRIAL RESPONSES (ITRs) FOR THREE DAYS (75 TRIALS) FOR CONTROL, GROUP I, AND GROUP II SUBJECTS

Group	Males Mean	Males S.D.	Males N	Females Mean	Females S.D.	Females N
			Avoidances			
Control	32.71	13.54	7	32.85	14.94	7
Group I	42.50	12.88	10	41.87	12.10	8
Group II	41.69	14.85	13	49.54	6.61	11
			Intertrial Responses			
Control	35.66	25.56	6	48.50	28.41	7
Group I	42.10	18.97	10	87.62	75.74	8
Group II	66.23	36.45	13	88.30	50.57	10

The other major data from the avoidance acquisition test concern intertrial responding. The behavior of two Ss, one Control male and one Group II female, was judged to be extremely abnormal (greater than 2.2 standard deviations from the mean) and the data from these Ss were discarded. These data and all other intertrial response data can be found in Tables 9, 10, and 11 in the appendix.

The mean number of intertrial responses (ITRs) for each group is illustrated in Figure 6. All three curves are widely separated with no overlap. The curves for each group show a sharp increase in the mean number of ITRs from Day 1 to Day 3 with the exception of the Control group's slight decrease on Day 2. The pattern of responding is the same across days with the Group II Ss making the greatest number of ITRs, the

