Early Auditory Deprivation and Visual Behavior

James Colin MacDougall

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Department of Psychology,
McGill University,
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The effect of early auditory deprivation on visual perceptual ability and exploratory behavior was studied. Rats deafened by an ototoxic drug were not different from hearing animals in their ability to learn a brightness and a pattern discrimination. Experiments comparing the performance of congenitally deaf and normally hearing mice raised in both a normal and enriched environment yielded similar results. Deaf mice raised in a normal environment showed a different pattern of exploratory behavior than similarly raised hearing mice when tested at maturity. This difference in exploratory behavior was even more striking when enriched early experience was provided. At two months of age deaf and hearing mice raised in an enriched environment showed no difference in their pattern of exploratory behavior. The results of the experiments on perceptual ability were interpreted as weakening the sensory compensation hypothesis. Also, it was suggested that deaf animals use their intact senses in a unique way to obtain information and stimulation from the environment. The implications of these findings for research with deaf children were discussed.
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Introduction

Recent evidence suggests that basic cognitive processes in deaf children are not essentially different from those of normally hearing children (Furth, 1968). However, on many specific psychological tasks, especially those involving reading and writing, the deaf do show marked deficiencies (Mykelbust, 1960). These deficiencies may be attributable to the relative absence of speech, and to the lack of normal social and educational experience, but there is the possibility that early auditory deprivation has a widespread effect on the development of basic psychological functions. A compelling reason for considering this possibility comes from the well-known research on the deleterious effects of sensory deprivation, especially isolation, on the development of normal intellectual and perceptual capacities (Hebb, 1949; Bexton, Heron, and Scott, 1954). Early deprivation in one sense modality may have not only the well documented effects on later perceptual functioning in the same modality (Riesen, 1961), but may also have an effect on development in other modalities, and perhaps on the way the organism as a whole deals with the environment. The present study is an attempt to explore one aspect of this notion—the effect of early auditory deprivation on visual development.
Evidence is available which indicates that in mature organisms stimulation in one modality can affect perception in the other senses. The Russian investigator Kravkov (1930, 1936) showed that concomitant auditory stimulation has a pronounced effect on both peripheral and foveal vision. He found that a tone of 2,100 cycles per second and 100 decibels greatly diminished light sensitivity for peripheral vision but increased the sensitivity of foveal vision to white light. He also demonstrated that visual acuity could be altered by a concomitant auditory stimulus. Similar effects were reported by Semenovskaia (1946), and Bogoslowski and Kravkov (1941). The theory offered to explain these findings involves the concept of irradiation. Kravkov and his colleagues suggest that excitation in the brain as a result of stimulation of one sense modality is not strictly localized but is transmitted to neurons in other sensory systems because of their anatomical proximity, and consequently, perception in these other modalities is affected.

In another series of experiments Child and Wendt (1938) studied the effect of a flash of light on the auditory threshold. They found that whether the auxiliary stimulus had a facilitating or inhibitory effect depended on
the time interval between the onset of the two stimuli. If the two were simultaneous or the light preceded the tone by a half second the auditory threshold was reliably lowered.

There have been many similar studies done by other Russian investigators and they have been summarized by London (1954). However, Dember (1960), in his review of various perceptual phenomena involving sensory interactions, suggests that the Russian work should be interpreted with caution because of the lack of controls used in their studies and the failure of American investigators to replicate most of the results.

A recent series of experiments reported by Zubec and his associates is relevant to the notion of intersensory effects. Duda and Zubec (1965) found that prolonged visual deprivation led to an increase in auditory sensitivity as measured by critical fusion frequency. Schutte and Zubec (1967) found that subjects who were placed in darkness for a week showed a significant increase in olfactory sensitivity, and an increase in gustatory sensitivity for salty and sweet solutions. Sensitivity to HCl and quinine however were not affected. In all the experiments the changes in sensitivity were relatively long lasting and persisted for several days.
after restoration of normal stimulation. Zubec and his colleagues interpret these intersensory effects as providing some experimental support for the sensoristatic model of the nervous system formulated by Schultz (1965), in which it is postulated that the organism attempts to maintain an optimum range of sensory variation. This maintenance of optimal stimulation is thought to be accomplished by the Reticular Activating System which is known to modulate the sensory activity of the organism (Lindsley, 1961). This regulating system apparently has an adaptation level and when this is disturbed by sensory restriction it changes its level of activity. This notion is consistent with Cohen's (1965) view that afferent stimulation not only provides specific information about the environment but also "sets tonic excitability levels in widespread areas of the nervous system...which then determine the general attitudinal relationship of the entire organism toward its environment".

