

ROBIN FRASER PATCHETT

THE EFFECT OF PATTERNED SOUND DEPRIVATION UPON  
AUDITORY DISCRIMINATION IN ALBINO RATS

Submitted for the degree of  
Doctor of Philosophy in Psychology  
at Victoria University of Wellington

Wellington, New Zealand

1975

### ACKNOWLEDGEMENTS

The material and editorial assistance of Professor A.J.W. Taylor and Professor L.B. Brown is very gratefully acknowledged. My thanks also to all the members of the staff of the Department of Psychology at Victoria University whose advice was always given willingly. I am grateful, also, to Mr. F. Lane and Mr. J. Bowden who made and serviced much of the equipment.

### ABSTRACT

To test the hypothesis that prior patterned or varied auditory experience was necessary for the development of auditory frequency discrimination and auditory pattern discrimination, groups of Sprague-Dawley albino rats were deprived of patterned sound from birth by the novel technique of rearing them in 'white' noise. The sound deprived rats learned a frequency discrimination as easily as controls reared in varied sound conditions, but showed inferior performance on an auditory pattern discrimination task.

Supporting experiments showed that the inferiority of varied sound deprived animals on the pattern discrimination task was not likely to have been due to their emotional state at the time of the testing nor to their inferiority in learning to respond in a discrimination task compared with non-deprived controls. Open-field testing showed that the sound deprived subjects did not differ from non-deprived controls in 'emotionality'. The sound deprived rats were not inferior, either, to controls on a complex visual discrimination task.

Experiments were also carried out to explore the effect of various durations of patterned sound deprivation and the effect of the deprivation at various times in the life cycle of the rat on auditory pattern discrimination. The results of these experiments favoured an explanation for the effect of varied sound

experience which proposed that patterned auditory discrimination development depended, simply, on prior experience with varied sound rather than an explanation which proposed that the effect depended on varied sound experience during a particular sensitive period in the life of the rat.

The research involved a total of seven different experiments, the similarities in the findings of which when compared with those of other investigators working in the area of the effects of deprivation of patterned light on visual discriminations were noted. The present experiments support generalizations about the role of prior experience on later behaviour, based largely on experiments in the visual mode, by supplying evidence from another sensory mode.



## CONTENTS

<u>CHAPTER</u>		<u>PAGE</u>
ONE	BACKGROUND TO THE EXPERIMENTS .....	1
	Previous Studies Pertaining to the Effect of Early Auditory Deprivation on Auditory Discrimination in Animals .....	6
	Conclusions from Previous Studies .....	22
TWO	THE AIMS AND DESIGN OF THE EXPERIMENTS .....	23
THREE	THE EFFECTS OF AUDITORY PATTERN DEPRIVATION ON LATER AUDITORY DISCRIMINATION IN THE ALBINO RAT .....	29
	Experiment Ia. The Effect of Patterned Sound Deprivation on Auditory Frequency Discrimination in Albino Rats .....	30
	Experiment Ib. The Effect of Patterned Sound Deprivation on Auditory Pattern Discrimination in Albino Rats .....	54
FOUR	THE EFFECTS OF REARING ALBINO RATS IN WHITE NOISE ON THEIR PERFORMANCE ON VARIOUS MEASURES OF EMOTIONAL AND COGNITIVE BEHAVIOUR ..	61
	Experiment IIa. The Effect of Rearing in White Noise on Weaning Weight and 'Emotionality' in the Albino Rat .....	63
	Experiment IIb. The Effect of Rearing in White Noise on Visual Discrimination in the Albino Rat .....	74
FIVE	THE EFFECT OF RESTRICTING PATTERNED SOUND FOR VARIOUS DURATIONS AND AT VARIOUS AGES ON AUDITORY PATTERN DISCRIMINATION IN THE ALBINO RAT .....	89
	Experiment IIIa. The Effect of 60 Days of Patterned Sound Deprivation During Adulthood on the Ability of the Albino Rat to Learn an Auditory Pattern Discrimination ..	91
	Experiment IIIb. The Effect of Patterned Sound Experience from Birth to 30 Days of Age on an Auditory Pattern Discrimination in the Albino Rat .....	97

CHAPTER

PAGE

Experiment IIIc. The Effect of Depriving Rats of Patterned Sound for the First 30 Days After Birth on Their Later Ability to Learn an Auditory Pattern Discrimination ....	97
SIX CONCLUSIONS .....	102
Further Research Possibilities .....	107
REFERENCES .....	110

PLATES

Plate 3.1. The Test Chamber .....	34
-----------------------------------	----

## CHAPTER ONE

### BACKGROUND TO THE EXPERIMENTS

Enquiry into the development of perception has been a topic of interest for centuries. It has been considered important to know the answer to the question which Molyneux is said to have put to Locke, whether a man born blind but later given sight could distinguish by sight alone a sphere from a cube. Research in the area has usually been based on the question of whether maturation follows a fixed pattern guided by genetically organized mechanisms or whether maturation is regulated by environmental stimulation. A suggestion for a compromise between the advocates of the two opposing viewpoints about the origins of psychological development, the 'nativist' and the 'empiricist', was made as early as 1895 by Roux who said of the nervous system, that although early development depended on intrinsic growth and self differentiation, later development was determined by environmental conditions.

The proposition that physical and psychological maturation, based on genetically arranged patterns, occurred through and because of environmental stimulation drew support from the "neurobiotaxis" doctrine formulated by Kappers (1920). According to this view, nerve fibres in the embryonic nervous system grew towards sources of stimulation. The concept of neurobiotaxis was conceived to account for neural development during the pre-

natal period, however, Hebb (1949) considered that the idea of neurobiotaxis could be extended to account also for later development. For Hebb, neurobiotaxis was the principle behind the functioning of the nervous system. Without stimulation, sensory systems would fail to develop or fail to persist.

Another concept, also originating from research in prenatal development, was introduced into theories of postnatal development after ethologists (e.g. Lorenz, 1950) began to recognize that there were periods during the early development of birds during which they were especially sensitive to particular environmental events, such as the appearance of others of their species. During these periods of heightened sensitivity, called critical periods, behaviour patterns were established which profoundly influenced subsequent behaviour.

Thus apparently, not only did the organism require stimulation for normal development but also particular stimulation at particular times especially early in life. Early stimulation, or the lack of it, was considered to make an important difference both in neural development and in behaviour capacity. These ideas led to considerable research in two directions - studies in early sensory deprivation and studies in early sensory augmentation or enrichment.

Another source of interest in the quality of environmental stimulation and its effect on early development came from an ancient suspicion that a generally impoverished rearing environ-

ment led to dull wittedness and maladaptive behaviour. In support of this notion, Spitz (1945) and Bowlby (1953) generated considerable interest amongst people concerned with child rearing when they demonstrated the detrimental effects of the cursory child care practices, involving deprivation of one sort or another, in institutions, hospitals and foundling homes. As a consequence of this interest, also, a great number of experiments were conducted with animals both to explore the effects of rearing in restricted environments on later behaviour and to explore the effects of adding extra stimulation to that usually encountered by animals during rearing.

The investigation of the effects of early experience on later behaviour continued in experiments which explored the effects of early physical stimulation, the effects of general sensory enrichment or general sensory impoverishment on later behaviour as well as other experiments which explored the effects of restricting enrichment or deprivation to a given sense modality (e.g. see reviews by Beach and Jaynes, 1954; Gibson, 1967). Experiments on early physical stimulation, such as those reviewed by Denenberg (1968), usually involved handling or physically stimulating infant animals which treatment had effects on later "emotionality" in the animals. General sensory enrichment, achieved by rearing animals in groups in complex environments with "toys" led to greater maze learning ability in rodents (e.g. Hymovitch, 1962) and to significant differences from less fortunate,

normally reared rodents on several measures of brain anatomy and physiology (e.g. Rosenweig, Bennett and Diamond, 1972). Experiments designed to test the effect of augmenting the sensory experience of young animals with particular stimuli, were usually successful in showing that exposure to particular stimuli early in life assisted animals to make discriminations involving those stimuli later in life (e.g. Meier and McGee, 1959). General restriction of stimulation and social contact, on the other hand, was found to lead to many behavioural disturbances in animals that ranged from more than usual arousal by novel stimuli to an inability to learn by painful experience (e.g. Thompson and Heron, 1954; Melzack and Scott, 1957). Restriction of stimulation of a particular sense, however, has been the most common technique used to investigate the role of experience in the development of discrimination behaviour in animals, and is the subject of the present investigation.

There are two aspects to the deficits afforded by sensory deprivation. One is that an animal which has been subjected to sensory deprivation from birth lacks experience of the sense deprived. The other aspect is that a deprived animal lacks stimulation of a particular sensory system. As the historical outline above has suggested, experiments which have used the method have been designed with one or other of these aspects of sensory deprivation primarily in view.

The experiments which have used sensory deprivation to deprive animals of experience have usually been concerned with separating those discriminations which animals are capable of learning in the absence of previous sensory experience from those discriminations which require animals to have particular sensory experience before they can be learned. Experimenters attempting such a separation regarded the technique of sensory deprivation as a method of prolonging the naivety of the animal in the sense deprived from birth until such time as the animal was physically matured enough to perform responses which were easily discernable. It was considered that by discovering what particular features of perceptual organization, what particular discrimination capacities were present to begin with before sensory experience commenced, baselines from which to explore the effects of early experience would be established. Whether, and what type of experience resulted in facilitation of learning a discrimination or whether the experience was detrimental to learning the discrimination could be gauged from such a baseline.

Experiments which have used sensory deprivation as a method of depriving animals of particular stimulation have been concerned with the effects of sensory deprivation on the development of discrimination behaviour. There was the possibility that sensory deprivation retarded development of discrimination behaviour based on the sense deprived, and the advance or restoration of development awaited the appropriate sensory stimulation. There was also

the possibility that sensory deprivation might cause already existing discrimination abilities to deteriorate. This aspect of the use of sensory deprivation to deprive animals of stimulation was, of course, very closely related to the other outlined in the preceding paragraph, and they are often both explored in the same experiment (e.g. Fantz, 1967).

By far the majority of the very large number of experiments which have investigated the effects of early sensory deprivation in animals have used visual deprivation. The concentration on one sense modality was not surprising considering the technical difficulties involved in attempting to rear animals in silence or without tactile experience. However, the concentration has meant that generalizations about the role of early sensory experience on later discrimination behaviour in animals must be made with caution until studies in other sense modalities produce results which agree with the findings in vision.

It is the purpose of this present investigation to demonstrate a method by which auditory deprivation of animals can be achieved in a manner which both avoids the problems associated with methods previously employed and explores the role of patterned auditory experience on auditory discrimination development in the rat.

#### Previous Studies Pertaining to the Effect of Early Auditory Deprivation on Auditory Discrimination in Animals

There were few studies in this area because of the difficulty in depriving an animal of auditory stimulation by methods



which leave its auditory system intact so that post-deprivation studies can be made of its auditory discrimination abilities. Sound deprivation achieved either by rearing an animal with ear occluding devices or in a sound attenuated chamber or both can be defeated by the animal generating its own noise. Also, it has been shown that chronically placed ear occluding devices can sometimes cause considerable damage to an animal's tympanic membranes and middle ear structures (Sterritt and Robinson, 1964). The separation of auditory discrimination deficiencies caused by middle ear damage from those caused by auditory deprivation is very difficult to achieve. Then, too, the effects of rearing animals in social isolation and visually impoverished conditions necessary for ensuring that they are reared in silence, may produce behavioural changes in the animals which overshadow the effects of the auditory deprivation (e.g. Melzack, 1968).

In spite of the practical difficulties involved, there have been several studies in which auditory deprivation, or at least auditory restriction, have been used to explore the effects of such treatment early in life on later behaviour towards auditory stimuli.

In 1943 Wolf conducted an experiment in which he reared albino rats with cotton and paraffin plugs in their ears from ten days of age until they were aged 25 days. Other rats were deprived of vision with plaster hoods over their heads from 16 to 25 days of age. Further rats were similarly treated for a

comparable duration beginning when they were 26, 50 and 75 days of age. Two weeks after the deprivation periods ended, all the rats were individually trained to run to a source of food when a signal was presented. The signal used on the first ten days of training was a light while on the second ten days of training, a buzzer was used. Immediately following this training, the rats were paired so that a previously vision deprived rat was paired with a previously auditorily deprived animal. Each pair was then put into competition for the food. Wolf found that when the starting signal for the competition was a light, the previously auditorily deprived rats won the competition significantly more often than their early vision deprived competitors. Then, with the same pairs of animals, when the signal for beginning the competition was a buzzer, the early auditorily deprived animals lost the competition. The groups deprived of hearing and vision later than during the pre-weaning period did not differ in their performance in the competition.

Wolf believed that his findings had implications for understanding some kinds of neurotic symptoms. His results did demonstrate, however, that deprivation of hearing (or vision) during an early period of development in the rat could have an effect on later behaviour controlled by the stimulus dimension deprived. Similar, although not such subtle effects of sensory deprivation were shown in several experiments in which animals were deprived of vision, (for a review, see Ganz, 1968). One

visual deprivation experiment with cats (Dews and Wiesel, 1970) showed that visual deprivation during a very short period early in the life of a kitten affected some behaviour based on vision during adulthood.

Sixteen years later Gauron and Becker (1959) set out to replicate Wolf's experiment, but they modified some of his techniques that were unsatisfactory with their rats. For example, they auditorily deprived their rats by plugging their ears with cotton and collodion rather than the wax used by Wolf, and they changed the plugs as the rats' ears grew and they reared their visually deprived rats in a dark box rather than with individual hoods. Also they counterbalanced the order of individual training to the two stimulus cues, so that some rats were trained first with the light and then the buzzer while with others the opposite arrangement held. Despite the modifications and other problems discovered such as the aversive nature of the buzzer to several rats, the results of Gauron and Becker's experiment supported those of Wolf's. Auditorily deprived rats won in competition with visually deprived rats significantly more often when the signal for beginning the competition was a light, and they lost when the signal was a buzzer. Gauron and Becker interpreted these results as "a limitation of sensory ability", (p.692) in the rats as a result of the deprivation experience. They did not attempt to define more closely what they meant by 'sensory ability'. Although both Wolf's and Gauron and Becker's results supported the proposition that sensory deprivation was

sometimes followed by an inability to use information presented in the affected modality, neither experiment appeared to present grounds for suggesting that the actual functioning of the sensory systems of the animals was affected by the deprivation.

Tees (1967a) reared rats with cotton and collodion in their ears from three to five days of age until they were 60 days old in sound-attenuating chambers. At 60 days of age they began training on an auditory frequency discrimination problem or one of two auditory pattern discrimination problems. In the frequency discrimination, the rats were expected to detect a change from one frequency to another in a continuously presented series of tone pulses, and to use the change as a cue for an avoidance response in a double compartment shuttle-box. The auditory patterns to be discriminated in the first pattern discrimination problem were groups of three tone pulses, continuously presented, the first and third being of one auditory frequency and the second tone of another. The rats were expected to respond when the patterns changed from one configuration, for instance high-low-high to the opposite, low-high-low. The second pattern discrimination task involved the subjects with a continuously presented negative stimulus arrangement of groups of three tone pulses with each alternate group of three being of the same auditory frequency. The positive stimulus, to which the subjects were expected to respond, consisted of a change from the negative stimulus presentation to one where the frequencies of the tones alternated within the groups of three as in the first auditory

pattern discrimination problem.

Tees found that his auditorily deprived rats were no different from colony reared controls in their acquisition of the frequency discrimination, but they took significantly more trials to learn both pattern discriminations than did their controls. Tees interpreted his results to mean that prior sensory experience of sound was not necessary for rats to learn an auditory frequency discrimination whereas the "capacity to process auditory input over time efficiency requires sensory pre-conditioning", (1967a, p.392). Parallel results to Tees' can be found in experiments in visual deprivation which show that visually deprived rats can make responses on the basis of discriminations made between (a) striations of various orientations (e.g. Woodruff and Slovak, 1965); (b) forms such as circles and triangles (e.g. Gibson, Walk and Tighe, 1959); and (c) relative light intensities (e.g. Hebb, 1937). These discriminations did not involve configurational aspects of the visual environment and did not require the abstraction of a relationship between a visual form and its surrounding forms. When such a configuration is involved in a visual discrimination task in which integration of meaningful visual information over an area is required, animals have difficulty making discriminations (e.g. Riesen 1961, 1966; Ganz, Hirsch and Tieman, 1972). The auditory patterns which Tees used can be viewed as configurational auditory stimuli, discrimination between which required animals to integrate auditory information over time.

The interpretations Tees made of his results can be criticised on several grounds. He found no differences in the number of trials taken to reach a criterion in the frequency discrimination task between the auditorily deprived rats and the normally reared group and concluded that auditory deprived rats could learn a frequency discrimination as easily as those normally reared. Another possible conclusion from these same results is that the test for frequency discrimination used may not have been sensitive enough to distinguish between the performance of the two groups. Thompson (1959) demonstrated that the method of stimulus presentation which required an animal to respond to a change of stimulus frequency, as used by Tees, resulted in a much more rapid acquisition of a frequency discrimination than any of the other methods he tested.

Further, Tees used 2kHz and 4kHz as the stimulus frequencies in his discrimination task. According to a careful study by Hack (1971), rats respond to 4kHz signals at an intensity 7dB less intense than to 2kHz signals. Tees varied his stimuli of both frequencies over the same range from 55 to 70dB SPL so that his subjects would not use the intensity variable as a cue. However, because of the 7dB difference in the two frequencies from the point of view of the 'sensation level' of the rat, the range of intensities of 4kHz stimuli that were presented to Tees' rats was some 7dB higher than the range of 2kHz stimuli. Thus Tees' rats may have learned an intensity discrimination rather than a frequency discrimination.

Tees' pattern discrimination results demonstrated a difference between auditorily deprived and normally reared rats in learning auditory pattern discriminations, and he attributed this to the fact that they had no prior experience of sound. However, the possibility existed that the two groups of rats differed on the discrimination test because of differences in heredity between the groups. The litters of rats that supplied the experimental animals were different from the litters that supplied the controls.

A final criticism is that Tees mentions that the pattern discrimination results suggest that "sensory contiguities inherent in an unrestricted auditory environment seem to be necessary so that later complex accoustical stimuli can gain faster control over responses" (1967a, p.392). He implied that the sound deprived rats learned the pattern discriminations more slowly because of their naivety of sound. However, it might also have been the case that they learned the pattern discriminations more slowly because they had recently been subjected to 60 days of sound deprivation irrespective of their ages at the time deprivation commenced, a conclusion with quite different implications from the one suggested by Tees.