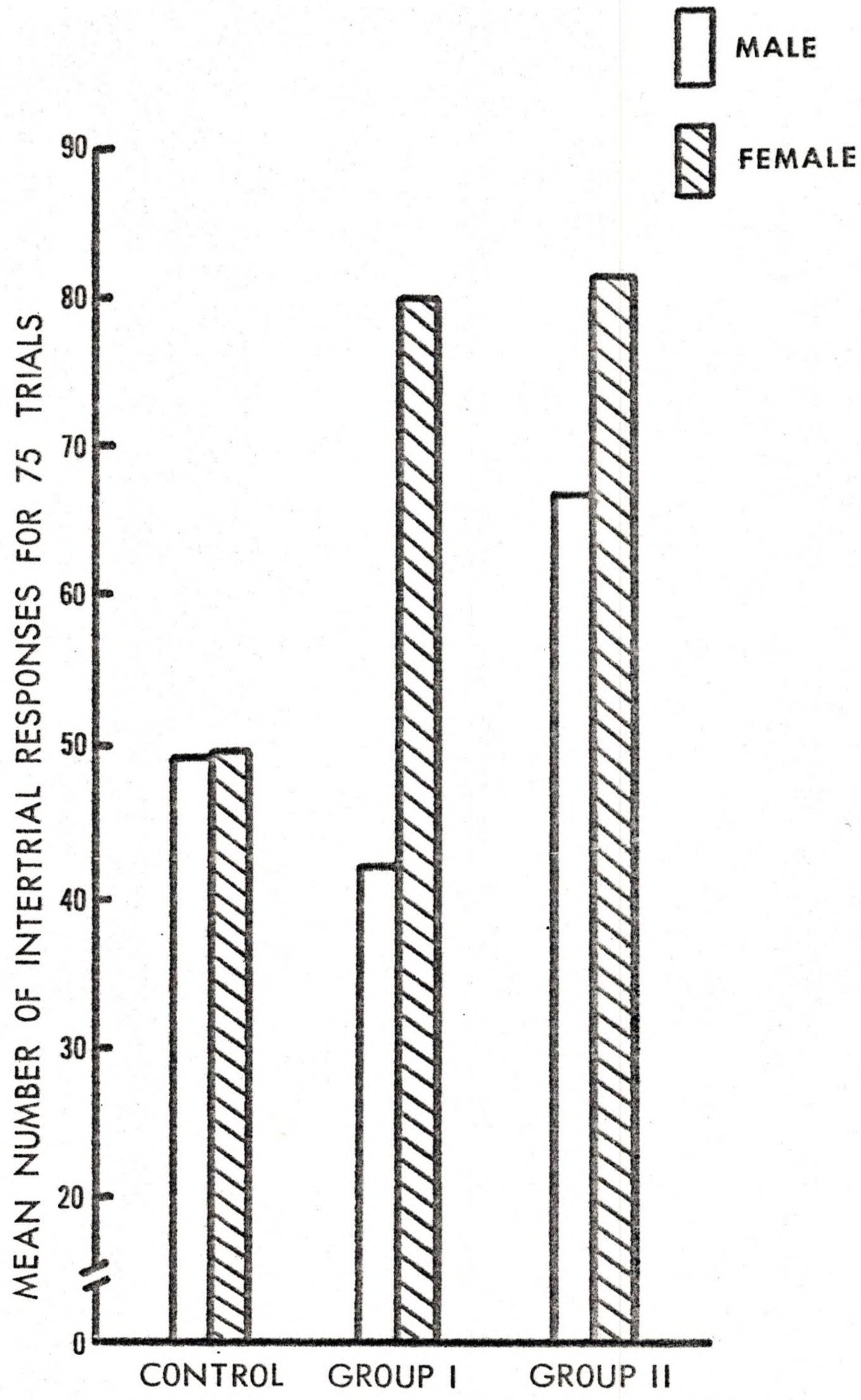

CONTROL
GROUP I
GROUP II
MEAN NUMBER OF INTERTRIAL RESPONSES
0
10
15
20
25
30
35
1
2
3
DAYS

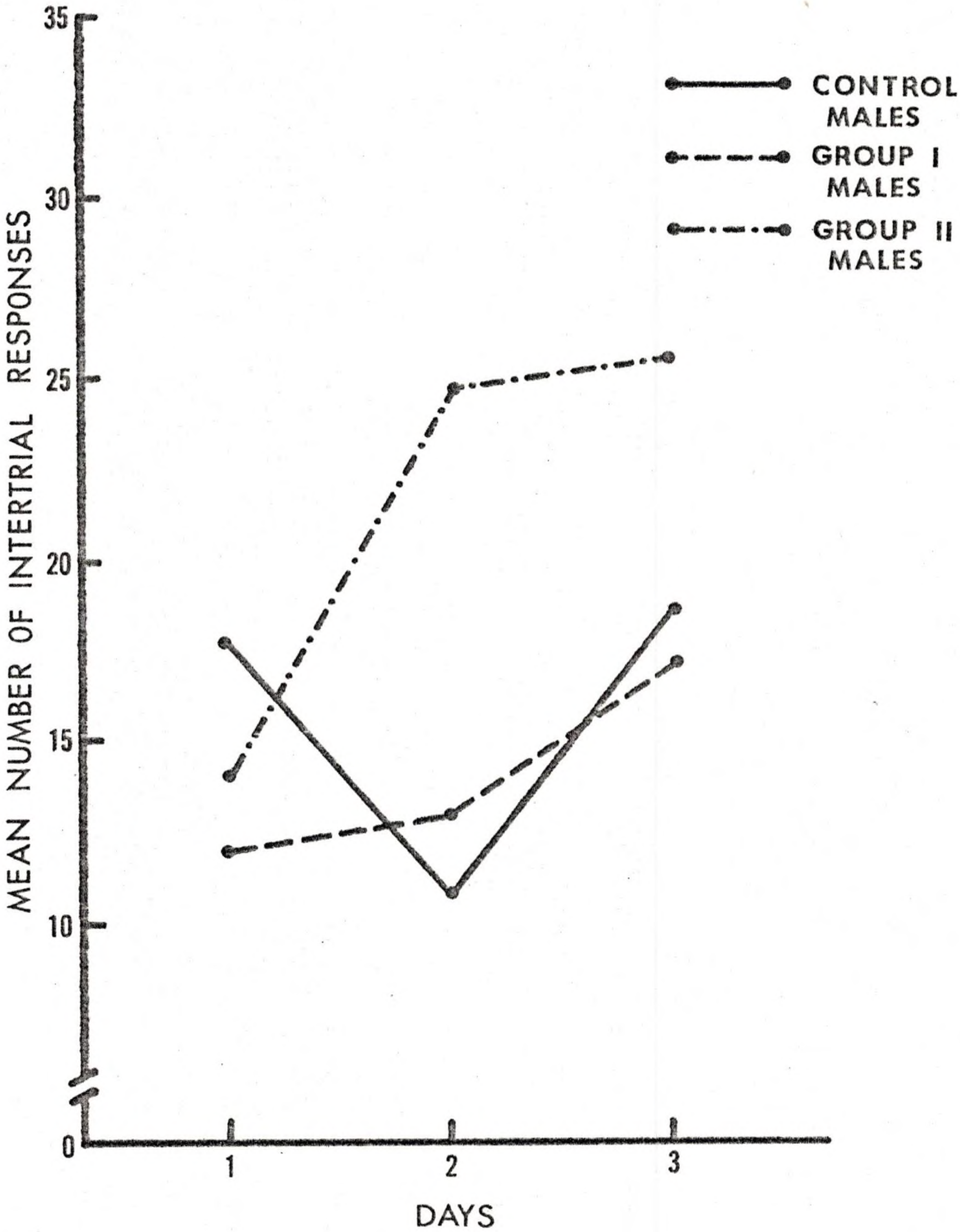
Controls making the least number, and the Group I Ss being intermediate. Although there is a substantial difference between the means of each group on each of the three days, the difference was significant only between the mean number of total ITRs for Group II and the Control Group ($p<.05$).