In general all these studies suggest that, at least in the mature organism, sensory functioning in one sense modality can be influenced by input (or lack of it) in other modalities. It is striking that even a few days of sensory deprivation can produce fairly long term effects. What might
be the effect of prolonged early deprivation in one modality on sensory and perceptual functioning in other modalities?

Another line of research which bears directly on the question of intersensory development has been reported over the past fifteen years by Krech, Rosenzweig, and their associates. In a long series of experiments reviewed by Rosenzweig (1966) these investigators have reported that variations in the complexity of early experience can lead to a change in brain weight and depth, as well as brain chemistry. The basic anatomical finding is that animals who have been raised in a complex environment show about a 5% increase in the weight of total cortex, the greatest weight increase being shown in the occipital region. The analysis of the activity of the enzymes acetylcholinesterase (AChE) and cholinesterase (ChE), both of which act on the transmitter substance acetylcholine, shows that there is a change in enzymatic activity in the cortex as a result of early enrichment of experience. The total cholinesterase activity in both cortex and subcortex of animals who have received enriched experience is about 3% greater than in the animals who have not had enriched experience. Since cortical weight shows a greater increase than does total ChE activity, ChE activity per unit of tissue weight decreases with
enriched experience at the cortex. In the remainder of the brain, since the rise of total ChE activity is not accompanied by a change in weight, specific ChE activity rises when the animal experiences a complex early environment. A corollary finding is that brain weight and biochemical activity (ChE, AChE) in the cortex increases as the degree of early impoverishment decreases.

The aspect of this general line of investigation that is particularly relevant to the present study concerns the finding that if a particular modality, in this case vision, is restricted in early life, there is an increase in weight and chemical activity of the surrounding sensory regions. Rats raised in a complex, but totally dark environment, showed an increase in weight and biochemical activity in the somesthetic areas of the cortex (Rosenzweig et al., 1962). In a similar experiment (Krech, Rosenzweig, and Bennett, 1963) rats were blinded and anatomical and chemical measurements were taken in the visual and somesthetic areas of the cortex. The main findings were an increase in weight and chemical activity in the somesthetic cortex, and surprisingly, a similar increase in chemical activity in the visual region of the cortex. Krech and Rosenzweig interpret this somewhat paradoxical increase in
the visual area as supporting the idea that visual areas in blinded animals participate in non-visual functions. The increase in weight and chemical activity of the somesthetic area was taken to be an indication of sensory compensation due to the presumed greater reliance on somesthetic cues by the blinded animals. In support of this they cite their previous finding that cortical injury in one hemisphere (Krech et al., 1960) results in increased ChE activity in the contralateral hemisphere.

More recently Rosenzweig et al. (1969) have confirmed their earlier results and, in addition, report that increases in cortical measures are independent of age of onset of experience, duration of the experience per day, strain of rat, and sex of the animal. They did report however, that some strains of mice and gerbils did not show the same magnitude of effect in the occipital region, but showed the greatest increases in somesthetic and other areas of the cortex.

Rosenzweig et al. (1969) replicated and extended the experiments which involved enucleation of the eyes and dark rearing. In the case of animals who had their eyes enucleated, they confirmed that brain weight increased as a result of environmental complexity training (ECT) in this group in the
same way as in a sighted group. Total AChE activity was found to be greater in the blinded rats (5.6%). Two experiments which varied the duration of ECT training were also done. In the first, 80 days of ECT were given and it was found that animals with visual experience developed greater weight of occipital cortex than did the dark reared animals. None of the other cortical areas showed a significant light-dark effect, and total cortex was heavier in the light reared animals. AChE activity per unit was significantly greater in both the occipital and total cortex of the dark raised rats than in the light raised litter-mates. In another experiment rats had both ECT and environmental impoverishment (IC) for 30 days in light and dark rearing conditions. The overall difference in occipital cortex between ECT and IC conditions for both light and dark raised groups was significant. Both groups showed significant ECT-IC differences in the weights of the other cortical areas as well. There was also a significant difference between ECT-IC in AChE weight for occipital and total cortex for both groups. However, in regard to ChE weight in occipital cortex, the light raised groups showed a significant effect while the dark raised group did not.