Tees (1967b) carried out another experiment in which he explored the effects of auditory restriction in rats on their later auditory intensity and auditory signal duration discriminations. The experiment was carried out in identical

fashion to the one reviewed above (Tees, 1967a) except that the stimuli for discrimination differed. In the intensity discrimination task, the rats were required to respond to an upward (more intense by 15dB) change in the intensity of a continuously presented series of tone pulses of the one auditory frequency. In the duration discrimination task, the negative stimulus was a series of 4kHz, 55dB pulses each 0.9 sec in length at 0.1 sec intervals. The positive stimulus was a change to pulses of the same frequency and intensity but 0.4 sec in length at 0.6 sec intervals. Tees' sound deprived rats learned the intensity discrimination as readily as normally reared controls, but control animals took significantly fewer trials than the deprived rats in learning the duration discrimination.

Tees concluded that the results of the auditory intensity experience seemed necessary to facilitate learning this discrimination; thus there was the possibility that an innate basis existed for the mediation of auditory intensity discrimination. Tees' conclusion was similar to others which have been made about visual intensity discrimination after visual deprivation (e.g. Hebb, 1937; Riesen and Arcns, 1959; Aarons, Halasz and Riesen, 1963; Tees 1968b), and it appeared reasonable in the light of the parallel studies in visual intensity discrimination. However, a more stringent test of auditory intensity discrimination than that used by Tees might have modified that conclusion.



From his auditory duration discrimination results, Tees concluded that the discrimination of auditory duration might be similar to the discrimination of auditory patterns and require a type of temporal integration which is difficult or impossible without early sensory experience of sound. He also considered that auditory duration discrimination might be analogous to visual acuity as both are measures of discernible space between units. The measure of visual acuity is the minimum interval of space that is perceived while auditory duration discrimination is the minimum time interval perceptible between auditory events. He speculated that if the two measures were indeed parallel, then animals deprived of patterned light during rearing might be inferior to light reared animals in visual acuity - just as his auditorily deprived animals were inferior to controls in auditory duration discrimination. Tees cited Siegel (1953) and Wilson (1964) both of whom found visual acuity as they measured it in doves and monkeys respectively, to be unaffected by early visual deprivation, and concluded that his speculation had no supporting evidence. However, both Riesen, Ramsay and Wilson (1964) and Wilson and Riesen (1966) found that rhesus monkeys reared in restricted light had lowered visual acuity immediately after they were released from light restrictions but heightened acuity as experience in the light increased. Then, Dews and Wiesel (1970) found that cats deprived of patterned light for as short a period as the first four to six

weeks after birth had lowered visual acuity when tested during adulthood. Consequently, Tees' speculation was subsequently supported by experimental evidence, although not from experiments with rodents.

As in his previous experiment (Tees 1967a), Tees did not control for the effects of heredity nor did he include a group deprived of auditory experience at some time other than from immediately after birth so that his claim that his results were the product of early deprivation could have been substantiated.

In a carefully conducted series of experiments designed to discover the origins of the species-specific behaviour elicited in Mallard ducklings when exposed to Mallard and only Mallard maternal calls, Gottlieb (1968) incubated Mallard eggs in individual isolation in a sound attenuated incubator. Gottlieb was able to demonstrate that some 12 to 24 hrs before hatching, Mallard ducklings incubated together with other Mallard embryos show an increase in bill clapping which is a specific response to the Mallard maternal call. When the sound isolated duck embryos were tested just before hatching with Mallard maternal calls, there was no increase in bill clapping. Gottlieb claimed that his results indicated that normally occurring auditory stimulation of the embryo plays a role in regulating the embryo's later ability to respond selectively to the maternal call of its species.

Gottlieb continued his investigations to determine whether the auditory deprivation induced a lag in the species-specific auditory development of the ducklings or whether the results of the deprivation were more permanent. He incubated Mallard eggs in sound isolation which continued for 14 to 30 hrs after the duckling had hatched. The ducklings were then placed individually in a situation in which they were required to choose between approaching an area with the sound of a Mallard maternal call or an area with the sound of a Wood duck maternal call. All of the ducklings which responded approached the Mallard call area of the apparatus, indicating to Gottlieb that the auditory deprivation induced only a temporal lag in the development of the embryo's ability to respond to the appropriate maternal call.

The results obtained by Gottlieb with ducklings and auditory deprivation were similar to those of Wilson and Riesen (1966), who reared rhesus monkeys in darkness with daily periods of diffuse light for periods up to 60 days after birth. Wilson and Riesen found that when they exposed the monkeys to normal light after the deprivation period, they were retarded in untrained visual behaviour such as visually fixating patterns and tracking moving objects compared with light reared animals of the same age. However, the timetabling of the appearance of items of visual behaviour in the visually deprived monkeys

counting from the time of first exposure to patterned light was strikingly similar to that of infant monkeys counting from the time of birth. Wilson and Riesen's results indicated that early visual deprivation in monkeys resulted in a lag in the development of visual behaviour, a conclusion very similar to that of Gottlieb.

Batkin, Groth, Watson and Ansberry (1970) did not show an effect of auditory deprivation on overt behaviour in an animal, but by implication their study suggested that auditory deprivation might alter auditory sensitivity in rats. They raised albino rats from birth in sound attenuated chambers for eight months then compared their extra-cranial auditory evoked potentials (AEPs) to auditory stimuli of various frequencies and intensities with those of colony reared litter-mates. The experimenters went to considerable lengths to deprive their subjects of sound. The experimental animals had their toes amputated at birth to preclude scratching noises and the nursing mothers were made aphonic by cauterization of the larynx. After weaning, each individual was isolated in a plastic-foam-lined cage in a sound attenuated room set inside the crater wall of an extinct volcano. Batkin et al. found that the auditorily deprived rats differed significantly from control subjects when the former were tested for AEP intensity thresholds immediately at the end of the deprivation period. The median threshold

response levels of the deprived rats were some 30dB less sensitive to auditory stimuli ranging from 500Hz to 10kHz in frequency. However, retests carried out with some of the deprived animals after they had experienced a sound environment for 48 hrs and three weeks indicated that their AEP thresholds improved after exposure to sound although after three weeks of sound experience, intensity thresholds of the deprived rats were still raised in comparison with controls.

The results of the Batkin et al. agree with the very many investigations using visual deprivation which have shown that such treatment for prolonged periods altered the usual functioning of appropriate units in the brain (e.g. reviews by Riesen, 1961, 1966; Hubel and Wiesel, 1970). The study implied that animals deprived of sound for prolonged periods may exhibit hearing losses when first exposed to a sound environment. Further experiments with behavioural tests of auditory capacities with such animals need to be made to settle the point.

Although Batkin et al. claim that their results reinforce an impression that adequate early auditory stimulation is important for the development of hearing capacities, such a conclusion is difficult to accept because the rats used by Batkin et al. were deprived for a long period of their lives. There is no way of discovering from the study results whether the AEP thresholds of the deprived rats did not develop to such levels as

those shown by the control rats (which was the Batkin et al. conclusion) or whether the threshold levels did develop or existed initially then deteriorated as a result of the deprivation of auditory stimulation. Then, too, it is not clear from the report presented by the authors that the effect they found was the result of the auditory aspect alone of the deprivation that their experimental rats suffered. The report does not indicate clearly how similar or different were the environments of the experimental and the control animals, except for the difference in sound treatment. Further, it is difficult to understand how the Batkin et al. rats were deprived of auditory stimulation by rearing them on plastic foam. In the quiet conditions of the sound attenuated room the sound of rats rustling on plastic foam must have been relatively intense.

Another report which suggested that auditory deprivation had effects on the functioning of the auditory cortex was that recently published by Stein and Schuckman (1973). Their study was reminiscent of the early experiment of Wolf (1943) in that they reared one set of rats from 13 days of age until they were 45 days old under conditions of auditory restriction or visual deprivation and other sets of rats under the same deprivation conditions beginning when they were 40 days of age for various durations. Visual deprivation was accomplished by suturing rats' eyelids closed and covering their heads with tape while auditory restriction was arranged by plugging rats' ears with cotton and

collodion. At the end of the deprivation period the rats were subjected to a surgical procedure to embed electrodes in both the auditory and the visual cortices of each animal. After post-operative recovery, the rats were trained to press a bar for water available only during intercranial electrical stimulation (ICS) of either cortical area.

The results Stein and Schuckman obtained were also similar to those of Wolf (1943). The rats which had been deprived of sound from 13 to 45 days of age had a slower rate of learning towards a criterion when the discriminative stimulus was ICS of the auditory cortex than when the discriminative stimulus was ICS of the visual cortex. The opposite arrangement held in the case of rats deprived of vision during the 13 to 45 day age period. Rats which had been deprived of vision or hearing from 40 days of age for durations of either five or 45 days showed no such effects of deprivation.

Stein and Schuckman concluded that early auditory or visual restriction resulted in significant retardation of learning when stimulation of the auditory cortex serving the deprived sensory mode served as the discriminative stimulus, suggesting that the behavioural consequences of early sensory restriction were due in large part to cortical dysfunction. They suggested that the deprivation resulted in retardation in learning rather than more permanent disabilities because in their experiment the

rats did eventually reach the criteria set. They were also able to claim, with evidence, that the effect they found was due to early deprivation, and that a sensitive period to the effects of sensory restriction might exist between 13 and 40 days of age in rats. Their results coincide in many respects with those of Hubel and Wiesel (1970) who claimed evidence for an early sensitive period to the effects of visual deprivation on single cell activity in the visual cortex of cats.

#### Conclusions from Previous Studies

Conclusions from the existing literature on the effects of auditory deprivation on auditory discrimination development in animals are difficult to draw because of the paucity of studies in the area and because of the shortcomings evident in the methods employed by several of the investigators. However, parallels which can be drawn between such information which has been gathered about the development of auditory capacities and information about the development of visual capacities suggest that the use of both sensory modalities develops similarly in some animal species.



## CHAPTER TWO

### THE AIMS AND DESIGN OF THE EXPERIMENTS

The experiments described in the following chapters were designed to extend current knowledge about the effects of early auditory deprivation on later behaviour towards auditory stimuli. Specifically, the studies examined some aspects of the development of auditory discrimination behaviour in albino rats by exploring the effects of early deprivation of patterned sound experience on the later ability of the rats to learn tasks involving either auditory frequency discriminations or auditory pattern discriminations.

The experimental animals were deprived of patterned sound by housing them under conditions which included the constant presence of 'white' noise, a technique of auditory deprivation which has not been previously used. It was assumed that the white noise would mask out most other ambient sound and thus restrict the animals' reception of structured or patterned auditory stimulation. The auditory environment produced by the white noise was considered to be analogous to the diffused light environment which has been used in visual deprivation experiments (e.g. Riesen, 1961; Wiesel and Hubel, 1965a).

The literature review suggested that experiments purporting to show effects of early sound experience on auditory discrimination in animals by the method of sensory deprivation should be designed so that:

a. the resulting deficiency could neither be attributed to damage of the sensory system nor alteration to it to the extent that the discrimination tasks set for the subject cannot be completed. A review by Riesen (1966) demonstrated clearly that total visual deprivation can cause atrophy in the visual system. The same review also pointed out that under conditions of prolonged diffuse light, kittens, monkeys and chimpanzees developed nystagmus in the absence of objects to fixate. With these gross organic defects, it was not surprising that the subjects had difficulty seeing, let alone discriminating, visual forms.

b. the incapacity demonstrated should reflect a perceptual deficiency, rather than a subject's inability to perform the responses required in the discrimination tasks because of either a disturbed capacity to learn or an altered emotional tone resulting from the deprivation experience. Several writers, for example McCleary (1960), Melzack (1962) and Tees (1968a) suggested that cognitive or emotional differences rather than perceptual inadequacies could account for the inferiority of stimulus deprived animals at learning tasks designed to demonstrate perceptual differences.

c. the deficit should be shown to be the result of early deprivation rather than of the deprivation as such. King (1958) indicated that a high proportion of the investigations into the effects of early sensory deprivation that he reviewed, failed to

include a group given the same deprivation later in life. Consequently, many experimenters who claimed to have investigated the effects of early sensory deprivation did not in fact do so.

The present investigation was divided into three groups of experiments, with the above three sources of criticism in mind.

Group 1. The results of this group of two experiments were expected to establish whether or not an effect of deprivation of patterned sound on auditory discrimination could be found in the albino rat. Experiment Ia investigated the effect of rearing rats in white noise from birth to 60 days of age then comparing them with control rats genetically and by experience as similar to the noise-reared rats as possible except for experience of sound, on a test of auditory frequency discrimination considered to be stringent. In Experiment Ib, similarly reared experimental and control subjects were subjected to a test of auditory pattern discrimination.

If no differences were found between the experimental and the control animals on the auditory tests, the possibilities existed either that the deprivation by white noise was ineffective or the rats could make the discriminations tested without prior experience of sound which varied in frequency and intensity over time. If differences between the animals were found on the discrimination tests which coincided with differences in rearing conditions, the reasons for those differences would require experimental investigation. In fact, an effect of the patterned sound deprivation was

not shown with the frequency discrimination test but there was a clear effect found with the auditory pattern discrimination test. The subsequent experiments were concerned with examining several possible explanations for the effect which was found.

Group 2. The two experiments of this group explored the possibility that rearing rats in white noise had an effect either on their early physical development or on their emotional or cognitive development. If the rats reared in white noise were emotionally or cognitively different from others reared in varied sound, such differences might explain the differences found between those two groups of rats on the auditory pattern discrimination test.

In Experiment IIa, the weights at weaning of rats reared in white noise were compared with those of rats reared in varied sound to establish whether the rearing environments affected early physical development differently. Then when the animals reached maturity at 60 days of age, they were subjected to an open-field test for 'emotional' behaviour. Experiment IIb was designed to investigate the effects of the white noise during rearing on the rats' ability to learn discriminations other than those involved in audition. Experimental and control group rats were compared on a 'difficult' test of visual discrimination.

Group 3. This group of three experiments investigated the effect of depriving rats of patterned sound at various times during their lives so that the effect of varied sound experience

on the development of auditory pattern discrimination in rats could be examined more closely.

In Experiment IIIa, rats were reared in varied sound until 60 days of age then deprived of patterned sound for the next 60 days. At 120 days of age they were compared with 120 day old control rats which had been reared entirely in varied sound, on the auditory pattern discrimination test used in the earlier Experiment Ib. The results were expected to show whether the effect of the patterned sound deprivation shown in the previous Experiment Ib could be attributable to the time of the deprivation, early in the life of the rat or whether the effect was the result of 60 days of sound deprivation in itself.

Experiment IIIb was conducted after the previous Experiment IIIa results had indicated that the effects of the deprivation depended on the time in the life of the rat the deprivation was suffered. Deprivation during the first 60 days after birth had an effect on auditory pattern discrimination in the rat, deprivation during the second 60 days did not. Experiment IIIb set out to extend this finding by examining the effect of the deprivation for periods within the first 60 days after birth in the rat. Rats were reared for the first 30 days from birth in varied sound then deprived of patterned sound for 30 days. At 60 days of age they were compared with 60 day old control rats on the auditory pattern discrimination test. It was expected that the results would show which period might contain a 'sensitive period' for the

effects of patterned sound deprivation, the first 30 days after birth or the second 30 days. Experiment IIIb results showed that the deprivation during the second 30 days of a rat's life since birth had no effect on its auditory pattern discrimination ability, thus it was possible that a 'sensitive period' for the effects of the deprivation existed during the first 30 days. This possibility was examined in Experiment IIIc in which rats deprived of patterned sound from birth to 30 days then reared in varied sound for 30 days were compared with 60 day old control animals on the auditory pattern discrimination test. The results of this last experiment favoured an explanation of the effect of early patterned sound deprivation on auditory pattern discrimination which did not include the likelihood of the existence of a 'sensitive period'.

### CHAPTER THREE

#### THE EFFECTS OF AUDITORY PATTERN DEPRIVATION ON LATER AUDITORY DISCRIMINATION IN THE ALBINO RAT

The two experiments described in this chapter were designed to study the effect of auditory pattern deprivation on two different types of auditory discrimination in rats, auditory frequency discrimination and auditory pattern discrimination. The auditory frequency discrimination required rats to compare a tone of one frequency with a tone of a second frequency while the auditory pattern discrimination required the animals to complete the more complicated task of integrating a temporal sequence of auditory stimuli.

The discriminations selected for testing were considered analogous to others which have been used to show the effects of visual pattern deprivation on later visual discriminations like hue (Ganz and Riesen, 1962, with chimpanzees) and visual patterns which required the integration of visual information over area (Tees, 1968a, with rats).

Deprivation of patterned sound was achieved by rearing rats in white noise of an intensity likely to mask out other ambient noise, a procedure not previously used but which was expected to deprive the animals of patterned sound as effectively as restricting their hearing with ear occluding devices, by social isolation and environmental sound attenuation without incurring the problems associated with these other techniques.

Experiment Ia

The Effect of Patterned Sound Deprivation on Auditory

Frequency Discrimination in Albino Rats

This experiment tested the hypothesis that experience with varied sound was necessary before rats could learn an auditory frequency discrimination, by rearing rats in white noise which deprived them of varied sound then comparing their performance on a frequency discrimination task with that of controls reared in varied sound.

The frequency discrimination task was purposely made 'difficult' by the stimulus presentation system employed because it was suspected that differences between the deprived and the non-deprived groups might not be discernible if learning took place too readily. The stimuli were presented in a discrete trial procedure and the subjects were expected to respond in each trial when a stimulus of one auditory frequency was presented but not to respond during a trial when a second frequency was presented. The subjects were thus required to 'remember' the frequency of the previous stimulus over the period of the inter-stimulus interval. This stimulus presentation system was found by Thompson (1959) to be considerably more difficult, in that animals took many more trials to reach a criterion of frequency discrimination learning, than a system which required subjects to respond when one auditory frequency presented continuously changed to a second frequency.



The frequency discrimination task was followed by a frequency generalization test which provided a measure of the degree to which stimulus control had been established during the discrimination procedure (after the procedure used by Randall, 1965). This generalization procedure was instituted, also, to gain information about the effects of the deprivation of patterned sound on later responding to a range of auditory frequencies. Studies reviewed by Ganz (1968) suggested that stimulus deprived animals produced steeper generalization gradients after discrimination training than did animals not so deprived.