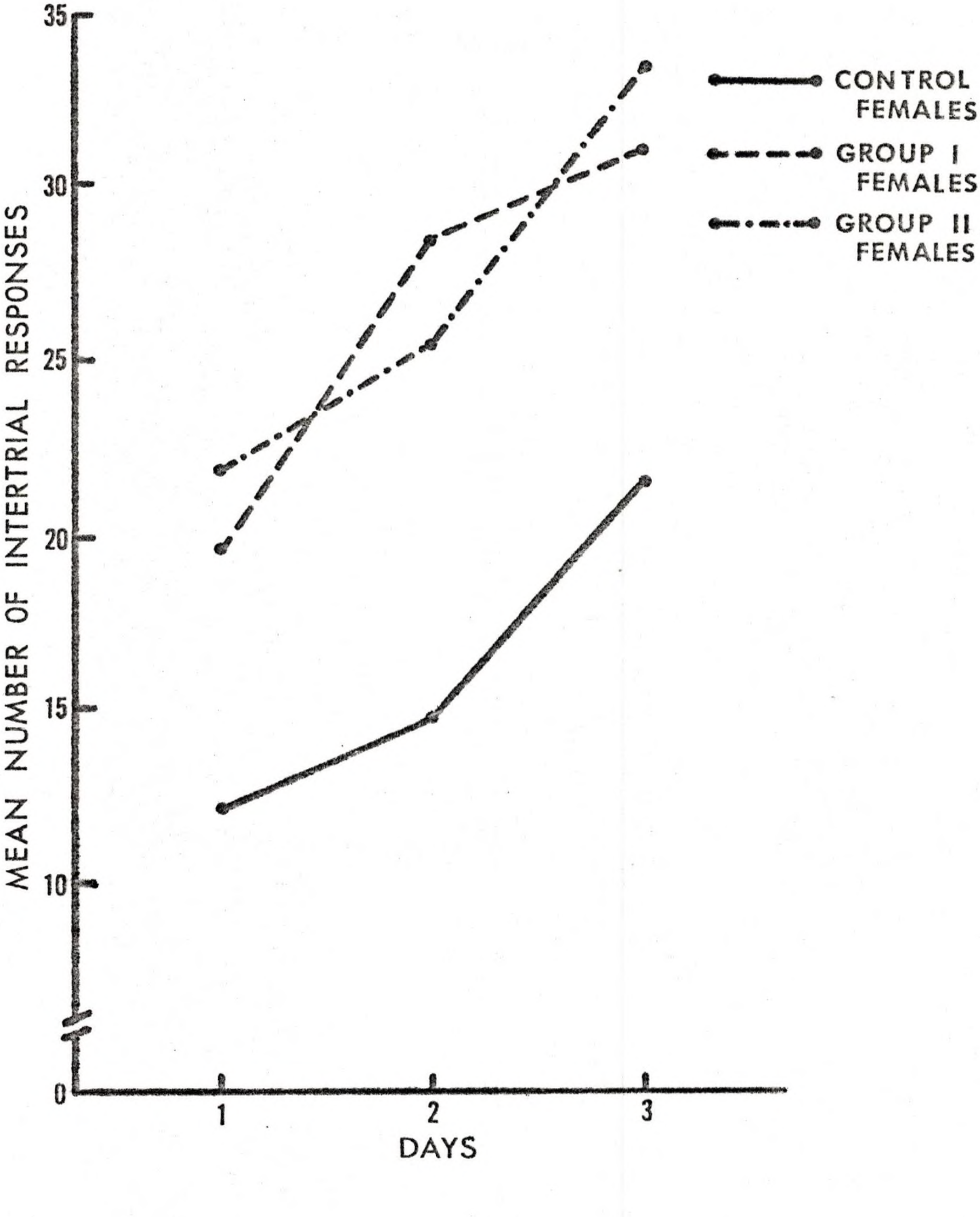
Sex appeared to be an important variable affecting the number of ITRs made by both treatment groups. A comparison of the mean number of ITRs made by each sex in each group for the 75 avoidance acquisition trials is graphically presented in Figure 7. While the performance of Control males and females is almost identical, there is a difference between the mean number of ITRs made by each sex in both the treatment groups with the females making substantially more ITRs in both groups. However, these difference were not significant ($p<.08$ for the Group I males versus females; $p<.10$ for the Group II males versus females). The ITR data are also presented in Table 2.

Figure 8 graphically portrays the ITR data for males only. The curves for the Control and Group I males do not differ significantly ($p<.10$). The Group II curve shows a large increase in the number of ITRs from Day 1 to Day 3. The Group II males made significantly more ITRs than either the Group I ($p<.05$) or Control males ($p<.005$).

The ITR data for the female Ss are graphically presented in Figure 9. A comparison of this figure with Figure 8 demonstrates that the females' performance pattern was quite different than the males. All three curves show a consistent acceleration across days. The females in both treatment groups show a greater number of ITRs than the Control females at all points. However, this difference was significant only for Group II females ($p<.05$).