In general then, these results confirm the
earlier findings that blinded animals show increases in cortical measures, even in the visual cortex, as a result of experience.

Further evidence for this general phenomenon is provided by Gyllensten et al. (1965) who studied the effect of dark rearing on development in the optic centres of growing and adult mice. They found that there was a highly significant decrease in relative volume of internuclear material in all visual centres (cortex and subcortex). In the cortex the decrease was most pronounced after two months and became less pronounced during prolonged stay in the darkness, but no similar normalization occurred in the sub-cortical centres. A similar effect was found in terms of thickness of visual cortex and diameter of cell nuclei. Gyllensten et al. (1965) in keeping with Krech et al. (1963) consider that the most likely explanation for this effect is that non-visual functions of the visual cortex increase during visual deprivation.

This group of studies can be interpreted as supporting the thesis that sensory compensation does occur, at least in the specific instance of visual deprivation and an enriched tactual environment. However, it is important to note that Krech, Rosenzweig et al. (1963), and Gyllensten et al. (1965) have not reported any direct behavioral evidence to
support their speculations about the effects of early experience on the brain. In fact, one difficulty with this type of research is that while some indications of the anatomical and biochemical mechanisms which underlie the well documented effects of early varied experience (Hebb, 1949) on later problem solving ability are offered, knowledge of these mechanisms does not seem to lead to any predictions about behavior which would not arise from consideration of the many behavioral studies on this subject. Rosenzweig himself seems to be aware of this when he states in his review article (1966) that "other experiments are being done to determine whether cerebral changes and the changes in ability go together regularly or whether they can be split apart." However, he states further that "...the results have not forced us to abandon our initial hypothesis that changes in the brain endured by experience underlie the changes in learning ability brought about by the experience." One notable exception to this limitation on the research concerns their speculation about sensory compensation. It appears, at least up to now, that their findings have not yet been directly tested on the psychological level. And, in the conclusion of his article Rosenzweig states that a reopening of the historical sensory compensation hypothesis (Donaldson, 1892) now seems
warranted.

The basic work of Rosenzweig et al. (1969) has been extended by MacNeil and Zubec (1967). Their findings however do not support the sensory compensation hypothesis. Two experiments were performed in order to determine whether a compensatory increase in cortical weight after dark rearing can occur in the absence of enriched environmental stimulation. A secondary aim was to determine whether an increase in the weight of the auditory cortex, similar to that observed in the somesthetic cortex, can result from visual deprivation. In the first experiment, two strains of visually deprived rats (hooded and albino), and two strains of sighted controls, were reared for 80 days in an impoverished environment. The main findings were that the visually deprived hooded animals showed no significant changes in the weight of somesthetic, visual, and auditory cortices relative to the sighted controls. The visually deprived albinos, on the other hand, showed a decrease in the weight of somesthetic and auditory cortices. When the animals were raised in an enrichment condition no differences were found between the blind and sighted animals in both strains. There was some suggestion based on a between-experiments comparison that animals exposed to an enriched
environment possessed a heavier sensory cortex than animals reared in an impoverished environment. Also, heavier visual and auditory cortices were found in the enriched animals but not in all subgroups. These latter observations however, involved comparisons between two different groups of animals obtained at different times of the year. If these latter data are disregarded, the major finding of this study is that dark rearing of rats under either an impoverished or enriched sensory environment does not have any effect on the weight of sensory cortex. This is not consistent with the Krech, Rosenzweig et al. (1963) findings, and MacNeil and Zubec offer a number of possible explanations which would account for the discrepancy in results. To begin with, there is the difference in strains used in the two sets of experiments. Also, different operative procedures were used in preparing the specimens for analysis of brain weights, and litter mate controls were not used in the MacNeil and Zubec experiment. Finally, the complex environment in the MacNeil and Zubec study was not as complex as that used by Krech, Rosenzweig et al. in their experiments. Nevertheless, these findings are not consistent with those of Krech, Rosenzweig et al. (1963), or with those of Gyllensten et al. (1965), and they must be interpreted as weakening the
sensory compensation hypothesis.