#### Method

##### Subjects

The subjects were 16 Sprague-Dawley strain albino rats from the Victoria University Psychology Department colony. They were ten males and six females from four litters that were all cast within 24 hrs of each other. Two litters were sired by one male and the other two by another. Originally there were 38 pups in the four litters. Sixteen pups were assigned to another experiment, four died soon after birth and two randomly selected male pups were discarded. The remaining 16 subjects were reared in two even sexed groups of eight.

##### Apparatus

Rearing environment. The subjects were reared in open wire mesh (2 X 1cm) cages (30 X 30 X 22cm) suspended above droppings trays partially filled with sawdust. The trays could

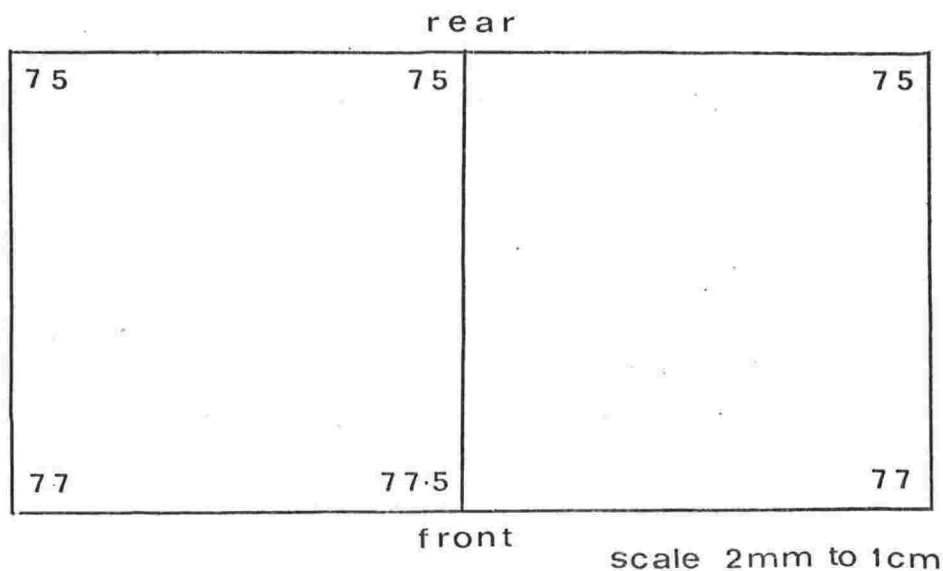


Fig.3.1. Plan of rearing cages showing sound intensities in dB re  $0.0002 \text{ dynes/cm}^2$  at the points indicated when the sound level was 75dB, linear scale, at the rear junction of the two cages.

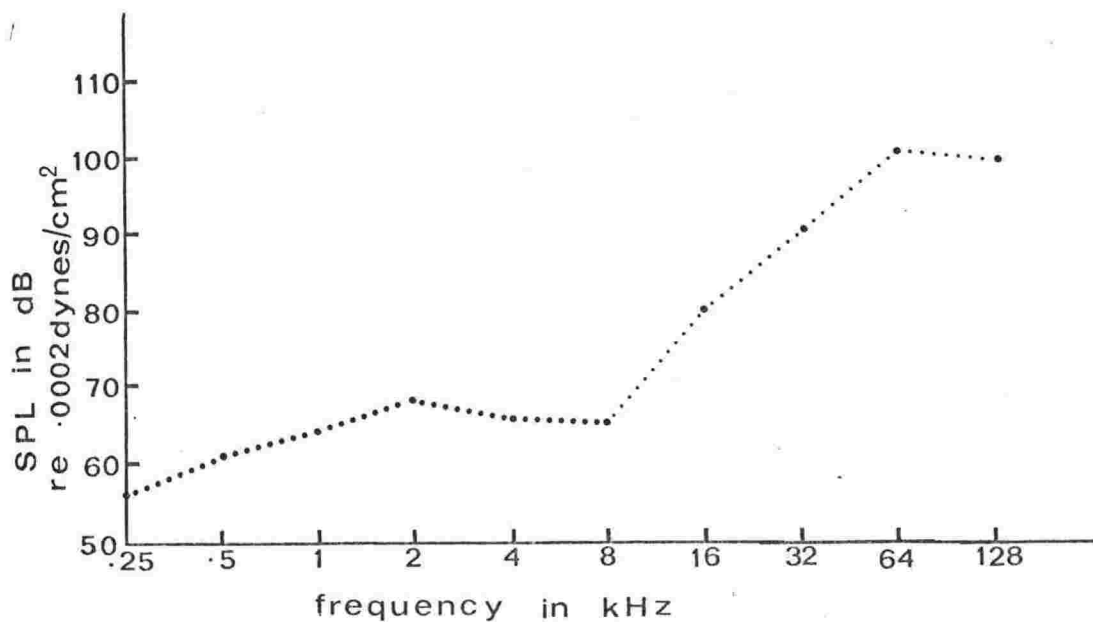


Fig.3.2. Octave band analysis of the 'white' noise when the overall (linear scale) sound level at the rear junction of the two rearing cages was 75dB SPL. Measurements up to 8kHz made with Philips PM6400 meter with PM6410 filter set. Levels at higher frequencies estimated from manufacturers' data for EST-2 transducer.

be removed silently for cleaning. Shredded paper was provided as nesting material.

Two cages were in one room together with white noise generating equipment. The latter consisted of a Grason Stadler Company Model 455c white noise generator modified by the addition of a stage of amplification, an Advanced Technology Center Inc. LTV-701 ultrasonic generator system comprising a Krohn-Hite Model DCA-10(R) amplifier and an LTV Type EST-2 electrostatic transducer and finally, a Radio Speakers of Canada Ltd. 8in "Twintone" loudspeaker.

The white noise generating apparatus was positioned with the loudspeaker and the electrostatic transducer aimed to produce white noise at an intensity level of  $75^{+1}\text{dB}^*$  at the rear junction of the two adjacent cages (Figure 3.1). The sound level, measured with a Philips PM-6400 meter set to its linear scale, was approximately 20 dB higher than the mean ambient noise level in the room and some 10dB higher than the most intense noise recorded earlier in the room with measurements made at two-hourly intervals during daylight hours over a period of five consecutive week days. The white noise range (Figure 3.2) included that spectrum of ultrasonic frequencies for which the hearing of a rat is

---

\* All sound intensity measurements made during this project were made in dB Sound Pressure Level where the reference pressure, 0dB, is  $0.0002 \text{ dynes/cm}^2$ .

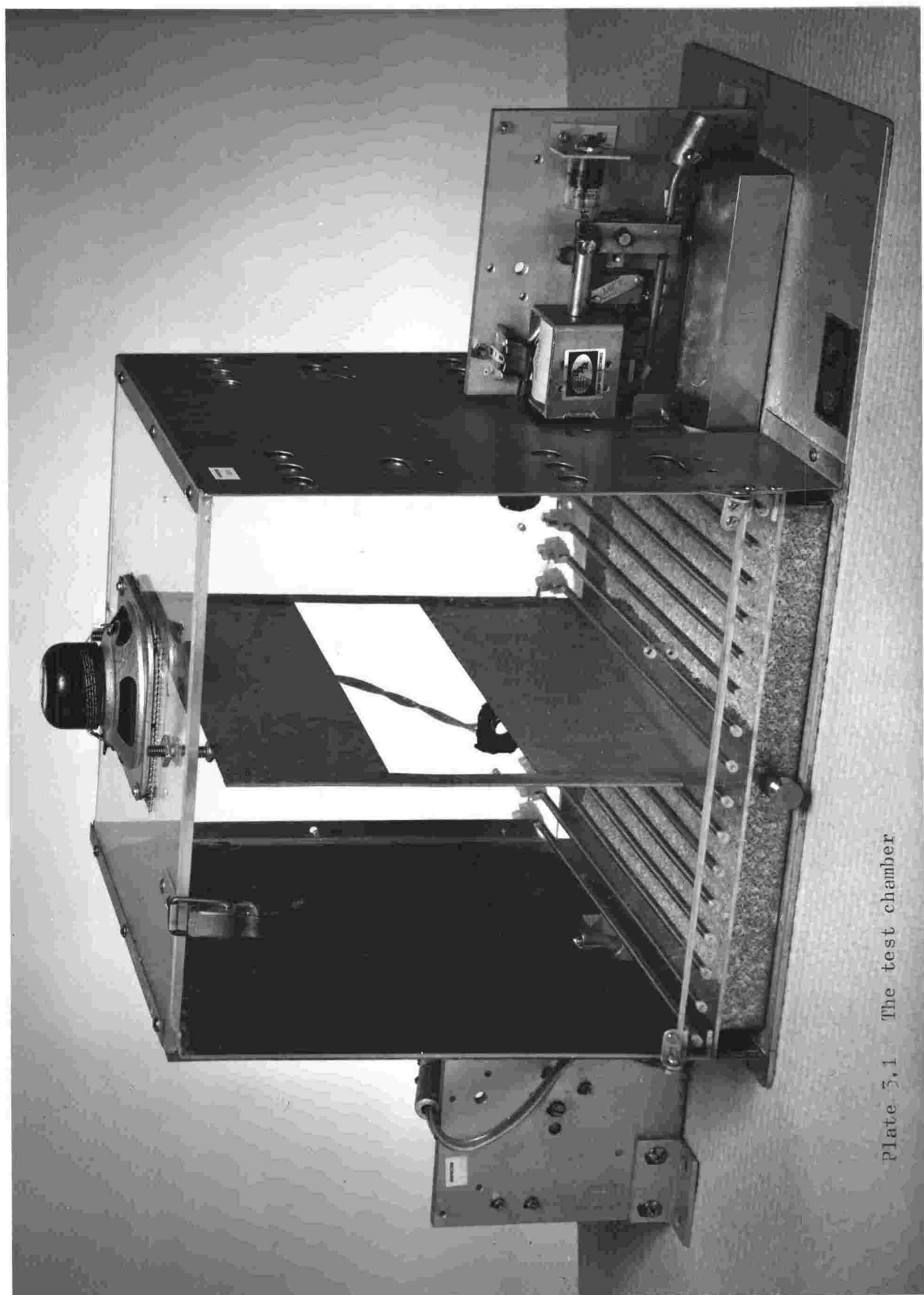


Plate 3.1 The test chamber

most sensitive, 20kHz to 60kHz (Clack and Harris, 1963; Gourevitch, 1965; Gourevitch and Hack, 1966).

Two more cages were in a second room and were so screened that rats housed in the cages could hear, but not see the cage cleaning activities which occasionally took place in the room. A radio tuned to a 24hr broadcast station was positioned so that peak intensities from the radio reached 77-78dB at the rear junction of the two adjacent cages.

Temperature in both rooms was thermostatically controlled to remain at  $22 \pm 3^{\circ}\text{C}$ . Humidity was controlled by soaking the sawdust in the droppings trays beneath the cages with water. Both rooms received normal daylight.

Electric power to the white noise generating equipment was from mains supply but a standby Honda Model E-300 electric generator provided emergency power over some 20hrs of periodic municipal power cuts.

Training and test apparatus. Discrimination training and testing was conducted in a test chamber as depicted in Plate 3.1. It measured 30cm long, 24cm wide and 27cm high. The chamber was divided in half by a barrier extending fully across the width and 9cm in height above the floor. The floor consisted of a grill of 4mm stainless steel bars placed 2cm apart parallel with the central barrier. The door front, top and back of the chamber were constructed of clear acrylic sheet ("Perspex") while the sides, parallel with the central barrier, were of steel. Set into each

steel side was the nose-cup shield of a Lehigh Valley Electronics Inc. Model 1351 liquid dipper in such a position that the 0.01ml dipper cup was in the centre of the side and 2cm above the grill floor. Centred in the top of the chamber was an 8cm hole over which was mounted a 4in loudspeaker (Richard Allen Radio Company, Type CB4).

Events in the test chamber were remotely controlled from the next room in which was located the electro-mechanical and electronic programming and recording equipment and the experimenter during the test sessions. A view of the test chamber was provided by a 28 X 20cm double glazed window, glazed on the one side with one-way-vision glass and on the other by plate glass. The attenuation of sound by the wall between the two rooms was measured to be  $22^{+2}$ dB.

The ambient noise in the test chamber room, measured at a point in the centre of the test chamber over two-hourly intervals for five consecutive week days, averaged 42dB. The highest sound level recorded during the measurement period was 57dB. When two exhaust fans which provided ventilation in the room were switched on, the ambient noise level in the test chamber rose to a steady 62dB. Hence the steady noise of the fans was expected to mask out most extraneous sound from the test chamber during test sessions.

The test chamber was lighted by one white 40w fluorescent tube some 2m overhead.

Alternate bars of the grill floor of the test chamber were

connected together and subsequently connected to a Lehigh Valley Model 1520 contact relay. The bars to the left of the barrier were connected to the contact relay independently from those to the right through a switch, operated by the experimenter, that determined which set of bars was connected with the relay. When animals touched any two adjacent floor bars on the appropriate side of the barrier during a positive auditory stimulus presentation through the loudspeaker, the liquid dipper arm on the same side was raised, making a drop of water available in the test chamber. That action also stopped an electronic timer, previously started simultaneously with the first tone of the auditory stimulus.

Another switch operated by the experimenter turned off the auditory stimulus, withdrew the dipper arm and started a second electronic timer used to indicate inter-trial intervals (ITI). This second timer was reset by the contact relay during ITIs, thus providing a stimulus postponement system to discourage incorrect ITI responding.

The auditory signals used as stimuli consisted of a series of groups of three tones of the same frequency and intensity. Each tone was 0.4sec in length with silent intervals of 0.1sec between tones. Each group of three tones was separated by a silent interval of 1.1sec. The tones were generated by a Philips PM-5140 low frequency generator with built-in 1dB step attenuator which was connected to the test chamber loudspeaker through a relay operated by a Grass Instruments Company Model S48 square wave stimulator set

to operate according to the temporal pattern described. The rise and fall times of the tones, measured by displaying the tones via a sound level meter onto the screen of a Philips PM-3210 cathode ray oscilloscope, were  $8^{+2}$ msec.

#### Procedure

Rearing. Within 12hrs of the birth of the last rat pup, the four litters were removed from their mothers and divided into four groups. The litters were evenly distributed over the four groups and each group had a similar proportion of both sexes. Two of the groups were then removed to another experiment leaving two groups of eight subjects each for the present study. One of those two groups was then placed with a mother which had been installed in a cage in the room with the white noise generating apparatus (the experimental condition) and the other in a cage in the room with the varied sound environment provided by the radio (the control condition).

The white noise was switched on during the subjects' first post-natal day at low intensity then increased in daily steps until on the fifth post-natal day it reached the intensity of 75dB at the rear junction of the two cages. This procedure of introducing the white noise was developed after preliminary experiments revealed that a mother rat tended to destroy her litter if she was placed in the noise at full intensity either before or within two days of casting the litter. The procedure adopted solved this problem but meant that the rat pups were not deprived of patterned sound



from birth or before that time. However, according to evidence reported by Wada (1923), Crowley and Hepp-Reymond (1966) and Volokhov (1968), it is unlikely that the rat auditory system is functional before the fifth post-natal day. The white noise remained on constantly until the end of the experiment and was found to vary not more than 1dB between measurements at weekly intervals.

Both groups were raised with the mothers until aged 21 days when all individuals were weighed and the mothers were removed. Rat diet (the formula for which was developed by Glaxo Laboratories Ltd. and produced by Farm Products Co-op. (Manawatu) Ltd.) and water were freely available to the animals during the rearing period. The sexes were segregated at 45 days of age to prevent breeding complications but beyond this, and apart from the periodic replenishment of food and water, the weekly removal and replacement of droppings trays and weekly measurements of sound level, the subjects were undisturbed until 60 days of age when auditory discrimination training and testing began. This age was selected because by then the rats had reached what was judged to be a sufficient size to perform the necessary response task effectively.

Frequency discrimination training method. Against a background of silence, the subject was presented with an auditory stimulus consisting of a series of three tone groups in the temporal sequence described above at a frequency of either 8kHz or 4kHz. The frequencies of 8kHz and 4kHz were chosen because rat mean hearing

threshold levels are within 2dB of each other at these frequencies (Hack, 1971). Thus it was unlikely that a subject would differentiate between the two stimuli on the basis of intensity. Also in order to prevent the subjects from using stimulus intensity as a cue, intensity of the two frequencies was altered after every five trials independently over a range extending from 60dB to 75dB measured at a point in the centre of the test chamber. The intensities were varied randomly except for a restriction which ensured that on 50 per cent of trials, stimuli of 8kHz were more intense than stimuli of 4kHz. Stimulus intensity at the subjects' ear varied also, according to where it was located in the test chamber.

If the animal responded to the 8kHz signal, the positive stimulus (S+), by crossing the central barrier in the test chamber, it was rewarded with a drop (0.01 ml) of water. If it crossed the barrier to the 4kHz signal, the negative stimulus (S-), it was not rewarded. S+ remained on until the subject was observed to have taken the drop of water. S- was terminated at the end of 10sec. A response was recorded when the subject touched two adjacent floor bars on the side of the barrier opposite to that on which it was located immediately before the beginning of the stimulus. The interval between the first tone of the stimulus and the response constituted a trial. The duration of each trial was recorded.

The ITI was 20<sup>+</sup>5sec except when a subject crossed the

barrier during the ITI in which case the subsequent trial was delayed for 15sec after the spontaneous response. The purpose of the stimulus postponement procedure, similar to that used by Trapold and Winokur (1967) and Levis (1971) was to discourage responding in the absence of the sound stimuli.

Frequency discrimination training. Three days before training began, the subjects were placed on a water deprivation schedule which allowed them 30min of water availability in 24hr. Eight of the subjects, four experimental subjects and four controls, began training on day 60 of age, while the second eight began at 67 days of age. The procedure was completed in four daily sessions of approximately 45min for each subject. Each subject was trained at the same time of day each day.

On the first day of training each subject was placed in the test chamber and allowed to locate and drink water from both liquid dipper cups. As soon as the subject had found both dipper cups and in the process had crossed the central barrier at least once, five training trials using only S+ were given. When these had been successfully completed, 40 trials were given in which S+ and S- were presented in a random sequence (identical for all subjects) with the restriction that there were no more than three consecutive S+ or S- trials. At the conclusion of the 40 trials, the subjects were returned to their home cages and given 30min access to water.

On the second and third training days each subject completed 80 trials so that at the end of the third day's session, each subject had completed 200 trials.