MALE
FEMALE
MEAN NUMBER OF INTERTRIAL RESPONSES FOR 75 TRIALS
90
80
70
60
50
40
30
20
0
CONTROL
GROUP I
GROUP II


MEAN NUMBER OF INTERTRIAL RESPONSES
35
30
25
20
15
10
0
1
2
3
DAYS
CONTROL MALES
GROUP I MALES
GROUP II MALES


35
30
25
20
15
10
0
MEAN NUMBER OF INTERTRIAL RESPONSES
1
2
3
DAYS
CONTROL FEMALES
GROUP I FEMALES
GROUP II FEMALES

CHAPTER IV

DISCUSSION

The results of this investigation support the hypotheses developed earlier and are congruent with the findings of Fazzaro (1971), Fulkerson (1971), Hutchings and Gibbon (1970), and Thompson, Watson, and Charlesworth (1962), which indicate that prenatal maternal stress of albino rats lowered the emotionality level of the offspring. The authors mentioned above interpreted increased activity in open-field tests and better performance in shuttlebox avoidance acquisition as indices of lower emotionality. In general, both experimental treatments, applied prenatally, lowered the level of offspring emotionality. The effect appears greatest for the offspring of the group which received the inescapable shock treatment. This is indicated by their superior performance in the avoidance conditioning task and their increased activity in the open-field.

Offspring whose mothers were stressed by escapable shock also performed better on the avoidance test than the Controls. Their performance was inferior to the Group II Ss but this comparison was not statistically significant. The open-field data indicate that Group I Ss were significantly less active than the Group II Ss but did not differ from the Controls. In general, it can be concluded that the Group I offspring were less emotional than Controls but more emotional than Group II offspring.

The open-field data also show a consistent decrease in activity across days for all groups. This is consistent with the findings of all the previously reviewed studies and probably reflects habituation to a novel situation.

The number of ITRs made in the avoidance conditioning task is also of interest. In the study by Satinder (1968), cited previously, it was found that ITRs correlated .46 with number of avoidances and .31 with open-field ambulation scores. Both correlations were significant beyond the .01 level. These correlations would suggest that increased ITRs are indicative of lowered emotionality. A study by Golub and Kornetsky (1972) also revealed a positive correlation between number of avoidances and ITRs. They found that rats from mothers treated with the tranquilizer cloropromazine during pregnancy showed more total avoidances and a higher rate of intertrial responding than controls.

It is possible that an increase in ITRs reflects an exploratory drive which decreases as the animal becomes more fearful (emotional). The data from the present study offer support for this hypothesis. The Group II Ss, the least emotional by the other criteria, made the most ITRs, followed by the Group I Ss (who were intermediate in emotionality between the Group II and Control Ss). The Controls made the least number of ITRs.

Sex appears to be an important variable affecting the number of ITRs and the open-field performance. The females in both treatment groups made more ITRs than did the males, while the number of ITRs for the Control males and females were nearly identical. However, these results are inconclusive as the statistical analyses for the treatment groups was not significant. Nonsignificance can be attributed mainly to a large amount of variability in the data. On the other hand, the sex difference in the open-field test is clear cut and highly significant. The females in all groups were substantially more active than the males on all days.

Hutchings and Gibbon (1970) raised the question concerning the possibility that simply removing the pregnant female from her nesting area constituted a stress great enough to effect the emotionality of the offspring and that this stress,and not any treatment factor, was the crucial variable. The results of their study indicated that there was no difference in the emotionality of offspring whose mothers had been stressed by handling and those whose mothers had been given 1.0 mA escapable shock. While the design of the present study does not allow a clear test of Hutchings and Gibbon's hypothesis, the results indicate that the treatment given the pregnant females had an effect above and beyond mere handling (i.e., removing the animal from the familiar nesting area). In the present study the Control mothers were removed from their home cages for the same amount of time as the Experimental mothers and yet there was a significant difference between the behavior of the Experimental and Control offspring.

From the design of the present study one cannot ascertain whether the difference in emotionality between the Group I offspring and the Control offspring was due to the affect of shock on the fetus, the maternal anxiety, or a combination of both. This also holds true for the difference between the Group II and Control offspring. However, the difference between the emotionality levels of the Group II and Group I offspring can be attributed solely to a difference in maternal anxiety as both groups received the same amount of shock.

Although it is impossible to separate shock effects from anxiety effects (except for the difference between Group I and Group II offspring), the author believes that maternal anxiety is the crucial variable affecting the offspring emotionality in both treatment groups and that intrauterine shock had little effect on the offspring. The study by Anderson (1968), which indicated that even electroconvulsive shock during pregnancy did not affect the behavior of the offspring, supports this contention. In addition, the studies by Thompson (1957), Hockman (1961), and Thompson *et al*. (1962) indicate that maternal anxiety *per se* can influence offspring emotionality.