There is a recent report by Gyllensten et al. (1966) however, which provides strong evidence that sensory interactions do occur in development. Gyllensten et al. (1966) studied morphological alteration in the auditory cortex of visually deprived mice. Some of the mice in their study were raised in darkness for 2-4 months; others were blinded at 8 months. The auditory cortex of the mice was examined at 2 and 4 months of age. At 2 months hypotrophy of the auditory cortex, in terms of volume of inter-nuclear material and nuclear size, was demonstrated. At 4 months hypertrophy in the auditory cortex was shown. The mice which were blinded in adulthood showed only hypertrophy. These findings led Gyllensten et al. to conclude that sensory deprivation does not exclusively affect the primary, directly deafferentiated sensory system, but has a more generalized influence on the whole sensory and motor system. Also, the supragranular and granular layers of the cortex exhibited greater hypertrophy than the infragranular levels. The experimenters offer several interesting hypotheses to explain their findings. Basically they suggest that the initial hypotrophy of the auditory cortex during the first two months of visual deprivation may depend on
partial deafferentiation, due to lack of associative stimuli from the visual cortex. They point out that at least in rats there are associative fibers between the auditory and visual cortex (Krieg, 1947). Also, various studies in rats and cats have shown that visual functions are related to large non-striate fields in the neocortex. In addition to this they quote the study of Wase and Christensen (1960) who reported that visual and auditory deprivation in mice has been shown to result in a decreased turnover of phospholipids in the whole brain. In this connection they also mention the Krech and Rosenzweig studies which, as has already been mentioned, showed that deprivation can lead to generalized effects on the whole brain. They suggest that these general effects are related to the "generalized activating system" which is depressed by sensory deprivation. Thus they postulate that "the initial hypotrophy may depend either on a specific, or on a general, or on a combined lack of afferent stimuli to the cortex during post-natal growth".

A further possible explanation in terms of hormonal changes as a result of visual deprivation is mentioned briefly. They point out that in several animal species functional connections are known to be present between the pituitary gland
and the optic system.

Gyllensten et al. offer two lines of explanation for the hypertrophy in the auditory cortex which is found at 4 months of age in blinded mice. The first suggestion, in keeping with Krech, Rosenzweig et al. (1963) is that the blind animals are required to rely on auditory cues more than sighted animals which results in an overdevelopment of their auditory sensory capacity. In support of this they point out that the supragranular and granular layers, rather than the infragranular layers, exhibited the greater hypertrophy. These superficial layers are thought to be more related to associative and afferent functions in the organism. In their view this strongly suggests that the auditory hypertrophy is compensatory and mediated by motivated training.

The second theory that is postulated suggests that the absence of normal stimulation of the visual cortex causes a lack of morphogenetic inhibition which would under normal circumstances depress the growth of the surrounding areas. They claim that this lack of inhibition would occur at a specific critical period, presumably after two months of age.

It should be noted that Gyllensten et al. do
not report in detail on the nature of the environment of the animals during development. This would be important in the light of the Krech, Rosenzweig et al. (1963) studies which showed that sensory compensation only occurred when visually deprived animals were raised in an enriched environment. If the animals were kept in a normal colony then there is no reason to suspect that the auditory environment would be in any way enriched, especially since the animals were never presented with any problem solving tasks. It is clear from an early study of Rosenzweig et al. (1955) that the rat can in fact echo-locate in a maze, and it could be expected that prolonged exposure to this type of problem especially for blinded animals would lead to some sort of increase in this ability as a result of auditory compensation. It appears however that the animals were not exposed to this type of environment. This fact would argue against an explanation of the Gyllensten effects in terms of compensatory activity, and suggest that one of the other explanations is correct. Further, it may well be that both types of process are occurring--that is, increased auditory ability could arise from both internal processes set off by the lack of visual stimulation and also from increased practice in the non-affected modalities.
The fact that Krech, Rosenzweig et al. (1963) observed anatomical and chemical changes only in an enriched environment condition may reflect a difference between the auditory and somesthesia modalities and their relation to vision, or it may be that the measures taken by Gyllensten et al. are more sensitive. In any case the general point that was made concerning the work on brain weight and chemistry applies to this study on size and density of inter-nuclear material. That is, it is not known what meaning these anatomical observations have on the behavioral level. It may be that changes, even of the magnitude reported by Gyllensten et al., are still not sufficient to produce any appreciable behavioral change on the part of the animal in terms of perceptual ability.