Frequency generalization test. On the fourth day a generalization test was administered by recording the subjects' response times to stimuli of the same temporal pattern as the training stimuli but of the frequencies 2kHz, 6kHz and 10kHz as well as to the training stimulus frequencies of 8kHz and 4kHz. Each successive stimulus was presented at a different intensity between 60dB and 75dB according to a random sequence. To maintain responding throughout testing, responses to 8kHz stimuli were rewarded. Fifty trials were given according to a Williams' latin square design (Edwards, 1960) in which each of the five stimulus frequencies was presented ten times and each stimulus frequency followed every other at least twice. In each trial the stimulus was presented until a response had been made or for 15sec, whichever occurred first. The ITI was 15<sup>+</sup>5sec. A stimulus postponement for spontaneous ITI responding procedure was found to be unnecessary. Trials in which no response was made within 15sec were assigned a response time of 15sec for recording purposes.

### Results and Discussion

#### Frequency Discrimination Training

To facilitate analysis of the results, the 200 trials each subject completed were divided into four blocks of 50 trials and the median response times of each block for each subject was accepted

as representative of that subject's performance over the trial block.

Table 3.1 shows that all 16 subjects mastered the response task without difficulty.

TABLE 3.1  
Mean Response Times to Stimuli of 8kHz and 4kHz in  
Successive 50 Trial Blocks for Varied Sound Reared  
and Patterned Sound Deprived Rats

Group	Mean Response Times in Seconds							
	Stimulus frequency 8 kHz				Stimulus frequency 4 kHz			
	Trial Block				Trial Block			
	I	II	III	IV	I	II	III	IV
Experimental (N=8)	6.74	4.91	5.07	3.92	9.55	7.52	8.02	8.99
Control (N =8)	8.03	5.91	4.25	3.38	8.80	8.54	7.39	7.69

Analysis of variance\* (four factor, repeated measures on two factors) of the response times of the experimental and the control group, divided by sex, to the two stimulus frequencies over the four trial blocks was carried out, (Table 3.2).

\* All parametric statistical techniques applied to the data of this and the subsequent experiments are derived from Bruning, J.L. and Kintz, B.L., Computational Handbook of Statistics, Glenview, Illinois: Scott, Foresman and Co., 1968.

TABLE 3.2

Summary of Analysis of Variance of Response Times in  
Four Blocks of Fifty Trials to 8kHz and 4kHz Stimuli  
by Varied Sound Reared and Patterned Sound Deprived Rats

Source	SS	df	ms	F	p
Total	883.19	127	-	-	
Between Subjects	183.67	15	-	-	
Rearing	0.00	1	0.00	<1.00	-
Sex	52.30	1	52.30	4.80	<.05
Sex X Rearing	.69	1	.69	<1.00	-
Error b	130.68	12	10.89	-	
Within Subjects	699.52	112	-	-	
Stimulus Frequency	278.51	1	278.51	67.59	<.001
Trial Blocks	103.97	7	14.85	3.60	<.01
Rearing X Frequency	5.27	1	5.27	1.27	ns
Rearing X Trial Blocks	26.79	7	3.82	<1.00	-
Frequency X Blocks	38.38	7	5.48	1.33	ns
Rearing X Trial Blocks X Frequency	4.88	7	.69	<1.00	-
Sex X Frequency	.19	1	.19	<1.00	-
Sex X Trial Blocks	9.53	7	1.36	<1.00	-
Sex X Frequency X Blocks	3.29	7	.47	<1.00	-
Rearing X Sex X Frequency	.66	1	.66	<1.00	-
Rearing X Sex X Blocks	4.87	7	.69	<1.00	-
Rearing X Sex X Blocks X Frequency	8.99	7	1.27	<1.00	-
Error W	214.29	52	4.12	-	

According to this analysis, the difference in rearing between the experimental group, deprived of patterned sound, and the control group reared in a varied sound environment, had no

significant effect on response times during the training trials. Both the Rearing X Trial Blocks and the Rearing X Trial Blocks X Frequency interactions were found to be non-significant, also, indicating that no significant differences existed between the two groups at any stage of the training, either early or late, and that differential responding to the two stimulus frequencies in both groups was of the same magnitude throughout the trial blocks. These results were open to the interpretation that rats require no prior experience of patterned sound before learning an auditory frequency discrimination as easily as rats with such prior experience. However, it is possible that the deprived subjects gained enough patterned sound experience early during the first block of trials to be indistinguishable from the non-deprived subjects later in that same block of 50 trials, a situation which may not have been discernible with the analysis used. Thus a further analysis was carried out to examine more closely the effect of rearing on response times to the two stimulus frequencies during the first block of 50 trials. The 50 trials were divided into blocks of ten and the difference between the median of the response times to 8kHz stimuli and to 4kHz stimuli in each block of ten trials was calculated for each subject in both experimental and control groups. These difference score data were subjected to analysis of variance (two factor, repeated measures on one factor) summarized in Table 3.3.

TABLE 3.3

Summary of Analysis of Variance of Differences Between Response Times to Stimuli of Two Auditory Frequencies in Five Blocks of Ten Trials by Two Groups of Differently Reared Rats

Source	SS	df	ms	F	p
Total	445.21	79	-	-	
Between Subjects	76.09	15	-	-	
Rearing	4.99	1	4.99	<1.00	-
Error b	71.10	14	5.07	-	
Within Subjects	369.12	64	-	-	
Trial Blocks	31.95	4	7.98	1.54	ns
Trials X Rearing	48.60	4	12.15	2.35	ns
Error W	288.57	56	5.15	-	

The analysis revealed no evidence that the subjects responded differently in the early stages of discrimination training because of differences in rearing. It is thus reasonable to conclude that prior sound experience, or lack of it, was irrelevant to the subjects' performance on the frequency discrimination task.

In the analysis summarized in Table 3.2, a highly significant difference found between response times to the stimulus frequency of 8kHz (mean response time = 5.28sec) and response times to the stimulus frequency of 4kHz (mean response time = 7.19sec) indicated that the speed of responding was under the control of the stimulus dimension of sound frequency and also that a discrimination was being made between the two frequencies by the subjects.



The variation in response times attributable to differences between blocks of 50 trials was significant. Duncan's multiple range tests, summarized in Table 3.4 indicated that responses made to 8kHz stimuli became significantly faster as trials proceeded from Block I to Block IV. Responses to 4kHz stimuli, however, showed no such pattern. This result is consistent with an interpretation that the subjects improved in discriminating between the two stimulus frequencies as trials proceeded.

TABLE 3.4

Summary of Duncan's Multiple Range Tests of Mean Response Times in Blocks of 50 Trials to Stimuli of 8kHz and 4kHz\* for all subjects combined (N=16)

Means of Response Times in Seconds to 8kHz Stimuli				
Trial Blocks	i	ii	iii	iv
Means	7.38	<u>5.41</u>	<u>4.66</u>	3.65
Means of Response Times in Seconds to 4kHz Stimuli				
Trial Blocks	i	ii	iii	iv
Means	<u>9.17</u>	<u>8.34</u>	<u>8.03</u>	7.71
* Means <u>not</u> underscored by the same line are significantly different (p < .05)				

There was a significant difference found in response times between male and female subjects. The mean response times for

females was 5.89sec, and for males 7.34sec; thus females responded significantly more rapidly than did males.

#### Frequency Generalization Test

All 16 subjects completed the 50 trial test in one session each. The median response times of the ten trials for each of the five stimulus frequencies for each subject were calculated and averaged over subjects in each group. Figure 3.3 summarizes the results of the frequency generalization test trials and indicates that the shortest mean response times occurred to 8kHz stimuli and response times increased as test stimuli became more distant along the frequency dimension from the 8kHz value.

The results of an analysis of variance (three factor with repeated measures on one factor) on the frequency generalization test data are shown in Table 3.5.

TABLE 3.5

Summary of Analysis of Variance of Response Times to Stimuli of Five Auditory Frequencies by Two Groups of Differently Reared Rats

Source	SS	df	ms	F	p
Total	1346.63	79	-	-	
Between Subjects	147.49	15	-	-	
Rearing	2.02	1	2.02	<1.00	-
Sex	74.05	1	74.05	13.37	<.005
Rearing X Sex	4.94	1	4.94	<1.00	-
Error b	66.48	12	5.54	-	
Within Subjects	1199.14	64	-	-	
Stimulus Frequency	778.73	4	194.68	29.81	<.001
Frequency X Rearing	54.57	4	13.64	2.09	ns
Frequency X Sex	35.69	4	8.92	1.37	ns
Frequency X Sex X Rearing	16.52	4	4.13	<1.00	-
Error w	313.63	48	6.53	-	

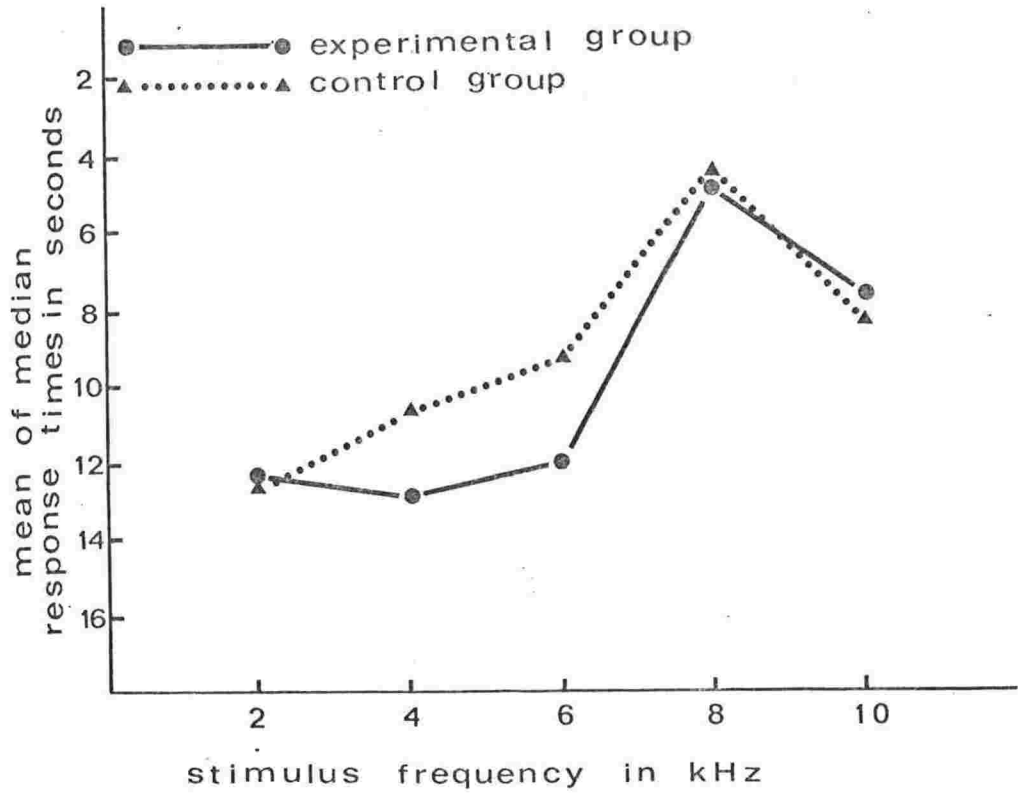


Fig. 3.3. Response time as a function of auditory stimulus frequency for normally reared and patterned sound deprived rats after frequency discrimination training.

Each point represents the mean of eight medians (one from each subject), each median derived from ten response times. Note that the ordinate scale has been reversed from its conventional direction so that the generalization gradients assume their more familiar orientation.

The analysis revealed, again, that the conditions of rearing were not a significant source of variance. Response times for the patterned sound deprived experimental group were not different from those of the varied sound reared controls.

The effect of stimulus frequency on response times was highly significant. A Duncan's multiple range test of the effect of frequency on response times, summarized in Table 3.6, indicated that the mean response times to four of the five stimulus frequencies differed significantly from one another. Responses to 8kHz stimuli were faster than to 10kHz stimuli, and they in turn were faster than responses to 6kHz. Responses to 2kHz stimuli were slowest. Responses to 4kHz stimuli did not differ from those to the flanking stimuli of 6kHz and 2kHz, but they did differ significantly from those to 8kHz and 10kHz stimuli. The results of this test showed that the gradient depicted in Figure 3.3 did, in fact, have a decremental slope and that response times were under the control of the stimulus dimension of auditory frequency.

TABLE 3.6

Summary of Duncan's Range Test of Mean Response Times in Seconds to Stimuli of Five Auditory Frequencies by 16 Rats with Ten Trials Each Per Frequency. \*

Means of Response Times in Seconds					
Stimulus Frequency	2kHz	4kHz	6kHz	8kHz	10kHz
Means	<u>13.14</u>	<u>12.25</u>	10.80	4.65	7.80

\* Means not underscored by the same line are significantly different ( $p < .05$ ).

As in the training trials, there was a significant sex difference in response times, females (mean response time = 8.48sec) being faster than males (mean response time = 10.47sec).

It was noted that the Frequency X Rearing interaction in the analysis of variance approached significance ( $F = 2.09$ ,  $df = 4/48$ ,  $.05 < p < .10$ ). A subsidiary calculation showed that at the stimulus frequency of 6kHz, the mean response times of the two groups differed significantly ( $t = 2.46$ ,  $df = 14$ ,  $p < .05$ ). Inspection of the frequency generalization gradients in Figure 3.3 suggests that if the two groups differ significantly at the 6kHz point, then the two graphs differ in shape, one being more sharply peaked than the other. The generalization gradient produced by the patterned sound deprived animals tended to be steeper than that produced by the rats reared in varied sound. These results do not give clear support to the contention of Ganz and Riesen (1962) that stimulus deprived animals produce steeper generalization gradients along the stimulus dimension of which they have been deprived, after discrimination training, than do animals not so deprived, but they did show a tendency in that direction.

### Conclusions

The experiment showed that rearing rats in conditions which deprived them of patterned sound had no significant effect on their later auditory frequency discrimination ability as shown on both a learning task involving responses to stimuli of two auditory frequencies and on a test of auditory frequency generalization. The

patterned sound deprived rats showed no differences from varied sound reared controls in learning the two frequency discrimination at any stage of the training procedure, nor did they show differences in responding to a range of auditory frequency stimuli on a test of frequency generalization.

The results were similar to those of Tees (1967a) who reared rats in conditions of total sound deprivation and found that the deprived rats did not perform differently from non-deprived controls on an auditory frequency discrimination which required the animals to respond to a stimulus change from one frequency to another.

There are several possible reasons why the differences in sound environment during rearing had no effect on later auditory frequency discrimination in the rats in this experiment. The reasons include:

- a. That the experimental rats were not, in fact, deprived of patterned sound.
- b. The discrimination task was so easy for the rats that any possible effect of rearing was masked by the relative speed with which both groups learned the task.
- c. That patterned sound deprivation may have no effect on simple frequency discrimination, but may have an effect on a more complex auditory discrimination.

Reasons a and b above would seem very unlikely because of the precautions taken to ensure that varied sound was excluded from the environment of the deprived animals and to ensure that the

discrimination task was one which allowed for the examination of the performance of the subjects at various early stages of the discrimination learning. Reasons a and c above should be supported or refuted by the following experiment which examines the effect of the same patterned sound deprivation on the ability of rats to learn a complex auditory discrimination.

### Experiment Ib

#### The Effect of Patterned Sound Deprivation on Auditory Pattern Discrimination in Albino Rats

This experiment was designed to explore the effect of rearing rats in patterned sound deprived conditions on their later performance on an auditory test which involved the discrimination of one pattern of auditory frequencies from another which differed from the first in temporal sequence.

### Method

#### Subjects

The subjects were 16 Sprague-Dawley strain albino rats, ten males and six females, litter-mates of the 16 used in Experiment Ia.

#### Apparatus

The rearing environment apparatus was the same as that used in Experiment Ia, as was the auditory discrimination test apparatus.

The auditory pattern discrimination stimuli consisted of three tone groups each 0.4sec in length with no silent intervals between the three tones. The switching arrangement was such that the fall time of the tone was overlapped by the rise time of the following tone. There was a 0.8sec silent interval between the groups of three tones and the rise and fall time of each group was  $8 \pm 2$ msec. The first and third tones of each group of three were of one auditory frequency and the second was of another frequency. All three tones were delivered at the same intensity measured with the



sound level meter microphone 20cm from the speaker diaphragm and at 0° angle of incidence.

The tones were generated by two transistor oscillators, one fixed to the frequency of 4kHz and the other to 8kHz. The oscillators were connected to the test chamber loudspeaker through relays operated alternately by contacts on two channels of a Friden Inc. Model SP-2 eight channel paper tape reader. The tape reader was advanced one step every 0.4sec by the Grass square wave stimulator. The pattern made up of the group of three tones could be reversed from high-low-high to low-high-low by a switch which reversed the output connections of the two oscillators. This reversal was automatically delayed until the next 0.8sec silent interval irrespective of when the switch was thrown. The Philips PM 3210 cathode ray oscilloscope was used to check the frequencies and the time intervals of the auditory signals.

#### Procedure

The 16 subjects, drawn from the mixed litters as described in Experiment Ia, were divided into two groups of eight with an equal proportion of both sexes in each group. One group, the experimental group, was placed with a mother in one of the two cages in the room containing the white noise generating apparatus, and the other group, the control group, was placed with a mother in the room with the varied sound environment. The rearing procedure was the same as that for the rats of Experiment Ia until the rats reached 60 days of age.

Auditory pattern discrimination training method

The stimuli consisted of a series of groups of three tones in a temporal arrangement described earlier with the first and third tones in each group of one frequency, the second of another frequency. The auditory pattern was similar to that used by Neff and Diamond (1958), Sharlock, Tucking and Strominger (1963) and Tees (1967a). The pattern selected to be the positive stimulus (S+) had the first and third tones of each group at a frequency of 8kHz and the second tone at 4kHz (high-low-high) while the negative stimulus (S-) was the reverse with the first and third tones at 4kHz and the second tone at 8kHz (low-high-low). The tones were set to an intensity of 68dB.

The method of stimulus presentation employed was the one usually used in discrete trial auditory discrimination procedures (e.g. Kappauf, 1943; Butler, Diamond and Neff, 1957; Thompson, 1959; Tees, 1967a). The subjects were required to respond to a change from the continuously presented S- to S+.

Each trial began with the first tone of the group of three after the stimulus had been changed from S- to S+ and ended when either the subject had responded by crossing the central barrier in the test chamber and touched two adjacent floor bars or when 30sec had elapsed, whichever occurred first. The duration of each trial was recorded. Responses made during trials were rewarded with drops (0.01ml) of water. The ITI was  $20^{+5}$ sec. To discourage ITI responding, an S+ postponement system was imposed so that no trial began before the subject had remained on one side of the

barrier for at least 15sec.