Further research in this area should include increased levels of prenatal shock to assess the effect of heightened anxiety. Theoretically, a point would be reached when the shock would no longer produce an innoculation effect (lower emotionality or decreased reaction to stress) but a sensitizing effect (increased emotionality or a heightened reaction to stress).

The generality of the conclusions drawn from this study must be considered in view of the complexity of the variables involved. A survey of the investigations reported in this area indicate that even the strain of rat is an important variable. Offspring of stressed albino mothers appear to have decreased emotionality (Thompson *et al*. 1962; Ader and Conklin, 1963; Hutchings and Gibbon, 1970; Fulkerson, 1971) whereas offspring of stressed Long-Evans hooded mothers show an increase in emotionality (Thompson, 1957; Hockman, 1961; Ader and Belfer, 1962). The inherent levels of emotionality in each strain could account for this finding. It may be that albino rats are inherently less emotional than hooded rats and that mild stress applied during pregnancy produces an innoculation effect on the offspring facilitating their reaction to their environment after birth. If the hooded rats have a higher emotional level to begin with, prenatal stress may sensitize the offspring, making them more emotional and disrupting their performance in stressful situations.

Further multidisciplinary research investigating differences in offspring behavior generated by prenatal stress would appear desirable. Any research that can ultimately shed some light on the etiology of abnormal behavior would seem exceedingly valuable and investigations in this area could be one of the approaches which eventually uncovers some of the answers concerning the problem of deviant behavior.

APPENDIX

RAW DATA AND STATISTICAL COMPARISONS

TABLE 3

t-TEST COMPARISONS FOR THE OPEN-FIELD TEST[a]

Comparison	t	df	P
1. Comparison between the mean number of squares entered by the Control and Group I males for three days.	0.18	18	>.10
2. Comparison between the mean number of squares entered by the Control and Group II males for three days.	1.42	22	=.088
3. Comparison between the mean number of squares entered by the Group I and Group II males for three days.	1.95	23	<.05
4. Comparison between the mean number of squares entered by the Control and Group I females for three days.	0.46	17	>.10
5. Comparison of the mean number of squares entered by the Control and Group II females for three days.	2.27	22	<.025
6. Comparison between the mean number of squares entered by the Group I and Group II females for three days.	2.75	18	<.01

[a]The values of P are given for a one-tailed test.

TABLE 4

t-TEST COMPARISONS FOR AVOIDANCES DURING AVOIDANCE ACQUISITION IN A TWO-WAY SHUTTLEBOX[a]

Comparison	t	df	P
1. Comparison between the mean number of avoidances made by Control and Group I Ss for 75 trials.	1.84	31	<.05
2. Comparison between the mean number of avoidances made by Control and Group II Ss for 75 trials.	2.40	37	<.01
3. Comparison between the mean number of avoidances made by the Group I and Group II Ss for 75 trials.	0.507	42	>.10

[a]The values of P are given for a one-tailed test.

TABLE 5

t-TEST COMPARISONS FOR INTERTRIAL RESPONSES (ITRs) DURING AVOIDANCE ACQUISITION IN A TWO-WAY SHUTTLEBOX[a]

Comparison	t	df	P
1. Comparison between the mean number of ITRs made by Control and Group I Ss during 75 trials.	1.16	28	>.10
2. Comparison between the mean number of ITRs made by Control and Group II Ss during 75 trials.	1.68	37	<.05
3. Comparison between the mean number of ITRs made by Group I and Group II Ss during 75 trials.	0.65	42	>.10
4. Comparison between the mean number of ITRs made by Control males and Group I males during 75 trials.	0.54	14	>.10
5. Comparison between the mean number of ITRs made by Control males and Group II males during 75 trials.	2.09	17	<.005
6. Comparison between the mean number of ITRs made by Group I males and Group II males during 75 trials.	1.96	21	<.05
7. Comparison between the mean number of ITRs made by Control females and Group I females during 75 trials.	1.26	13	>.10
8. Comparison between the mean number of ITRs made by Control females and Group II females during 75 trials.	1.94	15	<.05
9. Comparison between the mean number of ITRs made by Group I females and Group II females during 75 trials.	0.20	17	>.10
10. Comparison between the mean number of ITRS made by Control males and Control females during 75 trials.	0.83[b]	11	>.10

TABLE 5--Continued

Comparison	t	df	P
11. Comparison between the mean number of ITRs made by Group I males and Group I females during 75 trials.	1.55[b]	16	<.08
12. Comparison between the mean number of ITRs made by Group II males and Group II females during 75 trials.	0.73[b]	22	>.10

[a]The values of P are given for a one-tailed test.

[b]The values of P are given for a two-tailed test.