Krech, Rosenzweig et al. (1963), Gyllensten et al. (1966), and others have suggested that sensory compensation in a sensorily deprived animal might result from the animal having to rely more on the non-deprived modalities. If we accept Hebb and Thompson's (1954) notion that an organism seeks to maintain an optimal level of arousal, then it is possible that a sensorily deprived animal would actually engage in more activity, especially exploratory activity, in order to maintain this level of arousal. This conceptualization includes a
built-in mechanism for sensory compensation in that when an animal is deprived of stimulation in a particular modality the level of arousal is altered, and this could cause the animal to explore the environment more with the senses he has available to him. This increased use of the remaining senses may result in a greater perceptual ability in these modalities.

There is little work reported on whether peripheral sensory loss does produce increased exploration. In fact, Glickman (1958) stated that he was the first to study the effect of blindness on exploratory behavior. He tested blind and sighted rats for exploratory activity in the Y maze and the open field. The blind rats were found to engage in a greater amount of exploration than the controls, although this difference only reached significance when the animals had previous experience with one or the other of the test situations. One explanation that Glickman offers to account for the dependence of the effect on prior experience with a maze is that the absence of visual stimulation for 13 days in the blind animals led to a reduction in optimal level of excitation. The subsequent exposure of these animals to a new and highly stimulating environment is then thought of as reinstating an optimal level of excitation more closely approximating that prior to blinding.
In a similar experiment Zucher and Bindra (1961) studied the effect of both enucleation of the eyes and removal of vibrissae on exploration in the rat. In this study attention was paid to age of onset of loss as well as to the time interval between sensory loss and testing. Animals in their "Young-Young" condition were operated on at 23 days and tested at 35 days. In the "Young-Mature" condition the testing took place at 85 days, and in the "Mature-Mature" condition the operation was at 70 days, and the testing at 90 days. The results showed that animals in the "Young-Mature" condition, even in their control group, explored more than animals in the other conditions. This suggested that the effects of blinding were somewhat confounded with the operative procedures or other extraneous factors. For animals that were operated and tested in infancy, neither enucleation nor removal of vibrissae resulted in more activity, but the removal of both simultaneously did produce an effect. Blinding in the "Mature-Mature" condition did produce an increase in exploratory activity. This suggests that a greater sensory loss is required in young animals to produce changes in exploratory activity. This may mean, in terms of the optimal level of stimulation notion discussed by Hebb and Thompson (1954), and Glickman (1958), that
it is only after animals have prolonged experience with the
environment that an optimal level is developed. The loss of
sensory input in one modality in adult animals who have had
normal stimulation up to that time would produce compensatory
exploratory activity, while in animals with congenital sensory
loss a level of arousal appropriate to the amount of stimulation
would develop, so that no compensatory exploratory activity is
noted. This could mean that any perceptual compensation that
is found is due not to an increase in the use of a particular
modality, but to other internal factors such as hormonal
changes, or lack of morphogenetic inhibition (as mentioned by
Gyllensten et al., 1966). However, it is clear that the evidence
on exploration and sensory loss is meagre, and more important,
work on the effect of early auditory loss has not yet been done.