Auditory pattern discrimination training. Three days before training began, the subjects were placed on a water deprivation schedule which allowed them access to water for 30min every 24hrs. Eight of the 16 subjects, four experimental animals and four controls, began the procedure aged 64 days and the remaining eight began on post-natal day 71. Each subject was trained at the same time of day each day.

On the first training day each subject was placed in the test chamber and allowed to discover the location of the two liquid dippers and to drink from each. This procedure was carried out in silence. Then to establish "shuttling" behaviour, ten responses were elicited by allowing the subject to drink a drop of water whenever it crossed the central barrier and approached the liquid dipper. Finally, each subject was given ten trials with the sound stimuli but without the 30sec trial limitation so that eventually, responses were made to all ten S+ presentations. Each subject was then returned to its home cage and given access to water for 30min.

On the second and subsequent training days, 50 trials were administered daily, until a criterion of 18 out of 20 consecutive trials with trial durations of less than 10sec with no response having been made in the 15sec prior to S+ presentation had been reached. A limit of 500 trials per subject was set to lessen the likelihood that the criterion could be met eventually, by chance (Grant, 1947).

Results and Discussion

TABLE 3.7

Trials to Criterion\* for Rats Reared in Varied Sound  
and Auditory Pattern Deprived Rats on an Auditory  
Pattern Discrimination Task

Experimental Group (Auditory Pattern Deprived)		Control Group (Varied Sound Reared)	
Rat	Trials	Rat	Trials
E1	111	C1	58
E2	124	C2	58
E3	127	C3	70
E4	116	C4	57
E5	143	C5	50
E6	139	C6	52
E7	163	C7	36
E8	137	C8	44
Means	132.50		53.12
SDs	15.57		9.58

\*Excluding criterional trials.

The rats reared in the varied sound environment took significantly fewer trials to reach the criterion of auditory pattern discrimination than did the auditory pattern deprived animals (  $t = 11.70$ ,  $df = 14$ ,  $p < .001$  ).

The results coincide with those of Tees (1967a) who found that rats reared in the absence of all sound had difficulty learning a similar auditory pattern discrimination to that used in the present experiment. Tees concluded that some auditory experience was necessary before rats could learn an auditory pattern discrimination easily. However, the present experimental

group of rats, slower to learn the auditory pattern discrimination than the control group, was reared in an environment which included sound. Thus the results of the present experiment suggest a restatement of Tees' conclusion: Facility in learning an auditory pattern discrimination by rats depends on their prior experience with sound which varies in frequency and intensity.

Whether the white noise rearing affects just auditory pattern discrimination in rats, or whether it has a much more general effect on the later behaviour of rats needs to be investigated, however, before conclusions and implications can be drawn with confidence from the results of this experiment.

#### General Discussion

The two experiments described in this chapter together showed that albino rats, reared in patterned-sound-depriving white noise, when removed from the noise and tested for auditory discrimination, could discriminate between auditory frequencies just as easily as rats reared in a varied sound environment. However, the patterned sound deprived rats could not learn an auditory pattern discrimination as easily as others that were reared in a varied sound environment.

Experiment Ib results showed that rats were affected by the deprivation experience so a conclusion that an effect of deprivation was not shown on the frequency discrimination task in Experiment Ia because the rats were not deprived of patterned sound was not sustained. The alternative conclusion that rats can dis-

criminate auditory frequencies despite deprivation of patterned sound was supported.

A firm conclusion about the role of varied sound experience in the rat's ability to discriminate auditory patterns was difficult to draw from the results of Experiment Ib. One possible conclusion was that experience with varied sound was necessary for rats to be able to discriminate auditory patterns, i.e. the deprivation retarded the development of auditory pattern discrimination in the rats. Another possible conclusion was that cognitive or emotional differences between the two groups of rats tested in Experiment Ib could account for the differences in performance found. A further possible conclusion was that 60 days of patterned sound deprivation caused an originally existing ability of the rats to discriminate auditory patterns to deteriorate. These possible conclusions are examined in following chapters.

## CHAPTER FOUR

### THE EFFECTS OF REARING ALBINO RATS IN WHITE NOISE ON THEIR PHYSICAL DEVELOPMENT AND ON THEIR PERFORMANCE ON VARIOUS MEASURES OF EMOTIONAL AND COGNITIVE BEHAVIOUR

Rearing animals in darkness can have an effect on their attention, perception and accompanying responses which is not due simply to their lacking the opportunity for visual learning (Fantz, 1967). Similar treatment also affects emotional arousal and control in animals (e.g. Miller, 1948; Riesen, 1961), as does rearing in social isolation in some species (e.g. Harlow and Harlow, 1965; Melzack, 1968). At least two forms of deprivation, visual and social, appear to produce animals emotionally and cognitively different from non-deprived controls.

The experiments described in this chapter explored the possibility that deprivation of patterned sound in rats resulted in animals which differed either emotionally or in their ability to perform a complex visual discrimination from non-deprived controls. The primary intention of the experiments was to discover whether the results of the preceding Experiment Ib, which showed that patterned sound deprived rats were inferior on an auditory pattern discrimination task to non-deprived controls, could be explained by suggesting that emotional or cognitive differences between the two groups of rats accounted for the difference in the results. The secondary intention of the present experiments was

to discover whether the effects of auditory pattern deprivation on emotional behaviour and discrimination behaviour were similar to those reported for visual deprivation.



Experiment IIa

The Effect of Rearing in White Noise on Weaning Weight  
and 'Emotionality' in the Albino Rat

Stimulation of rats during infancy by handling (e.g. Hunt and Otis, 1963), shocking (Levine, Chevalier and Korchin, 1956), shaking (Levine and Lewis, 1959), cooling (Schaefer, 1963), or exposing to loud noises (Henderson, 1967), causes significant changes in a range of behavioural and physiological processes, especially those processes involved in emotional behaviour. As well as these procedures which involve the introduction of extrinsic stimulation to the existing ambient levels of stimulation during rat infancy, the ambient levels themselves have been shown to have an effect on later physiological states and later behaviour. Levine and King (1965) found weight differences at weaning between rats reared in a sound attenuated chamber and those reared in a normal colony. Following on from Levine and King, a study by Denenberg, Schell, Karas and Haltmeyer (1966) showed differences in weaning weight and in behaviour on an open-field test between rats reared in a quiet room and others reared in a laboratory colony. The amount of activity shown and the number of faecal boluses dropped in the novel open space of an open-field test were generally regarded as indications of emotionality in rat subjects (cf. Broadhurst, 1957; Whimbey and Denenberg, 1967).

In the light of the Denenberg et al. (1966) study, it was

considered possible that rats reared under the patterned sound deprived conditions described in Experiment Ib reported in Chapter Three could differ in weaning weight and in emotionality as measured by open-field behaviour from others reared in a varied sound environment. If there were differences in emotional responsiveness between early patterned sound deprived rats and normally reared animals, then the implications of such differences for conclusions drawn from the results of Experiment Ib would need to be examined.

#### Method

##### Subjects

The subjects were 72 Sprague-Dawley albino rats, 36 males and 36 females, the progeny of two fathers and four mothers. The 72 were from four groups of litters, each group consisting of litters cast at the same time. The groups were formed over the period of 12 months.

##### Apparatus

The apparatus used in rearing the subjects was described in Experiment Ia, as was the auditory discrimination testing apparatus.

The device used to weigh the subjects on day 21 after birth was a "Dialogram" Ohaus Scale Corp. weighing machine capable of weighing 0.5gm.

The open-field test apparatus was a flat, white painted surface 86 X 86cm surrounded by 8cm walls also painted white. The

space was subdivided into 12 X 12cm squares by black lines. Directly above the centre of the field and some 60cm from the surface was suspended a 150w electric light bulb. The open-field apparatus was situated in the same room as the auditory discrimination test chamber and was thus similarly isolated from extraneous events.

#### Procedure

The subjects were mixed within 12hrs of birth in the manner described in Experiment Ia so that no rat mother raised more than half of her own litter at any one time. The experimental group, 35 of the subjects, was reared under the white noise conditions also described in Experiment Ia. The remaining 37 subjects formed the control group and were reared in the varied sound environment supplied by the 24hr radio broadcast and various casual ambient noises.

All subjects were weaned on the 21st day after birth by the removal of the rat mothers. On that day also, they were weighed.

On the 60th post-natal day the subjects were allotted to groups to undergo auditory discrimination testing. One batch of 20 animals, ten from the experimental group and ten from the control group, was assigned to experience an auditory frequency discrimination procedure, identical for each subject, followed by the open-field test. This batch was selected from the rest of the subjects on the basis that all members were the same age on the same day.

Over a period of four daily sessions, each subject completed an auditory frequency discrimination test, details of which were

given in Experiment Ia in the preceding chapter.

At the conclusion of each daily auditory discrimination session, each subject was taken directly from the test chamber and placed in the centre of the open-field apparatus. The 150w light was switched on and the subject was observed for 120sec. The number of lines on the floor that the subject crossed with all four feet and the number of faecal boluses dropped during the 120sec interval were recorded. The subjects were returned to their home cages immediately after the open-field test each day. To collect a large sample and to allow for typical behaviour to develop, the open-field testing was continued for five consecutive days, as recommended by Broadhurst (1957) and Levine and Broadhurst (1963). On the fifth day, because the auditory discrimination procedure ended on the fourth day, each rat was placed in the open-field directly from its home cage at approximately the same time of day as on the previous four days.

Results

Weaning Weight

Table 4.1 presents a summary of the results.

TABLE 4.1

Means and Standard Deviations of Body Weight in Grams at 21 Days of Age of Albino Rats Normally Reared and Reared under White Noise Conditions

Experimental Group (White noise reared)	N		Means	SDs
	Males	18	48.50	6.02
Control Group (Normally reared)	Females	17	45.47	7.54
	Males	18	54.72	7.20
	Females	19	49.57	5.62

A 2 X 2 analysis of variance of the data, summarized in Table 4.2, indicates that the effect of the rearing conditions was highly significant. The white noise reared animals were lighter (mean weight = 47.02gm) than the controls (mean weight = 52.08gm). The analysis also revealed that the effect of sex was significant. Females were lighter (mean weight = 47.63gm) than males (mean weight = 51.61gm). The effect of the interaction Sex X Rearing was not significant.

TABLE 4.2

Summary of Analysis of Variance of Body Weight at 21 Days of Age of Normally Reared and White Noise Reared Albino Rats.

Source	SS	df	ms	F	p
Total	3760.88	71	-	-	
Rearing	459.14	1	459.14	10.48	<.005
Sex	284.01	1	284.01	6.48	<.05
Rearing X Sex	40.73	1	40.73	<1.00	ns
Error	2977.00	68	43.77	-	

#### Open-field Test

Activity measure. The summary Table 4.3 indicates the amount of activity of the subjects in the open-field measured by the number of times the lines on the open-field floor were crossed during the 120sec testing sessions over the five day period. The results for males were separated from those for females as a sex difference was expected (Broadhurst, 1957).

TABLE 4.3

Means and Standard Deviations of Activity Scores in an Open-field by Normally Reared and White Noise Reared Albino Rats

		N	Means	SDs
Experimental Group (Noise reared)	Males	6	82	38.85
	Females	4	112	25.15
Control Group (Normally reared)	Males	6	102	36.22
	Females	4	123	10.39

These data were subjected to a 2 X 2 analysis of variance which is summarized in Table 4.4. The experimental group did not differ significantly from the control group on this measure of activity. Nor was there a significant difference between the sexes in activity in the open-field.

TABLE 4.4

Summary of Analysis of Variance of a Measure of Open-field Activity by Normally Reared and White Noise Reared Albino Rats.

Source	SS	df	ms	F	p
Total	20895.20	19	-	-	
Rearing	1344.80	1	1344.80	1.31	ns
Sex	3121.20	1	3121.20	3.05	ns
Rearing X Sex	97.20	1	97.20	<1.00	ns
Error	16332.00	16	1020.75	-	-

Defecation. The results of the faecal bolus count over the five day period is summarized in Table 4.5.

TABLE 4.5

Means and Standard Deviations of Numbers of Faecal Boluses dropped in an Open-field by Normally Reared and White Noise Reared Albino Rats.

		N	Means	SDs
Experimental Group (Noise reared)	Males	6	11.16	6.24
	Females	4	7.50	2.38
Control Group (Normally reared)	Males	6	9.50	4.51
	Females	4	5.75	3.86

An analysis of variance (2 X 2) of the bolus count data is summarized in Table 4.6. There was no significant difference between the two groups in the number of boluses dropped over the period of the experiment. There was no significant difference between the sexes on this measure, either.

TABLE 4.6

Summary of Analysis of Variance of Number of Faecal Boluses Dropped in an Open-field by Normally Reared and White Noise Reared Albino Rats.

Source	SS	df	ms	F	p
Total	438.55	19	-	-	
Rearing	14.45	1	14.45	<1.00	ns
Sex	66.00	1	66.00	2.94	ns
Rearing X Sex	0.01	1	0.01	<1.00	ns
Error	358.09	16	22.38	-	

### Discussion

The results showed that rats reared under the white noise conditions described in the experiment weighed less at weaning age but showed no significant differences on an open-field test from others reared under constantly varying noise conditions.

The weaning weight results are very similar to those of Levine and King (1965) and Denenberg, Schell, Karas and Haltmeyer (1966) who found that rearing rats in a sound attenuated chamber or in a quieter room than the usual laboratory colony room resulted in reduced weight gain by the time of weaning compared with controls. The even consistency of the sound environment used in the current experiments to deprive rats of patterned sound had a similar effect to a quiet environment on rat early weight gain. Levine and King (1965) suggested that the quiet condition of their experiment probably affected the mother rats rather than the infants directly. Levine and King's reasoning was based on their finding in the same experiment that rat litters born in the sound attenuated conditions they used, seldom survived intact



to the age of weaning because they were destroyed by their mothers. Thus Levine and King felt that maternal behaviour was disorganized by the sensory restriction imposed, resulting in a weight loss amongst the surviving offspring. It is of interest to note that during the development of the sound environment manipulation procedures for the present series of experiments, the mortality rate was very high amongst litters born in the white noise conditions of the study. Whatever the explanation for the difference in weight at weaning between the differently reared subjects, their physiological status at weaning did not appear to have had an effect on later emotionality as measured by open-field test behaviour.

Denenberg et al. (1966) compared rats reared in quiet and noisy rooms with rats which had been subjected to the extra stimulation of having been handled during the pre-weaning period of development. They were surprised that their hypothesis that the rats reared in the noisy room would be similar to handled rats in weaning weight and in open-field behaviour was not upheld by their experimental results. The usual finding is that rats stimulated by handling before weaning weigh less than non-handled controls at weaning (Denenberg and Karas, 1961; Levine and Otis, 1958; Levine, 1957) and show less emotionality on an open-field test by being more active and defecating less (e.g. Whimbey and Denenberg, 1967; Levine and Broadhurst, 1963). These usual findings were reported in the Denenberg et al. (1966) study for their animals handled prior to weaning. The same

findings were also reported, however, for the animals reared in the quiet rather than the noisy conditions. The lack of noise appeared to affect the subjects in a manner similar to handling during infancy. They showed less emotionality as adults.

The results of the present experiment suggest that although the white noise rearing condition was similar to the Denenberg et al. (1966) quiet rearing condition in that it provided a steady background stimulation rather than a series of brief fluctuations in stimulation such as that provided by handling, the effects differed. The animals reared under the white noise condition were neither more nor less emotional than animals reared under fluctuating noise conditions when measured for emotional behaviour on the open-field test.

It is possible that the white noise rearing had no effect on the development of emotional behaviour of the experimental subjects. They were thus no different from controls on the open-field test. It is also possible that the white noise rearing did affect the development of emotional behaviour in the experimental subjects either directly or through the mother rats, but the control subjects were equally affected in their emotional development by some aspect of their rearing environment such as the constantly fluctuating sound environment provided by the radio. A consideration of the Denenberg et al. (1966) results suggests that the second explanation for the present results is the more likely one of the two.

The finding in this experiment that there were no significant sex differences in open-field behaviour appears to be unusual. Female rats usually defecate less and ambulate more than male rats in an open-field (Broadhurst, 1957; Levine, 1966). However the present results are similar to those of Broadhurst (1957) who reported that he found no clear indication of sex differences in open-field behaviour in rats until they were at least 100 days old. The rats in the present study were 60 to 70 days of age.

Experiment Ib described in Chapter 4 indicated that rats reared in a white noise environment differed from those reared in a patterned sound environment on a test of auditory discrimination. The present experiment found no evidence that the rearing conditions produced emotionally different animals. Thus it cannot be claimed that the reason that the differently reared rats behaved differently on the auditory discrimination test was that they differed in emotionality and thus one of the two groups was handicapped in learning the response task.

Experiment IIb. The Effect of Rearing in White Noise  
on Visual Discrimination in the Albino Rat

Several writers have raised the possibility that animals subjected to sensory deprivation early in life may not learn a particular discrimination as easily as normally reared animals because their capacity either to make fine discriminations in general or to learn the response task involved in the discrimination test has been affected by the deprivation experience. Representative of these writers is Melzack (1968) who, on the basis of his experience with dogs raised in isolation, suggested that animals subjected to sensory deprivation early in life may have difficulty both in attending selectively to stimuli and in inhibiting irrelevant response patterns because such animals appear to be excessively 'aroused' by ambient stimuli. A similar suggestion was made by Zimbardo and Montgomery (1957) who noted that rats reared in an 'enriched' environment spent much less time exploring the novel environment of a problem-solving test than did rats reared in 'impoverished' conditions. As a consequence, Zimbardo and Montgomery suggested, the 'enriched' rats were able to solve the test problems more rapidly than the 'impoverished' rats.

McCleary (1960) proposed that sensorily deprived subjects might be able to discriminate between complex stimuli but might not be able to link the perceived differences between stimuli with responses demanded by the experimenter. McCleary was reporting the results of an experiment where monocularly deprived fish showed interocular transfer when heart rate was used as a response measure.

Other previous experimenters using more complicated response measures had not been able to show interocular transfer in monocularly deprived fish, (e.g. McCleary, 1954). The response task is clearly an important factor in determining discrimination test results, a point well recognized by researchers who advocate using a battery of tests before concluding that a sensorily deprived animal can or cannot make a particular discrimination (Rosenzweig, 1971).