TABLE 6

RAW DATA FOR CONTROL OFFSPRING FOR THREE DAYS OF OPEN-FIELD TESTING

	Number of Squares Entered		
Males	Day 1	Day 2	Day 3
$M5_1$	50	53	27
$M5^2$	57	29	43
$M4_1$	53	9	21
$M4_2$	71	71	44
$M21_1$	15	7	4
$M20_1$	30	75	20
$M20_2$	28	6	4
$M20_3$	35	76	7
$M20_4$	98	35	3
Females			
$F20_1$	125	85	47
$F21_1$	74	9	5
$F21_2$	50	11	4
$F21_3$	70	74	26
$F21_4$	70	52	13
$F21_5$	64	35	8
$F22_1$	80	63	48
$F22_2$	82	95	52
$F22_3$	146	73	41
$F4_1$	65	13	83
$F4_2$[a]	7	11	10
$F5_1$	63	45	21
$F5_2$	108	90	41

[a]Data discarded because it deviated more than 2.2 standard deviations from the mean.

TABLE 7

RAW DATA FOR GROUP I OFFSPRING FOR THREE DAYS OF OPEN-FIELD TESTING

	Number of Squares Entered		
Males	Day 1	Day 2	Day 3
$M1_1$	23	9	5
$M2_1$	69	66	39
$M2_2$[a]	79	75	88
$M3_1$	90	42	42
$M3_2$	35	8	8
$M8_1$	66	3	7
$M8_2$	20	57	23
$M8_3$	50	13	4
$M16_1$	70	31	11
$M16_2$	33	32	25
$M16_3$	75	14	25
Females			
$F1_1$	65	57	--[b]
$F1_2$	28	63	21
$F1_3$	47	50	22
$F2_1$	106	52	--[b]
$F2_2$	82	74	--[b]
$F2_3$	71	47	87
$F3_1$	70	15	31
$F3_2$	24	22	--[b]
$F3_3$	31	30	7
$F8_1$	59	78	--[b]
$F8_2$	137	33	--[b]
$F16_1$	74	63	43
$F16_2$	93	68	42
$F16_3$	78	62	41

[a]Data discarded because it deviated more than 2.2 standard deviations from the mean.

[b]Data were misplaced and never recovered.

TABLE 8

RAW DATA FOR GROUP II OFFSPRING FOR THREE DAYS OF OPEN-FIELD TESTING

	Number of Squares Entered		
Males	Day 1	Day 2	Day 3
$M17_1$	64	20	21
$M17_2$	69	31	48
$M17_3$	81	5	5
$M17_4$	94	29	20
$M18_1$	74	11	27
$M19_1$	63	42	55
$M19_2$	41	31	46
$M19_3$	93	57	49
$M19_4$	93	33	43
$M23_1$	66	39	21
$M23_2$	22	20	5
$M23_3$	85	119	43
$M23_4$	120	49	25
$M23_5$	56	66	42
$M24_1$	51	5	5
$M24_2$[a]	22	5	3
Females			
$F18_1$	117	89	40
$F18_2$	96	67	11
$F18_3$	92	101	51
$F17_1$	134	104	27
$F17_2$	80	138	23
$F17_3$	121	149	55
$F17_4$	31	52	9
$F19_1$	38	43	64
$F19_2$	96	59	70
$F19_3$	62	41	36
$F19_4$	88	93	85
$F19_5$	114	118	112
$F23_1$	67	37	--[b]
$F23_2$	77	25	--[b]
$F23_3$	93	29	--[b]

[a]Data discarded because it deviated more than 2.2 standard deviations from the mean.

[b]Data were misplaced and never found.

TABLE 9

RAW DATA FOR CONTROL OFFSPRING FOR THREE DAYS OF AVOIDANCE ACQUISITION

	Number of Avoidances			Number of Escapes			Number of ITRs		
	Day			Day			Day		
Males	1	2	3	1	2	3	1	2	3
$M5_3$	6	11	14	19	14	11	6	18	17
$M5_4$	19	20	17	6	5	18	45	23	54[a]
$M4_2$	8	17	18	16	8	7	42	19	20
$M21_1$	4	5	5	21	20	20	3	9	24
$M20_1$	3	4	10	22	21	15	6	5	16
$M20_2$	6	7	17	19	18	8	5	3	6
$M20_4$	4	16	18	21	9	7	11	1	3
Females									
$F20_1$	3	20	18	22	5	7	14	34	44
$F21_1$	8	17	19	17	8	6	3	21	30
$F21_2$	5	10	11	20	15	13	8	2	7
$F21_3$	1	6	4	24	19	21	17	4	7
$F22_1$	7	16	21	18	9	4	4	10	34
$F22_2$	8	1	4	17	23	21	6	5	5
$F22_3$	12	19	20	13	6	5	32	28	24

[a]Data discarded because it deviated more than 2.2 standard deviations from the mean.