Most of the studies reported thus far support
the notion that prolonged early sensory deprivation can have
an effect on the development of perception in the non-deprived
modalities. There is some direct evidence on this question
from studies of visual perception in the deaf, and auditory and
kinesthetic perception in the blind. The two most famous cases
relevant to the problem of sensory compensation are that of
Laura Bridgman and Helen Keller. Jastrow (1894) reported that
Helen Keller had greater sensitivity in her tactual sense, and G. Stanley Hall (1879) reported sensory compensation in Laura Bridgman. In an early review of the literature on sensitivity in the blind, Hayes (1941) reported that most experiments (Seashore and Ling, 1918) found either insignificant differences between the blind and the sighted, or more interestingly, some evidence was offered which suggested that the sighted were actually more sensitive than the blind (Griesbach, 1899). Plata (1941) reported that there was no difference between blind and sighted for touch and kinesthesia.

In a rather extensive study of the performance of blind and sighted children on tactile and auditory tasks, Axelrod (1959) found that early blinded subjects had lower two point limens on the right index finger than sighted subjects. This he attributed to perceptual learning from practice with braille. On more complex tactile and auditory tasks such as the abstraction of a common characteristic from pairs of objects, early blind subjects were found to be inferior to sighted subjects. This inferiority on complex tasks was interpreted in terms of the importance of early visual learning on later problem solving ability (Hebb, 1949). Axelrod also mentions the possibility that brain damage associated with
blindness could account for this deficit. However, examination
of subjects who were most likely to have brain damage (children
blind due to retrolental fibroplasis), showed that these
subjects performed no worse than the other blind subjects.
In general then, Axelrod found no evidence for simple sensory
compensation per se, but did find that in more complex perceptual
tasks the blind did not perform as well as the sighted subjects.

Evidence on sensory compensation in the deaf
is also somewhat confusing and contradictory. In some aspects
of visual perception the deaf seem to show a deficit, while in
others they equal or sometimes even surpass the hearing in
visual ability. In their extensive study of visual perception
in deaf children Mykelbust and Brutten (1953) found that on
most tests the deaf were inferior while on a few they at least
equalled the performance of the hearing. The deaf could not
reconstruct marble patterns and could not recognize dot patterns
presented for brief intervals as well as hearing children. Also
deaf children were atypical in their ability for bringing
objects or designs into relief from structured backgrounds,
indicating a deficit in the ability to distinguish figure-
ground relations. The authors concluded that lack of intersensory
facilitation or what they call "heteromodal reciprocity" accounts
for this deficit. They point out that this is consistent with Bartley's (1958) discussion of perception which emphasizes the importance of intersensory facilitation in development. In a later series of studies Doehring (1960a, 1960b) subsequently found evidence both for and against the position that deafness affects visual perception. In the first study he found that deaf children used colour as a basis of classification while comparable hearing children used shape cues. He interprets this to mean that the visual development of the deaf child is retarded. However, in another study (Doehring, 1960b), deaf children were shown to be equal to hearing children on a task which involved memory for the location of visual stimuli.

Suchman (1966) replicated Doehring's experiment on colour-form attitude and found that 86% of the hearing and only 33% of the deaf children preferred form, while only 14% of the hearing and 67% of the deaf preferred colour. Also there was a difference in discriminative accuracy scores between the groups. The hearing had higher accuracy scores for form than deaf children and conversely deaf were better than hearing children on colour discrimination. On another task which involved discrimination learning the hearing performance was better than that of the deaf on the form test, while on the
colour learning task both groups were equal. In another related study Costa, Rapin, and Mandel (1964) found that visual reaction time was similar in deaf and hearing children.

The main problem with research which uses human subjects in order to evaluate the effect of deafness on various psychological functions is that it is very difficult to ascribe any effects to the lack of auditory stimulation per se, rather than to limited social, educational, and linguistic experience. It is important to distinguish between these causal factors especially when attempting to formulate an educational program for deaf children. If auditory deprivation does have an effect on the development of various psychological functions, especially visual perception, then this would have to be taken into account in any educational program, particularly when attempting to deal with the reading and writing problems shown by deaf children (Mykelbust, 1960). On the other hand, if the lack of auditory stimulation per se does not affect perceptual or cognitive functions (Furth, 1968), then more attention should be paid to modifying the experiential and speech deficiencies which are common to deaf children.