Support for the notion that perceptual differences found between sensorily deprived animals and non-deprived controls may be the result of differences in general problem-solving ability rather than differences in particular perceptual abilities can be found in some of the studies which show the effects of 'enriched' and 'impoverished' living conditions on later rat behaviour. Rats reared in cages which feature visual and somesthetic-kinesthetic stimuli such as wheels, ladders and childrens' toy blocks are able to solve the problems involved in various mazes such as the Hebb-Williams maze and visual reversal discrimination problems more readily than rats reared in isolation in cages with solid, visually restricting walls (Hymovitch, 1952; Woods, 1959; Forgays and Read, 1962; Rosenzweig, 1971). Rosenzweig (1971) suggested that the advantages shown by rats reared in enriched conditions on these tests of general learning ability were not merely the result of the enriched environment providing sensory experiences similar to those encountered in the tests. Such specific experience has been shown to exert a clear effect on later specific discriminations in rats (Meier and McGee, 1959; Gibson, Walk and Tighe, 1959). On his

visual reversal test, for instance, Rosenzweig found that there was no difference between enriched and deprived rats on the initial dark-light discrimination, an illumination difference which the enriched rats could have experienced more often than the deprived rats which were kept in constantly dim light. However, there was a marked difference between the two groups of rats in the speed at which they learned the first and subsequent reversals of the stimuli between light-reinforced and dark-reinforced. It is difficult to imagine what sensory elements would be present in the enriched environment used in Rosenzweig's experiment which would give rats experience in behaviour towards stimulus reversals. The enrichment or impoverishment of the rearing environment, then, could affect the general learning ability of the organism.

A seldom raised aspect of sensory deprivation is that of the possibility of the existence of 'sensory compensation', the supranormal development of the use of other senses to compensate for a defective one. Rosenzweig (1966) reported that in a series of experiments using either blinded or visually deprived rats, weights and biochemical activity of the non-visual cerebral cortical areas of these animals were significantly greater than those found in sighted controls. Gyllenstein, Malmfors and Norrlin (1966) reported similar findings with mice. MacDougall (1970) and MacDougall and Rabinovitch (1971) followed the finding of Rosenzweig's by attempting to discover whether these brain differences between sensorily deprived and normal animals could be paralleled by behavioural differences. They examined visual

exploration behaviour and visual pattern discrimination (vertical and horizontal striations) in rats deafened by an ototoxic drug. They found no differences on the visual tests they used between deafened and normally hearing rats. However, several studies have demonstrated that a vertical-horizontal striation discrimination can be accomplished even by rats reared in darkness as easily as non-visually deprived controls (Woodruff and Wickens, 1951; Woodruff and Slovak, 1965; Tees, 1968a). The results obtained by MacDougall and Rabinovitch are thus not surprising considering that the striation discrimination test was the most taxing visual task they required their rats to accomplish. If normally sighted rats had no advantage on the test over visually deprived rats, then deafened rats cannot be expected to show greater ability than normally hearing rats on the same test. It is possible, however, that 'sensory compensation' may be able to be demonstrated using a more sensitive discrimination test than that used by MacDougall and Rabinovitch.

The present experiment was designed to discover the effect of rearing rats in white noise, depriving them of patterned auditory experience, on their later ability to solve a 'difficult' visual discrimination problem. Both the response task and the visual discrimination were made deliberately difficult so that the general learning ability of the rats could be tested as well as their ability to make complex visual discriminations. The testing was accomplished (a) with the response task by requiring the subjects to make a sequence of responses rather than the more usual single

responses to the discriminative stimuli and (b) with the visual discrimination by expecting the subjects to discriminate between two visual forms which rats reared in darkness have difficulty discriminating, an X and an N (Tees, 1968a).

It was considered possible that rats reared in a varied sound environment might be able to learn the response task and make the difficult visual discrimination more easily than others reared in white noise because the deprivation experience had affected the general learning ability of the deprived animals or had caused them to be easily distracted by noises in the novel sound environment of the test situation. Conversely, it was considered possible that the patterned sound deprived rats might prove superior on the visual task because of 'sensory compensation'.

Whether the results indicated a superiority or an inferiority of the white noise reared rats on the visual discrimination task, the implications of the results for the conclusions that could be drawn from Experiment Ib need to be examined.

#### Method

##### Subjects

The subjects were 12 Sprague-Dawley albino rats from two litters of 14 and 13 pups which were born on the same day and which had a father in common. Within 12hr of the birth of the last rat pup, neonates were randomly culled from both litters so that 12 remained, six males and six females.



### Apparatus

Rearing was carried out using the same apparatus as was described in Experiment Ia above. Two cages were located in separate rooms; one room also containing white noise generating apparatus, the other a radio tuned to a 24hr broadcasting station.

The visual discrimination apparatus was a fully automated device designed for a discrete trial simultaneous visual discrimination procedure. The test chamber was a clear acrylic ("Perspex") box 30 X 16cm and 16cm high with a floor of 4mm aluminium rods set 2cm apart to form a grill across the short width of the box. At one end of the chamber were two 4.5 X 6cm translucent plastic ("Mylar") panels set 3cm apart with their bases 5cm from the grill floor. A 4.5 X 2cm stainless steel plate was set immediately beneath each of the translucent panels. The plates were connected with contact relays (Lehigh Valley Model 1520) which were also connected with the floor bars. Touching any of the floor bars and either one of the steel plates simultaneously, tripped one or other of the contact relays.

The two translucent panels were separated by a clear acrylic divider which extended from the floor to the roof and from the wall between the two translucent panels, 10cm out into the test chamber. The lower corner of the divider on the edge attached to the panel wall was cut away to accommodate the nozzle of a Lehigh Valley Model 1527 liquid solenoid valve which extended through the panel wall into the test chamber. The divider, nozzle and steel

plates were arranged so that a small animal could receive liquid from the nozzle on one side of the divider or the other, but could not reach past the nozzle to touch the steel plate on the opposite side of the divider.

From the centre of the opposite end wall of the test chamber from the translucent panels and 5cm above the floor, extended a 5 X 6cm aluminium plate on the same plane as the floor. The plate was attached to a microswitch so that an 11gm pressure on the outer edge of the plate tripped the switch. Set centrally in the wall 3cm above the plate was an 8mm diameter dim yellow light bulb.

The test chamber was painted inside and out with non-reflecting black paint except for the area behind the two translucent panels, the divider and an area on the front wall through which the subjects in the chamber could be observed.

A Kodak Carosel S slide transparency projector was positioned some 50cm from the test chamber. An image from the left half of a slide transparency could be projected onto one of the two translucent panels in the test chamber at the same time that an image from the right side of the same transparency was projected onto the other translucent panel.

The visual stimuli used in the discrimination test were projected images of an X and an N originating from a Letraset International Ltd. letter sheet No. 453. The two letters were juxtaposed on a clear plastic film in such a way that when placed in the projector, an image of one letter appeared centrally on one

translucent panel in the test chamber while the other letter appeared centrally on the second panel. The transparency constructed was photographically copied and reversed so that the final transparency was projected as lighted letters on a dark background. The 2.5 X 2.5cm stimuli images on the translucent panels, after having been projected through a battery of neutral-density filters to reduce the light intensity from the projector lamp, were measured to each have a luminance of  $43.12\text{cd/m}^2$  by a Salford Electrical Instruments Ltd. photometer.

There were two slide transparencies used, one bearing the stimuli in the order X N and the other in the opposite order, N X. The projector was programmed with an alternating switch so that the slide change mechanism operated alternately forwards and backwards. This arrangement resulted in the stimuli alternating between the translucent panels in the test chamber each time the slide changer of the projector was activated.

The apparatus was operated by the animal subjects through an array of electro-mechanical programming equipment which provided for the following sequence of events:

A touch on the steel plate immediately beneath either of the two visual stimuli began the sequence. If the visual stimulus selected was the one designated positive (S+), the touch on the steel plate activated the liquid solenoid valve which delivered one drop (approximately 0.1ml) of water. The liquid solenoid valve was not operated if the steel plate beneath the stimulus designated negative (S-) was touched. One second after the steel

plate beneath S+ had been touched, the projector lamp was extinguished and the small lamp lit above the plate serving as a response key at the opposite end of the test chamber from the translucent panels. As a 'time out' arrangement to discourage responses to S-, one second after the steel plate beneath S- had been touched the projector lamp was extinguished and the chamber remained in darkness for 8sec after which the small lamp above the response key was lit. Depression of the response key while the small lamp was lit turned off the small lamp and turned on the projector lamp, re-presenting the stimuli. During the time that the projector lamp was extinguished, the slide change mechanism operated or did not operate according to control exerted by a Lehigh Valley Model 253-11 probability gate pre-set to operate on 50% of the impulses it received. The arrangement ensured that the S+ appeared equally often on the right as on the left and that the position of S+ at any presentation was independent of S+ positions on previous presentations.

Circuitry was arranged so that only the first touch operated the mechanisms controlled from the steel plates beneath the visual stimuli. Further manipulation beyond the first touch was fruitless until the mechanism had been reset by operation of the response key at the other end of the test chamber.

Two electro-mechanical counters were connected with the steel plates and synchronized with the projector slide change mechanism so that one counted responses to S+ while the other counted S- responses.

A Lehigh Valley predetermining counter was used to organize testing sessions into blocks of trials.

The equipment was located in the two room suite described in Experiment Ia with the test chamber and slide projector being separated from the programming and recording equipment by the wall between the rooms. Most extraneous sound was prevented from reaching the test chamber by the isolation of the chamber and by the masking noise provided by exhaust fans as described in Experiment Ia. The only illumination in the test chamber came from the visual stimuli and, while they were not being presented, from the small yellow lamp.

#### Procedure

The rearing procedure was exactly as described in Experiment Ia. The two litters were mixed within 12hr of birth of the last rat pup and divided into two groups of six. One group was reared with one mother in the white noise room while the other remained in the varied sound environment with the second mother. The mothers were removed when the pups were 21 days old.

At 60 days of age, four subjects from the white noise reared group (the experimental group) were randomly selected to begin visual discrimination training as were four subjects from the group reared under the varied noise conditions (the control group). The remaining subjects began training at 72 days of age.

Three days before training began, the subjects were placed on a 23.5hr water deprivation schedule. Each subject was trained at the same time each day and subjects from the experimental group

were alternated with those from the control group. A training session for an individual subject lasted until 45min had elapsed or until the subject had made 200 responses, whichever the earlier event. The subjects were trained to choose one of the two visual stimuli by touching the steel plate beneath the chosen stimulus. Then, when the stimuli were removed, the subjects were expected to retreat to the far end of the chamber and depress the response key to reinstate the stimuli for the next trial. To encourage rapid discrimination acquisition, a 'time out' procedure was instituted so that for 8sec after the S- plate was touched, the chamber was in darkness and the response key inoperable. Each trial began with the presentation of the stimuli and ended with the depression of the response key by the subject.

Each subject was trained on a schedule involving the method of successive approximations first to touch one or other of the steel plates for water reward; then to touch only that steel plate above which was a visual stimulus, the other panel being dark; then finally to light a stimulus panel by depressing the key at the far end of the chamber before touching the plate beneath the lighted stimulus panel. During these training sessions only one stimulus form was used. Half the subjects were trained to respond to a lighted X as S+ and a dark panel as S- and half were trained to respond to a lighted N as S+. It was found necessary to use a very large (10 X 7cm) response key at the end of the chamber opposite the stimulus panel during the early stages of training. Manipulation of this large key could scarcely be avoided by the subjects

as they explored the test chamber. Training was regarded complete when a subject reached a criterion of having completed two consecutive 100 trial blocks where the frequency of the responses to S+ was significantly greater than chance at the .05 level.\* The criterion was met when it was reached in two consecutive blocks either on the one day or across two days. After each daily session, each subject was given 30min free access to water, then returned to its home cage.

Visual form discrimination testing for each subject began with the 100 trial block immediately following that on which the subject had reached the single form stimulus versus the dark panel discrimination criterion. S+ for six of the subjects was X and S- was N, while for the remaining six S+ was N and S- was X. For each animal, the S+ was the same as that for the earlier training sessions. During testing, checks were instituted to ensure that the subjects did not develop left or right position preferences.

---

\* Using the method of approximating binomial probabilities from the table of the normal curve with the formula 
$$z = \frac{(X - .5) - NP}{\sqrt{NPQ}}$$
 (Siegel S. Nonparametric Statistics for the Behavioural Sciences, New York, McGraw Hill, 1956), with N = 100, a z score value of 1.65 is reached when x = 8.75. Thus in a 100 trial block, when a score of 50 per cent correct responses can be interpreted as chance responding, a score of 59 per cent correct differs from chance responding at above the .05 level of significance.

On the very few occasions that such behaviour was observed, it was counteracted by stopping the slide change mechanism so that S+ was not presented on the subject's preferred side for a number of trials until the subject began choosing either side again. Testing continued with each subject completing two 100 trial blocks daily until it reached the criterion of having completed two consecutive trial blocks with responses to S+ being significantly more frequent at the .05 level of significance than expected by chance.

### Results and Discussion

The results (see Table 4.7) when analysed showed that the experimental and control groups did not differ significantly in their performance on the visual discrimination test ( $t = .54$ ,  $df = 10$ ,  $p > .05$ ). The experiment provided no evidence to show that rearing rats in white noise affected their visual discrimination learning.

TABLE 4.7

Number of Blocks of 100 Trials to Criterion\* for Rats Reared in White Noise and Others Reared in Varied Sound on a Visual Discrimination Test.

Experimental Group (Noise reared)		Control Group (Varied Sound reared)	
Rat	Trial Blocks	Rat	Trial Blocks
EV1	8	CV1	8
EV2	6	CV2	7
EV3	4	CV3	8
EV4	4	CV4	10
EV5	10	CV5	5
EV6	7	CV6	5
Means	6.50		7.16
SDs	2.14		1.77

\* Excluding criterional trial blocks.



It was possible that whatever differences between the two groups in visual discrimination existed before training commenced might have disappeared during the training procedure. This possibility cannot be ruled out but was not considered likely because the criterion of learning selected was the trial block in which it first became clear that the rats were beginning to respond differentially to the stimulus patterns. The results indicated that whatever factors influenced the subjects to begin to respond differently to the two stimulus patterns, sound experience during rearing was probably not one of those factors. It was therefore reasonable to conclude that rats reared in white noise could learn a 'difficult' visual discrimination as easily as rats reared in varied sound, suggesting that they were no different in general learning ability or in the ability to make 'difficult' discriminations.

#### General Conclusions

The results of Experiments IIa and IIb cast serious doubt on the possibility that the effect of deprivation of patterned sound on auditory pattern discrimination found in Experiment Ib could be attributable to either emotional or general learning ability differences between the auditorily deprived rats and rats reared in varied sound. Such a possibility cannot be entirely eliminated by the present evidence, of course, because emotional or learning ability differences might have been found had other tests been used. However, inspection of the present data did not reveal noticeable trends which suggested that more extensive

testing would have produced different results. The one difference between the groups which was found, a difference in weight at weaning, apparently had no effect on later emotional behaviour or discrimination learning in the rats as tested in the experiments. It is difficult to imagine therefore, that the weaning weight difference reflected a difference between the groups which might have affected auditory discrimination learning.

The results of the experiments of this chapter suggested that as the effect of patterned sound deprivation in rats discovered in Experiment Ib was probably not attributable to emotional or to general learning differences between the auditorily deprived and the rats reared in varied sound, the effect was likely to have been specific to auditory discrimination.

## CHAPTER FIVE

### THE EFFECT OF RESTRICTING PATTERNED SOUND FOR VARIOUS DURATIONS AND AT VARIOUS AGES ON AUDITORY PATTERN DISCRIMINATION IN THE ALBINO RAT

Hebb (1949) hypothesised that experience early in life had a substantial effect on later behaviour and subsequent experimenters have shown the importance of many varieties of early experience on a diversity of later behaviour. The research in the area tended to flow along the familiar empiricism/nativism lines. One group of investigators following Hebb (1949) proposed that the young organism was poorly developed physically and psychologically and required environmental stimulation if it were to develop further at all. Early experience was held to be important simply because it preceded and thus influenced later behaviour. Another group of researchers followed the work of ethologists such as Lorenz (1950) and postulated that the young organism was not merely disorganized and awaiting organization to be imposed by the environment, but was genetically 'programmed' to accept some particular forms of stimulation from the environment at particular maturational points in its development. They held that stimulation at crucial stages of development had a more lasting effect on later behaviour than similar stimulation at some other stage of development. Experience early in life was important because without particular stimulation within delineated 'critical periods'.

most of which appeared to occur early in life, the subsequent adaptation was in jeopardy. The term 'critical period' was replaced by the less restrictive term 'sensitive period' by Hinde (1970).

The appropriateness of either explanation for the effects of early stimulation on later behaviour has yet to be resolved, but it becomes important when cases of environmental deprivation are considered. If, for instance, early deprivation of particular experience has effects judged to be adverse on behaviour, and the organism simply lacks experience with the stimulus dimension of which it has been deprived, then a supply of that experience should modify the subsequent behaviour. However, if deprivation occurs during a sensitive period for receiving the stimulation that is linked to a particular stage in the physiological maturation process of the organism, then later behaviour towards stimuli of the deprived dimension should be difficult to modify.

The three experiments described in this chapter were designed to explore firstly, whether the effect of patterned sound deprivation on auditory pattern discrimination in rats was the result of deprivation early in the life of the rats or whether it was simply the result of deprivation as such. Secondly, the experiments attempted to explore which of the two explanations suggested above for the importance of early experience of patterned sound for later auditory pattern discrimination was appropriate.

### Experiment IIIa

#### The Effect of 60 Days of Patterned Sound Deprivation During Adulthood on the Ability of the Albino Rat to Learn an Auditory Pattern Discrimination

The results of Experiment Ib, described in Chapter Three, showed that 60 days of patterned sound deprivation affected the ability of rats to learn an auditory pattern discrimination. In that experiment, the rats were deprived from birth. The present experiment was designed to explore, in conjunction with the results of Experiment Ib, whether the effect of the patterned sound deprivation could be attributed either to the time in the life of the rat that the deprivation occurred, or alternatively, whether the effect could be attributed to some other factor such as the duration of the deprivation, irrespective of the age of the rat. The experiment was conducted by depriving 60 day old rats of patterned sound for 60 days and comparing them with 120 day old litter-mates never deprived of patterned sound on a test of auditory pattern discrimination. The results of the experiment were compared with those of Experiment Ib.