TABLE 10

RAW DATA FOR GROUP I OFFSPRING FOR THREE DAYS OF AVOIDANCE ACQUISITION

	Number of Avoidances			Number of Escapes			Number of ITRs		
	Day			Day			Day		
Males	1	2	3	1	2	3	1	2	3
$M8_1$	13	20	17	12	5	8	1	26	35
$M8_2$	2	5	9	23	16	16	12	2	2
$M8_3$	8	14	18	15	11	7	1	3	2
$M8_4$	11	18	21	14	7	4	9	24	15
$M3_1$	14	20	22	11	5	3	18	3	32
$M2_1$	12	21	18	13	4	7	17	9	22
$M2_2$	18	16	15	7	9	10	37	12	11
$M16_3$	9	20	19	16	15	6	6	16	33
$M16_5$	14	16	15	11	9	10	15	28	9
$M16_6$	3	12	5	22	13	19	3	9	9
Females									
$F2_1$	15	21	20	10	4	5	22	21	14
$F2_2$	7	7	10	18	18	15	9	6	14
$F3_1$	20	22	23	5	3	2	12	33	76
$F3_2$	4	13	19	21	12	5	21	8	7
$F8_1$	6	14	19	19	10	6	19	68	80
$F8_2$	9	20	19	16	5	5	67	94	82
$F16_1$	14	7	18	11	14	7	6	11	2
$F16_2$	16	19	17	10	6	8	13	13	5

TABLE 11

RAW DATA FOR GROUP II OFFSPRING FOR THREE DAYS OF AVOIDANCE ACQUISITION

	Number of Avoidances			Number of Escapes			Number of ITRs		
	Day			Day			Day		
Males	1	2	3	1	2	3	1	2	3
$M17_1$	14	16	19	11	8	6	9	89	38
$M17_2$	14	16	19	11	9	6	18	20	36
$M17_3$	12	18	21	13	7	4	21	13	13
$M17_4$	8	17	21	12	8	4	17	55	28
$M24_1$	18	24	23	7	1	2	23	27	24
$M18_1$	10	7	10	15	18	15	13	9	42
$M19_1$	16	22	20	9	3	5	40	35	39
$M19_3$	4	8	5	21	17	19	14	12	1
$M19_4$	1	4	8	24	21	17	9	10	6
$M23_1$	10	20	19	15	5	6	26	29	59
$M23_2$	15	16	16	10	9	9	11	8	13
$M23_3$	5	14	21	20	11	4	2	8	18
$M23_4$	6	10	15	19	15	10	6	16	14
Females									
$F17_1$	17	18	21	8	7	4	5	18	22
$F17_2$	14	15	16	11	10	9	24	22	72
$F17_3$	14	17	18	11	8	7	29	33	31
$F18_1$	7	16	20	18	9	5	16	7	11
$F19_1$	16	20	22	9	5	3	52	52	56
$F19_2$	7	18	24	18	7	1	17	30	50
$F19_4$	3	15	22	22	10	4	15	10	18
$F19_5$	12	19	20	13	6	5	48	69	69
$F23_1$	11	20	20	15	5	5	11	29	31
$F23_2$	20	20	23	5	5	2	18	9	9
$F23_3$	4	17	21	21	8	4	5	2	0[a]

[a]Data discarded because it deviated more than 2.2 standard deviations from the mean.

REFERENCES

Ader, R., & Belfer, M. L. Prenatal maternal anxiety and offspring emotionality in the rat. Psychological Reports, 1962, 10, 711-718.

Ader, R., & Conklin, P. M. Handling of pregnant rats: Effects on emotionality of their offspring. Science, 1963, 142, 411-412.

Anderson, A. The effects of electroconvulsive seizures during pregnancy on behavioral development of the offspring. Dissertation Abstracts, 1968, 29(6-B), 2189.

Anderson, E. E. The interrelationship of drives in the male albino rat: II. Intercorrelations between 47 measures of drives and learning. Comparative Psychological Monograph, 1938, 14, 1-119.

Broadhurst, P. J. Emotionality and the Yerkes-Dodson law. Journal of Experimental Psychology, 1957, 54, 345-352.

Courts, F. A. Relations between muscular tension and performance. Psychological Bulletin, 1942, 39, 347-367.

Fazzaro, J. M. The effects of prenatal stimulation and postnatal factors on aversive and appetitive conditioning in the adult rat. Dissertation Abstracts International, 1971, 31(11-B), 6929.

Fraser, F. C., Fainstat, T. A., & Kalter, H. The experimental production of congenital defects with special reference to cleft palate. Neonatal Studies, 1953, 2, 43-57.

Freeman, G. L. The relationship between performance level and bodily activity level. Journal of Experimental Psychology, 1940, 26, 602-608.

Fulkerson, J. R. The interaction of pre- and postnatal stimulation on the stress responses of the rat. Dissertation Abstracts International, 1971, 31(11-B), 6932-33.

Furchtgott, E., & Echols, M. Activity and emotionality in pre- and neonatally X-irradiated rats. Journal of Comparative and Physiological Psychology, 1958, 51, 541-545.