### Method

#### Subjects

Twelve Sprague-Dawley strain albino rats served as subjects. There were six males and six females from two litters of 14 and 11 pups born within 24hr of each other. Both litters were sired by the same male which, together with the two mother

rats, had been used in this same capacity in Experiments Ia and Ib. The subjects were randomly selected from the two litters with selection being restricted so that three females and three males were selected from each of the two litters.

#### Apparatus

The equipment used to produce the patterned sound deprived and the varied sound environments was described in Experiment Ia above. The auditory pattern discrimination training and testing apparatus was previously described in Experiment Ib.

#### Procedure

The 12 subjects were drawn from their two litters within 12hr of the birth of the last rat pup. The litters were then mixed by exchanging two males and one female between the litters. The resultant two groups, each with three males and three females, were placed with the mother rats in separate cages in the varied sound environment. The subjects remained undisturbed until they were 60 days old except for the removal of the mothers and weight measurements 21 days after birth, segregation of the sexes on post-natal day 45 and minor disturbances associated with feeding, cleaning and monitoring of sound levels.

At 60 days of age one of the groups of three males and three females was selected by tossing a coin, to be the experimental group, was removed from the varied sound environment and placed in the cages in the room with the white noise generating apparatus. The noise was switched on and set to an intensity of 75dB measured

at the rear junction of the two cages. To maintain a similarity of experience with the experimental group, the remaining six subjects forming the control group were placed in a carrying cage and transported around the corridor approximately the same distance as the experimental group, then replaced in the varied sound environment, but in the unfamiliar cages recently vacated by the experimental group.

The two groups remained in their different sound environments from 60 days of age for 60 days. Commencing on post-natal day 120, and after three days of a 23.5hr water deprivation schedule, all subjects began an auditory pattern discrimination task using the same procedure as that described in Experiment Ib above.

#### Results and Discussion

Sixty days of patterned sound during adulthood did not affect the ability of rats to perform an auditory pattern discrimination. Analysis of the results of the discrimination test (Table 5.1) indicated that the difference between the mean number of trials to criterion of the experimental group and that of the control group was not statistically significant ( $t = .74$ ,  $df = 10$ ,  $p > .05$ ).

Since the earlier Experiment Ib showed that patterned sound deprivation from birth for 60 days did affect the ability of rats to perform an auditory pattern discrimination, it was concluded that deprivation had an effect if it was administered early

in the life of the rats. Hence it would appear that early experience of patterned sound is important for rats to learn an auditory pattern discrimination.

TABLE 5.1

Trials to Criterion\* for Rats Deprived of Patterned Sound for 60 Days and Rats Not Deprived of Sound on an Auditory Discrimination Test.

Experimental Group (Sound deprived)		Control Group (Not Sound deprived)	
Rat	Trials	Rat	Trials
EA1	52	CA1	50
EA2	54	CA2	46
EA3	50	CA3	52
EA4	59	CA4	59
EA5	57	CA5	56
EA6	53	CA6	52
Means	54.16		52.50
SDs	3.02		4.15

\* Excluding criterional trials.



Experiment IIIf

The Effect of Patterned Sound Experience from Birth to  
30 Days of Age on an Auditory Pattern Discrimination  
at 60 Days of Age in the Albino Rat

This experiment was devised to extend the findings of the previous Experiments Ib and IIIa by showing that if a sensitive period for auditory pattern experience existed during the first 60 days in the life of the rat, then it existed either during the first 30 days after birth or, conversely, during the second 30 days after birth. Hence rats were reared in varied sound for 30 days from birth then in white noise for the subsequent 30 days. It was postulated that a difference between auditory pattern discrimination test results for the experimental rats and their controls never deprived of patterned sound would indicate that a sensitive period might exist during the second 30 day period in a rat's life. Alternatively, if no difference was found between the groups on the discrimination test, the first 30 day period after birth might contain such a sensitive period.

Method

The method was exactly that of the previous Experiment IIIa except that 16 rats were used rather than 12, eight as experimental animals and eight as controls. The procedure differed from that of Experiment IIIa in that all the subjects were reared in the varied sound environment until they were 30 days old when the experimental group was removed to the white noise environment where it remained for the next 30 days. Both groups began auditory

pattern discrimination training when they were 60 days old.

### Results and Discussion

Fifteen subjects completed the discrimination test but the 16th was rejected from the experiment because it could not be induced to learn the response task. The results (Table 5.2) showed that the rats deprived of patterned sound for 30 days from 30 days of age did not differ on the auditory discrimination test from those not so deprived ( $t = .30$ ,  $df = 13$ ,  $p > .05$ ). The results suggested that if a sensitive period for the effect of patterned sound experience on auditory pattern discrimination existed in rats, then it did not exist during the period between 30 days and 60 days of age.

TABLE 5.2

Trials to Criterion\* for Rats Reared in Varied Sound for 60 Days and Others Reared in Varied Sound for 30 Days Then Deprived of Patterned Sound for 30 Days on an Auditory Pattern Discrimination Test.

Experimental group (Sound deprived)		Control Group (Not Sound deprived)	
Rat	Trials	Rat	Trials
EB1	53	CB1	45
EB2	72	CB2	77
EB3	56	CB3	--
EB4	47	CB4	40
EB5	55	CB5	62
EB6	46	CB6	66
EB7	50	CB7	48
EB8	42	CB8	46
Means	52.62		54.12
SDs	8.63		12.92

\* Excluding criterional trials.

### Experiment IIIc

#### The Effect of Depriving Rats of Patterned Sound for the First 30 Days After Birth on Their Later Ability to Learn an Auditory Pattern Discrimination

This experiment was designed to discover whether a sensitive period for the effect of patterned sound on auditory pattern discrimination was likely to exist within the first 30 days after a rat's birth.

### Method

The method was exactly the same as that for the previous Experiment IIIb except that the experimental group was deprived of patterned sound from birth to 30 days of age then placed in the varied sound environment for a further 30 days. Both experimental and control groups, the latter never having experienced sound deprivation, began auditory pattern discrimination training when the rats were aged 60 days.

### Results and Discussion

The results of the discrimination test are presented in Table 5.3. The rats which had been deprived of patterned sound for the first 30 days after birth did not perform significantly differently from others not so deprived on the discrimination test ( $t = .18$ ,  $df = 14$ ,  $p > .05$ , one tailed test). The results did not provide evidence for the existence of a sensitive period for the effects of varied sound during the first 30 days after birth in the rat.

TABLE 5.3

Trials to Criterion\* for Rats Reared in Varied Sound and Others Reared in White Noise for 30 Days Then in Varied Sound on an Auditory Pattern Discrimination Test Commencing on Post-Natal Day 60.

Experimental Group (Sound deprived)		Control Group (Not Sound deprived)	
Rat	Trials	Rat	Trials
EC1	40	CC1	46
EC2	46	CC2	56
EC3	39	CC3	38
EC4	55	CC4	53
EC5	43	CC5	36
EC6	67	CC6	44
EC7	40	CC7	61
EC8	58	CC8	47
Means	48.50		47.62
SDs	9.65		8.07

\* Excluding criterional trials.

### General Discussion

The group of experiments described in this chapter had two objectives. They were designed to discover whether the effect of deprivation of patterned sound on later auditory pattern discrimination was an effect of early deprivation or simply the effect of having deprived rats of patterned sound with white noise at any time in their lives. They were also designed to narrow down the possible explanations of the phenomenon.

The results of Experiment IIIa in conjunction with the results of Experiment Ib showed that deprivation of patterned sound during the early period from birth to 60 days affected auditory pattern discrimination, but the same deprivation had no such

effect during the second 60 days in the life of the rat. It was deduced that the early experience of patterned sound was more important to the development of auditory pattern discrimination than was later experience with patterned sound.

One explanation for the effect found was that a critical period for varied sound stimulation existed for some duration during the first 60 days of a rat's life. Stimulation by varied sound during this sensitive period might have been necessary for later facility in making auditory pattern discriminations. In an attempt to locate this sensitive period the 60 day period in which it might have existed was broken into two 30 day periods and the second of these periods tested for the presence of a sensitive period in Experiment IIIb. The results indicated that it was probable that no sensitive period existed during the time from 30 to 60 days of age in the rat's life, so the first 30 day period was examined in Experiment IIIc. The results of this experiment showed that there was no discernible effect on later auditory pattern discrimination by rats deprived of patterned sound for this early period when the test for discrimination was made after a subsequent period of varied sound. To comply with the usual criteria for a sensitive period, the effect of stimulation (or deprivation) during the period should be long-lasting (Denenberg, 1968) and irreversible (Reisen, 1961). In the present research, the effect of patterned sound deprivation did not survive through 30 subsequent days of varied sound experience. Further, the effect was not irreversible because the rats which showed the

effect after having been deprived of patterned sound, did eventually reach the criterion of discrimination.

However, the present experiments did not rule out entirely the possibility that a sensitive period exists in rats for varied sound experience. For example, Nyman (1967) in an experiment exploring sensitive periods in rats for the effects of 'free' environment experience on later problem solving behaviour, showed that the duration of the experience was an important factor. It could be that the 30 day period of deprivation of patterned sound suffered by the rats in Experiments IIb or IIIc was not long enough to affect their later auditory pattern discrimination learning. Woods (1959) and Denenberg and Morton (1964) also showed that the effects of deprivation of some forms of stimulation during sensitive periods in rats could be substantially negated by their experience subsequent to the deprivation. Hence it is possible that in Experiment IIIc, the rats deprived of patterned sound during their first 30 days after birth did not show a later effect of the deprivation because the experience of the subsequent 24hr-a-day varied sound environment largely negated the effects of the earlier deprivation even though the deprivation occurred during a relevant sensitive period. It is also possible that the test used in the experiments was not sufficiently sensitive to detect any residual effects of the deprivation in the rats. A conclusion must be that the case for sensitive periods for the effects of varied sound experience on later auditory pattern discrimination

in rats remains open for future research.

A second explanation for the phenomenon was possible. The view that early experience of varied sound was important for later auditory pattern discrimination learning in the rat not because of its priority in the life of the rat but because of its priority over later sound experience was supported. In Experiment Ib, deprivation of patterned sound before rats had experienced varied sound did affect their auditory pattern discrimination learning. But in Experiments IIIa, IIIb and IIIc, auditory discrimination learning was apparently not affected by deprivation of patterned sound when the rats were given some experience of varied sound before the discrimination test. The conclusion could be drawn that patterned sound deprivation in rats did not affect their later auditory pattern discrimination learning provided that they also had some experience with varied sound. The age at which the rats experienced the patterned sound appeared to be immaterial; it was the necessity for the varied sound experience to precede the auditory pattern discrimination test that was important. This more parsimonious explanation for the importance of early varied sound experience for auditory pattern discrimination in the rat, appeared to be more plausible than that involving a sensitive period. However, the issue would be made clearer by further experiments in which not only the length of the deprivation period was varied, but also the duration of the varied sound experience after the deprivation.

## CHAPTER SIX

### CONCLUSIONS

The series of experiments reported in this study used specially designed methods to manipulate the auditory experience of rats in order to assess its role in the development of auditory frequency discrimination and auditory pattern discrimination.

Auditory frequency discrimination. Prior experience of patterned sound did not appear to play an important part in the development of a discrimination between two frequencies. Rats with no experience of patterned sound before the discrimination test reached a criterion of frequency discrimination learning as easily as rats with varied sound experience. The several possible interpretations of these results were examined before a conclusion was drawn. Firstly, a test of auditory frequency generalization was completed at the end of discrimination training which indicated that the rats did, in fact, respond to the differences in the auditory frequencies during training rather than to some other cue for responding. Secondly, analysis of the performance of the rats at the beginning of the frequency discrimination training showed no differences between the sound deprived and the normally reared rats which might have suggested that a difference existing before training began, disappeared during the training process. When these possible interpretations for the



results of the experiment were eliminated, it was concluded with confidence that rats could discriminate auditory frequencies without prior experience of patterned sound.

The results of the present series of experiments were very similar to those of Tees (1967a) who, with his less refined procedures, found no difference between rats reared in silence and normally reared controls on a test of auditory frequency involving responses to a change of frequency of an auditory signal. He concluded that with no sound experience at all, rats were able to learn a frequency discrimination as easily as rats with sound experience. However, the present experiments extend Tees' study by showing that without experience of patterned sound, rats could discriminate auditory frequencies on a most rigorous test of that discrimination.

Previous experimenters who explored the visual modality in animals came to similar conclusions about the necessity for experience of light as a preliminary to the development of simple visual discriminations. For instance, discrimination between hues has been observed in chickens (Hess, 1956), ducklings (Oppenheim, 1968), and rhesus monkeys (Fantz, 1967; Ganz, 1968), before these animals have had any or very little experience of patterned light. Similarly, discrimination of forms such as triangles and circles did not appear to require experience in patterned light in rats (Gibson, Walk and Tighe, 1959), doves (Siegel, 1953), chickens (Fantz, 1957), cats (Myers and McCleary, 1964), and monkeys (Fantz, 1967). It seems then, that some visual

and auditory discriminations can be made by animals without prior sensory experience of the dimension of the stimuli to be discriminated.

Auditory pattern discrimination. The present experiments showed that experience of patterned sound did play a role. Rats deprived of patterned sound from birth until the time of the discrimination test learned the discrimination more slowly than others that had been reared in varied sound.

The pattern discrimination test used the same auditory frequencies to form the patterns as had been used in the frequency discrimination task. Therefore the patterned sound deprived rats were able to discriminate the frequencies used in the patterns. Subsidiary experiments indicated that it was unlikely that the patterned deprived rats were handicapped on the pattern discrimination task either because they were emotionally different from the varied sound reared controls or because they were not able to make 'difficult' discriminations in any sense modality. The deleterious effects of the patterned sound deprivation were apparently confined to auditory discrimination in the deprived rats. Discrimination of the auditory patterns required the rats to respond to differences in the temporal arrangement of the tonal stimuli which could be accomplished in two ways, at least. Either the rats could respond to the change from, for instance, a 'high-low-high' series of tones to a 'low-high-low' configuration of the group of three tones or they could respond to the change in the predominance of signals of one or other of the frequencies. For instance, in the 'high-low-

high' series, 'high' occurred twice as often as 'low' and when the pattern changed to 'low-high-low' the number of 'highs' per time interval decreased. Whichever arrangement the rats used as a cue for responding, successful discrimination depended on their relating the tones together within a time interval framework - a task which was difficult for the patterned sound deprived rats.

The effect found was the result of a period of patterned sound deprivation beginning at birth rather than for a similar duration later in life, according to the results of an experiment conducted to establish which of these two possibilities was likely; thus it was an effect of early deprivation. The conclusion was drawn that since early deprivation of patterned sound affected auditory pattern discrimination in rats, early experience of patterned sound was necessary for auditory pattern discrimination learning.

Further experiments explored whether the deprivation of patterned sound during the early period of the life of the rat had an effect on auditory pattern discrimination because the rat was deprived during a sensitive period for varied sound stimulation or whether the deprivation had simply delayed development of the discrimination because the rat had never experienced varied sound. The experimental results provided no clear answer to this question, although it was considered that the latter explanation for the effects of early deprivation of patterned sound was the more reasonable in the light of the evidence uncovered by the experiments. However, the conclusion that experience of varied sound either during

a sensitive period or at some time during the early life of the rat facilitated its ability to discriminate auditory patterns.

Tees (1967a) in a similar experiment using an auditory pattern discrimination with rats reared in near-silence produced similar results to the present experiment. Tees considered that his results indicated that experience in an environment with sound was necessary for animals to discriminate complex auditory stimuli. The present experiments extended Tees' conclusion by showing that experience not only of sound itself was required for auditory pattern discrimination in rats, but also sound which varied in frequency and intensity over time.

There have been several experiments in which animals deprived of patterned light were shown to have difficulty in discriminating visual configurations involving the abstraction of visual information from the context of the surrounding area (e.g. Riesen, 1961; Tees, 1968a; Ganz, Hirsch and Tieman, 1972). The present experiments demonstrated that patterned sound deprivation resulted in slow learning of an auditory pattern discrimination involving the abstraction of auditory information within time periods. It is possible, then, that the role of auditory experience in the development of auditory discriminations is similar to the role of visual experience in visual discriminations. A result in a visual deprivation study not paralleled in the present series of experiments in audition in rats was that of Dews and Wiesel (1970). These researchers located a sensitive period for the effects of visual deprivation on several types of visual discrimination in cats.

The present experiments in audition provided no clear evidence for a sensitive period for the effects of patterned sound deprivation on auditory pattern discrimination in rats. However, the previously cited (Chapter I) experiments of Wolf (1943), Gauron and Becker (1959) and Stein and Schuckman (1973) suggested that if a sensitive period for auditory experience was to be found in rats, the effects of stimulation during the period might be more subtle than could be detected by the discrimination test procedures adopted in the present study. Thus the question of a sensitive period is still open for future investigation.

It was noted that the results of the present experiments with rats arrived at similar results to those of studies showing the effects of ablation of parts of the auditory cortex in cats (Diamond and Neff, 1957; Neff and Diamond, 1958; Sharlock, Tucker and Strominger, 1963; Thompson, 1960). Cats from which auditory cortex was removed were able to learn an auditory frequency discrimination as easily as unoperated controls but had difficulty learning auditory pattern discriminations such as the one used in the present study. Facility for discriminating auditory patterns appears to require both an intact auditory cortex and experience in varied sound, while facility for frequency discriminations needs neither of these prerequisites.

#### Future Research Possibilities

The method used to deprive the animals of patterned sound in the present experiments provided similar results to other experiments in which animals were deprived of auditory stimulation

by rearing them in silence (Tees, 1967a) without the problems often associated with rearing animals in isolation or with ear occluding devices. Now that a practicable method of auditory deprivation has been tested, the study of the development of auditory discrimination in various animal species and of the effects of auditory deprivation on this development, can proceed. Findings from visual deprivation studies can then be compared with those from another sensory mode thus acquiring further information about sensory development.

Further experiments should be conducted to explore the effects of varying the duration of the patterned sound deprivation, the time of onset of the deprivation and the interval between the deprivation and the discrimination test. Such experiments should demonstrate whether the effect found in the present study represents a deterioration of an auditory discrimination ability occasioned by a lack of varied sound stimulation during an early stage of development in the animal or whether the effect found demonstrated a simple delay in the development of an auditory discrimination.