Furchtgott, E., Echols, M., & Openshaw, J. W. Maze learning in pre- and neonatally X-irradiated rats. Journal of Comparative and Physiological Psychology, 1958, 51, 178-180.

Golub, M., & Kornetsky, C. Prenatal chlorpromazine treatment and adult avoidance learning. Paper presented at the 13th annual meeting of the Psychonomic Society, St. Louis, Missouri, Nov. 41, 1972.

Grey, J. A. The psychology of fear and stress. New York: McGraw-Hill, 1971.

Hall, C. S. Temperament: A survey of animal studies. Psychological Bulletin, 1941, 38, 909-943.

Hamilton, H. C. The effect of the administration of sodium bromide on the behavior of the offspring: IV. Emotionality (timidity and experimentally induced seizures. The Journal of Psychology, 1945, 19, 17-30.

Hayes, K. J. Exploration and fear. Psychological Reports, 1960, 6, 91-93.

Hebb, D. O. Drives and C.N.S. (Conceptual nervous system). Psychological Review, 1955, 62, 243-254.

Hockman, C. H. Prenatal maternal stress in the rat: Its effects on emotional behavior in the offspring. Journal of Comparative and Physiological Psychology, 1961, 54, 679-684.

Hutchings, D. E., & Gibbon, J. Preliminary study of behavioral and teratogenic effects of two "stress" procedures administered during different periods of gestation in the rat. Psychological Reports, 1970, 26, 239-246.

Joffe, J. M. Prenatal determinants of behavior. Oxford: Pergamon Press, 1969.

Jones, J. M., Lloyd, C. W., & Wyatt, T. C. A study of the interrelationships of maternal and fetal adrenal glands of rats. Endocrinology, 1953, 53, 182-191.

Kaplan, A. R. Influence of prenatal maternal anxiety on emotionality in young rats. Science, 1957, 126, 73-74.

Kolstoe, R. H. Introduction to statistics for the behavioral sciences. Illinois: Dorsey Press, 1969.

Martin, R. F., & Hall, C. S. Emotional behavior in the rat: V. The incidences of behavior derangements resulting from air-blast stimulation in emotional and non-emotional strains of rats. Journal of Comparative Psychology, 1941, 32, 191-204.

Montgomery, K. C., & Monkman, J. A. The relations between fear and exploratory drive. Journal of Comparative and Physiological Psychology, 1955, 48, 132-136.

Moot, S. A., Cebulla, R. P., & Crabtree, J. M. Instrumental control and ulceration in rats. Journal of Comparative and Physiological Psychology, 1970, 71, 405-410.

Nicholas, J. S. Experimental methods and rat embryos. In E. J. Farris & J. Q. Griffith (Eds.), The rat in laboratory investigation. Philadelphia: J. B. Lippincott, 1949. Pp. 53-54.

Page, I. H. Sertonin, last four years. Physiological Review, 1958, 38, 277.

Pasamanick, B., Rogers, M. E., & Lilienfeld, A. M. Pregnancy experience and the development of behavior disorder in children. American Journal of Psychiatry, 1956, 112, 613-618.

Rogusa, D. M. Shemberg, K. M., & Rasbury, W. Escapable-inescapable shock and body weight. Psychonomic Science, 1968, 13, 45-46.

Satinder, P. K. A note on the correlation between open-field and escape-avoidance behavior in the rat. The Journal of Psychology, 1968, 69, 3-6.

Sontag, L. W. The significance of fetal environmental differences. American Journal of Obstetrics and Gynecology, 1941, 42, 996-1003.

Thompson, W. D., & Sontag, L. W. Behavioral effects in the offspring of rats subjected to audiogenic seizure during the gestational period. Journal of Comparative and Physiological Psychology, 1956, 49, 454-461.

Thompson, W. R. Influence of prenatal maternal anxiety on emotionality in young rats. Science,1957, 125, 698-699.

Thompson, W. R., & Schaefer, T. Early environmental stimulation. In D. W. Fiske & S. R. Maddi (Eds.), Functions of varied experience. Illinois: Dorsey Press, 1961. Pp.81-105.

Thompson, W. R., Watson, J., & Charlesworth, W. R. The effects of prenatal maternal stress on offspring behavior in rats. Psychological Monographs: General and Applied, 1962, 76:38, 1-26, Whole No. 557.

Warkany, J., & Nelson, R. C. Skeletal abnormalities induced in rats by maternal vitamin A deficiency. Archives of Ophthalmology, 1940, 35, 140-169.

Werboff, J., Gottlieb, J. S., Havlena, J., & Word, T.J. Behavioral effects of prenatal drug administration in the white rat. Pediatrics, 1961, 27, 312-323.

Whimbey, A. E., & Denenberg, V. H. Two independent behavioral dimensions in openfield performance. Journal of Comparative and Physiological Psychology, 1967, 63, 500-504.