It is envisaged that the auditory deprivation technique used in this study will be of great value in neurophysiological studies of the auditory systems of animals in the same manner as visual deprivation by diffuse light has served in the study of the visual system (e.g. Wiesel and Hubel, 1963, 1965a, 1965b). Neurophysiological studies indicating which particular neural functions are affected by sensory deprivation can provide leads to be followed by behavioural studies as well as provide information

about the functioning of sensory systems. For instance, two highly informative recent behavioural studies about the development of visual discrimination in cats, that of Dews and Wiesel (1970) and Ganz, Hirsch and Tieman (1972) were both suggested by the results of a series of studies of cat visual cortex single cell recordings after the cats had been visually deprived (Wiesel and Hubel, 1963, 1965a, 1965b; Hubel and Wiesel, 1970). Similar behavioural studies, based on neurophysiological findings in the auditory systems of auditorily deprived animals can be expected to be more informative and more efficient than behavioural studies based on other behavioural studies in gaining information about the development of auditory abilities. The eventual aim of such studies, of course, is to reach conclusions which will be useful in the alleviation of the auditory deprivation caused by deafness in people.

REFERENCES

- Aarons, L., Halasz, Z.H. and Riesen, A.H. Interocular transfer of visual intensity discrimination after ablation of striate cortex in dark-reared kittens. Journal of Comparative and Physiological Psychology, 1962, 55, 813-815.
- Batkin, S., Groth, H., Watson, J.R. and Ansberry, M. Effects of auditory deprivation on the development of auditory sensitivity in albino rats. Electroencephalography and Clinical Neurophysiology, 1970, 28, 351-359.
- Beach, F.A. and Jaynes, J. Effects of early experience upon the behavior of animals. Psychological Bulletin, 1954, 51, 239-263.
- Bowlby, J. Child Care and the Growth of Love. London: Pelican, 1953.
- Broadhurst, P.L. Determinants of emotionality in the rat: Situational factors. British Journal of Psychology, 1957, 48, 1-12.
- Bruning, G.L. and Kintz, B.L. Computational Handbook of Statistics. Glenview, Illinois: Scott, Foresman, 1968.
- Butler, R.A., Diamond, I.T. and Neff, W.D. Role of auditory cortex in discrimination of changes of frequency. Journal of Neurophysiology, 1957, 20, 108-120.
- Clack, T.D. and Harris, J.D. Auditory thresholds in the rat by a two-lever technique. Journal of Auditory Research, 1963, 3, 53-63.



- Crowley, D.E., and Hepp-Reymond, M.C. Development of cochlear function in the ear of the infant rat. Journal of Comparative and Physiological Psychology, 1966, 62, 427-432
- Denenberg, V.H. A consideration of the usefulness of the critical period hypothesis as applied to the stimulation of rodents in infancy. In Newton, G., and Levin, S. (Eds) Early Experience and Behaviour. Springfield, Illinois: Charles C. Thomas, 1968
- Denenberg, V.H. and Karas, G.G. Interactive effects of infantile and adult experiences upon weight gain and mortality in the rat. Journal of Comparative and Physiological Psychology, 1961, 54, 685-689
- Denenberg, V.H. and Morton, J.R.C. Effects of pre-weaning and post-weaning manipulations upon problem solving behavior. Journal of Comparative and Physiological Psychology, 1962, 55, 1096-1098
- Denenberg, V.H., Schell, S.F., Karas, G.G. and Haltmeyer, G.C. Comparison of background stimulation and handling as forms of infantile stimulation. Psychological Reports, 1966, 19, 943-948
- Dews, P.B. and Wiesel, T.N. Consequences of monocular deprivation on visual behavior in kittens. Journal of Physiology, 1970, 206, 437-455
- Diamond, I.T. and Neff, W.D. Ablation of temporal cortex and discrimination of auditory patterns. Journal of Neurophysiology, 1957, 20, 300-315

- Edwards, A.L. Experimental Design in Psychological Research.  
New York: Holt, Rinehart and Winstone, 1960.
- Fantz, R.L. Form preferences in newly hatched chicks. Journal of Comparative and Physiological Psychology, 1957, 50, 422-430.
- Fantz, R.L. Visual perception and experience in early infancy: a look at the hidden side of behavioral development.  
In Stevenson, H.W., Hess, E.H. and Rheingold, H.L. (Eds) Early Behavior: Comparative and Developmental Approaches.  
New York: Wiley, 1967, pp 181-224.
- Forgays, D.G. and Read, J.M. Crucial periods for free-environment experience in the rat. Journal of Comparative and Physiological Psychology, 1962, 55, 816-818.
- Ganz, L. An analysis of generalization behavior in the stimulus deprived organism. In Newton, G. and Levine, S. (Eds) Early Experience and Behavior. Springfield, Illinois: Charles C. Thomas, 1968.
- Ganz, L., Hirsch, H.U.B. and Tieman, S.B. The nature of perceptual deficits in visually deprived cats. Brain Research, 1972, 44, 547-568.
- Ganz, L. and Riesen, A.H. Stimulus generalization to hue in the dark-reared macaque. Journal of Comparative and Physiological Psychology, 1962, 55, 92-99.
- Gourevitch, G. Auditory masking in the rat. Journal of the Acoustical Society of America, 1965, 37, 439-443.

- Gourevitch, G. and Hack, H.M. Audibility in the rat. Journal of Comparative and Physiological Psychology, 1966, 62, 289-291.
- Gauron, E. and Becker, W. The effects of early sensory deprivation on adult rat behavior under competition stress. Journal of Comparative and Physiological Psychology, 1959, 52, 689-694.
- Gibson, E.J. Principles of Perceptual Learning and Development. New York: Appleton-Century-Crofts, 1967.
- Gibson, E.J., Walk, R.D. and Tighe, T.J. Enhancement and deprivation of visual stimulation during rearing as factors in visual discrimination learning. . Journal of Comparative and Physiological Psychology, 1959, 52, 74-81.
- Gottlieb, G. Prenatal behavior of birds. Quarterly Review of Biology, 1968, 43, 148-174.
- Grant, D.A. Additional tables of the probability of 'runs' of correct responses in learning and problem solving. Psychological Bulletin, 1947, 44, 276-282.
- Gyllensten, L., Malmfors, T. and Norrlin, M. Growth alterations in the auditory cortex of visually deprived mice. Journal of Comparative Neurology, 1966, 126, 463-470.
- Hack, M.H. Auditory discrimination in the rat. Journal of Comparative and Physiological Psychology, 1971, 74, 315-318.
- Harlow, H.F. and Harlow, M.K. The affectional systems. In Schrier, A.M., Harlow, H.F. and Stollnitz, F. (Eds) Behavior of Non-Human Primates. New York: Academic Press, 1965.

Hebb, D.O. The innate organization of visual activity II.

Transfer of responses in the discrimination of brightness and size by rats reared in total darkness. Journal of Comparative Psychology, 1937, 24, 277-299.

Hebb, D.O. The Organization of Behavior. New York: Wiley, 1949.

Henderson, N.D. Effects of preweaning noxious stimulation on later behavior in rats: Role of experimenter contact and spacing of stimulation. Psychological Reports, 1967, 21, 97-104.

Hess, E.H. Natural preferences of chicks and ducklings for objects of different color. Psychological Reports, 1956, 2, 477-483.

Hinde, R.A. Animal Behaviour. A Synthesis of Ethology and Comparative Psychology, Tokyo: McGraw-Hill Kogakusha, 1970.

Hubel, D.H. and Wiesel, T.N. The period of susceptibility to the physiological effects of unilateral eye closure in kittens. Journal of Physiology, 1970, 206, 419-436.

Hunt, H.F. and Otis, L.S. Early 'experience' and its effects on later behavioral processes in rats: I. Initial experiments. Transactions of the New York Academy of Sciences, 1963, 25, 890-901.

Hymovitch, B. The effects of experimental variations on problem solving in the rat. Journal of Comparative and Physiological Psychology, 1952, 45, 313-321.

Kappauf, W.E. The application of conditioning methods to the study of discrimination and the measurement of differential

- thresholds in animals. Journal of Psychology, 1943, 15, 129-135.
- Kappers, C.U.A. On structural laws in the nervous system: The principles of neurobiotaxis. Brain, 1920, 43, 125-129.
- King, J.A. Parameters relevant to determining the effect of early experience upon the adult behavior of animals. Psychological Bulletin, 1958, 55, 46-58.
- Levine, S. Infantile experience and resistance to physiological stress. Science, 1957, 126, 405.
- Levine, S. Sex differences in the brain. Scientific American, 214, 84-90.
- Levine, S. and Broadhurst, P.L. Genetic and ontogenetic determinants of adult behavior in the rat. Journal of Comparative and Physiological Psychology, 1963, 56, 423-428.
- Levine, S., Chevalier, J.A. and Korchin, S.J. The effect of early shock and handling on later avoidance learning. Journal of Personality, 1956, 24, 475-493.
- Levine, S. and King, D.L. Effect of auditory restriction during pregnancy on offspring survival. Psychonomic Science, 1965, 3, 275-276.
- Levine, S. and Lewis, G.W. The relative importance of experimenter contact in an effect produced by extra-stimulation in infancy. Journal of Comparative and Physiological Psychology, 1959, 52, 368-369.
- Levine, S. and Otis, L.S. The effect of handling before and after weaning on the resistance of albino rats to later deprivation. Canadian Journal of Psychology, 1958, 12, 103-108.

- Levis, D.J. Short and long term auditory history and stimulus control in the rat. Journal of Comparative and Physiological Psychology, 1971, 74, 298-314.
- Lorenz, K.Z. The comparative method in studying innate behavior patterns. In Symposia of the Society for Experimental Biology No. IV: Physiological Mechanisms in Animal Behavior. New York: Academic Press, 1950, 221-268.
- McCleary, R.A. Neural implications of interocular transfer in the goldfish. American Psychologist, 1954, 9, 423.
- McCleary, R.A. Type of response as a factor in interocular transfer in the fish. Journal of Comparative and Physiological Psychology, 1960, 53, 311-321.
- MacDougall, J.C. Early deprivation and visual behaviour. Dissertation Abstracts International, 1970, Vol. 30 (11-B) Abstract 5260.
- MacDougall, J.C. and Rabinovitch, M.S. Early auditory deprivation and sensory compensation. Developmental Psychology, 1971, 5, 368.
- Meier, G.W. and McGee, R.K. Effect of early experience on discrimination. Journal of Comparative and Physiological Psychology, 1959, 52, 390-395.
- Melzack, R. Effects of early perceptual restriction on simple visual discrimination. Science, 1962, 137, 978-979.
- Melzack, R. Early experience: a neuropsychological approach to heredity-environment interactions. In Newton, G. and Levine, S. (Eds) Early Experience and Behavior. Springfield, Illinois: Charles C. Thomas, 1968, 65-82.

- Melzack, R. and Scott, T.H. The effects of early experience on the response to pain. Journal of Comparative and Physiological Psychology, 1957, 50, 155-161.
- Miller, M. Observation of initial visual experience in rats. Journal of Psychology, 1948, 26, 223-228.
- Meyers, B. and McCleary, R.A. Interocular transfer of a pattern discrimination in pattern deprived cats. Journal of Comparative and Physiological Psychology, 1964, 57, 16-21.
- Neff, W.D. and Diamond, I.T. The neural basis of auditory discrimination. In Harlow, H.F. and Woolsey, C.N. (Eds) Biological and Biochemical Basis of Behavior. Madison, Wisconsin: University of Wisconsin Press, 1958.
- Nyman, A.J. Problem solving in rats as a function of experience at different ages. Journal of Genetic Psychology, 1967, 110, 31-39.
- Oppenheim, R.W. Color preferences in the pecking response of newly hatched ducks. Journal of Comparative and Physiological Psychology, 1968, 66 Monograph Supplement, No. 3, Part 2.
- Randall, W.L. Generalization after frequency discrimination in cats with central nervous system lesions. In Mostofsky, D.I. (Ed) Stimulus Generalization, Stanford, California: Stanford University Press, 1965.
- Riesen, A.H. Stimulation as a requirement for growth and function in behavioural development. In Fiske, D.W. and Maddi, S.R. (Eds) Functions of Varied Experience. Homewood, Illinois: Dorsey, 1961, 57-80.

- Riesen, A.H. Sensory deprivation. In Stellar, E. and Sprague, J.M. (Eds) Progress in Physiological Psychology. Vol. I. New York: Academic Press, 1966, 117-147.
- Riesen, A.H. and Aarons, L. Visual movement and intensity discrimination in cats after early deprivation of pattern vision. Journal of Comparative and Physiological Psychology, 1959, 52, 142-149.
- Riesen, A.H., Ramsay, R.L. and Wilson, P.D. Development of visual acuity in rhesus monkeys deprived of patterned light during early infancy. Psychonomic Science, 1964, 1, 33-34.
- Rosenzweig, M.R. Environmental complexity, cerebral change and behavior. American Psychologist, 1966, 21, 321-332.
- Rosenzweig, M.R. Effects of environment on development of brain and behavior. In Tolbach, A., Aronson, L.R. and Shaw, E. (Eds) The Biopsychology of Development. New York: Academic Press, 1971, 303-342.
- Rosenzweig, M.R., Bennett, E.L. and Diamond, M.C. Brain changes in response to experience. Scientific American, 1972, 226(2), 22-29.
- Roux, W. Quoted by Riesen, A.H. Sensory deprivation. In Stellar, E. and Sprague, J.M. (Eds) Progress in Physiological Psychology. Vol. I. New York: Academic Press, 1966, 118.
- Schaefer, T. Early 'experience' and its effects on later behavioral processes in rats: II. A critical factor in the early handling phenomenon. Transactions of the New York Academy of Sciences, 1963, 25, 871-889.



- Scharlock, D.P., Tucker, T.J. and Strominger, N.L. Auditory discrimination by the cat after neonatal ablation of temporal cortex. Science, 1963, 141, 1197-1198.
- Siegel, A.I. Deprivation of visual form definition in the ring dove: I. Discrimination learning. Journal of Comparative and Physiological Psychology, 1953, 46, 115-119.
- Siegel, S. Nonparametric Statistics for the Behavioral Sciences. Tokyo: McGraw-Hill Kogakuska, 1956.
- Spitz, R. An inquiry into the genesis of psychiatric conditions in early childhood. In Eissler, R.S., Freud, A., Hartman, H. and Kris, E. (Eds) The Psychoanalytic Study of the Child. Vol. I. New York: International University Press, 1945.
- Stein, B.E. and Schuckman, H. Effects of sensory restriction upon responses to cortical stimulation in rats. Journal of Comparative and Physiological Psychology, 1973, 82, 182-187.
- Sterritt, G.M. and Robinson, D.G. Pathology resulting from chronic paraffin ear plugs: methodological problems in auditory sensory deprivation research. Perceptual and Motor Skills, 1964, 19, 662.
- Tees, R.C. Effects of early auditory restriction in the rat on later adult pattern perception. Journal of Comparative and Physiological Psychology, 1967a, 63, 389-393.
- Tees, R.C. Duration discrimination in the rat after early auditory restriction. Perceptual and Motor Skills, 1967b, 25, 249-255.
- Tees, R.C. Effect of early restriction on later form discrimination in the rat. Canadian Journal of Psychology, 1968a, 22, 294-301.

- Tees, R.C. Effect of early restriction on later visual intensity discrimination in rats. Journal of Comparative and Physiological Psychology, 1968b, 66, 224-227.
- Trapold, M.A. and Winokur, S. Transfer from classical conditioning and extinction to acquisition, extinction and stimulus generalization of a positively reinforced instrumental response. Journal of Experimental Psychology, 1967, 73, 517-525.
- Thompson, R.F. The effect of training procedure upon auditory frequency discrimination in the cat. Journal of Comparative and Physiological Psychology, 1959, 52, 186-190.
- Thompson, R.F. Function of auditory cortex of the cat in frequency discrimination. Journal of Neurophysiology, 1960, 23, 321-334.
- Thompson, W.R. and Heron, W. The effects of restricting early experience on the problem solving capacity of dogs. Canadian Journal of Psychology, 1954, 8, 17-31.
- Thompson, W.R. and Schaefer, T. Early environmental stimulation. In Fiske, D.W. and Maddi, S.R. (Eds) Functions of Varied Experience. Homewood, Illinois: Dorsey, 1961, 81-105.
- Volokhov, A.A. Comparative studies of the functional development of analyzer systems in animals in the process of ontogenesis. Progress in Brain Research, 1968, 22, 527-540.
- Wada, T. Anatomical and physiological studies on the growth of the inner ear of the albino rat. American Anatomical Memoirs, 1923, 10, 1-174. From Gottlieb, G. Ontogenesis of sensory function in birds and mammals. In Tobach, A., Aronson, L.R.

- and Shaw, E. (Eds) The Biopsychology of Development.  
New York: Academic Press, 1971, p. 75.
- Whimbey, A.E. and Denenberg, V.H. Two independent behavioral dimensions in open-field performance. Journal of Comparative and Physiological Psychology, 1967, 63, 500-504.
- Wiesel, T.N. and Hubel, D.H. Single cell responses in the striate cortex of kittens deprived of vision in one eye. Journal of Neurophysiology, 1963, 26, 1003-1017.
- Wiesel, T.N. and Hubel, D.H. Comparison of the effects of unilateral and bilateral eye closure on cortical unit responses in kittens. Journal of Neurophysiology, 1965a, 28, 1029-1040.
- Wiesel, T.N. and Hubel, D.H. Extent of recovery from the effects of visual deprivation in kittens. Journal of Neurophysiology, 1965b, 28, 1060-1072.
- Wilson, P.D. Visual development in rhesus monkeys neonatally deprived of patterned light. Unpublished PhD dissertation, University of Chicago, 1964. Quoted by Tees, R.C. Duration discrimination in the rat after early auditory restriction. Perceptual and Motor Skills, 1967b, 25, 249-255.
- Wilson, P.D. and Riesen, A.H. Visual development in rhesus monkeys neonatally deprived of patterned light. Journal of Comparative and Physiological Psychology, 1966, 61, 87-95.
- Wolf, A. The dynamics of the selective inhibition of specific functions in neurosis. Psychosomatic Medicine, 1943, 5, 227-238.

- Woodruff, A.B. and Slovak, M.L. The effects of severely restricted visual experience on the perception of 'identity'. Psychonomic Science, 1965, 2, 41-42.
- Woodruff, A.B. and Wickens, D.D. The effect of severe restriction of visual experience on form perception in the white rat. American Psychologist, 1951, 6, 281.
- Woods, P.J. The effects of free and restricted environmental experience on problem solving in the rat. Journal of Comparative and Physiological Psychology, 1959, 52, 399-402.
- Zimbardo, P.G. and Montgomery, K.C. Effects of 'free environment' rearing upon exploratory behavior. Psychological Reports, 1957, 3, 589-594.