The purpose of the present study was to investigate the effects of early auditory deprivation on
visual behavior in animals. In animal studies early environment can be closely controlled and linguistic ability is not a relevant factor. The assumption is that evidence based on animal experiments is useful information which can eventually be applied to the problems of deafness in man. The animal studies which have already been reviewed are very provocative on the question of sensory interactions, but the physiological and anatomical findings need to be substantiated by behavioral data. In the present experiments two species of animals were used—the rat and the mouse. The rat was used because a good deal is already known about its visual behavior, and the mouse was used because there is one particular strain (dn/dn) which is congenitally deaf (Deol and Kocher, 1958). The basic experimental procedure was to deafen rats by the administration of an ototoxic drug. Then the deafened rats and the deaf mice were studied on various visual discrimination tasks. Also, the exploratory behavior of deaf mice was studied. Since the weight of the physiological and anatomical evidence suggested that sensory compensation would occur, it was expected that deaf animals would be superior to hearing animals in their ability to perform visual discriminations. Also, it was hypothesized that deaf animals, because of their need for
additional stimulation, would engage in more compensatory exploratory activity than normally hearing animals. Finally, the effect of providing deaf animals with enriched early experience was studied, in order to examine the suggestion of Krech, Rosenzweig et al. (1963) that this type of experience is a necessary prerequisite for sensory compensation to occur.
Method

Before investigating visual discrimination in deaf and hearing rats it was necessary to establish a procedure for deafening animals and evaluating the resulting extent of hearing loss.

Deafening Procedure in Rats. Twenty-five male hooded rats were divided into three groups according to the split-litter method. The first group (n=11) was given 400mg/Kg Kanamycin Sulfate (0.5gm/cc) for twenty days, beginning on the third day after birth. The second group (n=8) was given the same dosage of Tetracycline Phosphate (250mg/cc), and a third group (n=6) was given a comparable amount of Ringer's Solution over the same period. Of the possible ototoxic antibiotics (e.g. Streptomycin, Neomycin) Kanamycin was chosen because it appeared to have the least side effects. The literature on Kanamycin indicates that slight loss of body weight (which returns to normal after cessation of the drug, see Figure 1) and possible vestibular damage in a small percentage of the animals given the drug, are the only adverse side effects (Lundquist and Wersäll, 1966; Weyer, 1966). Tetracycline was chosen as the antibiotic control drug because it is a broad spectrum bacteriostatic antibiotic which is similar to
Fig. 1  Mean weight of rats given Kanamycin, Tetracycline, and Ringer's Solution from day 3 to day 20. At day 21 drug administration was stopped.
Kanamycin except for the ototoxic effect. The literature on Tetracycline indicates that toxicity of any type is rare (Lew and French, 1966). Ringer's Solution (Ringer's Injection U.S.P.) was used as the drug control because it is known to be physiologically neutral. All three solutions were administered by subcutaneous injection. For the first ten days a Hamilton Microlitre Syringe and a 30 gauge needle were used, and for the remaining ten days, a 1cc B-D disposable syringe with a 26 gauge needle was used.

Deafening Procedure in Mice. Since it was possible to obtain congenitally deaf mice no experimental deafening procedure per se was necessary. The mice were bred from genetically standardized dn/dn (deaf) and dn/+ (hearing) animals who were obtained from the Animal Genetics Department, University College, London, England. This particular strain of mouse was first described by Deol and Kocher (1958) and was used in the present study rather than other deaf strains, (df/+, df/df) (Deol, 1956), because of the relative absence of vestibular dysfunction (Deol and Kocher, 1958; Mikaelian et al., 1965). Also, with the appropriate breeding procedure it was possible to obtain both dn/dn and dn/+ animals in the same litter - i.e. if a dn/+ male is bred with a dn/dn female the result should theoretically be 50% dn/+,
and 50% dn/dn, according to the following schedule:

\[
\begin{array}{ccc}
\text{dn} & \text{dn} \\
\text{dn} & \text{dn/dn} & \text{dn/dn} \\
+ & \text{dn/+} & \text{dn/+}
\end{array}
\]

**Audiometric Procedure.** After pilot experimentation with various procedures including an avoidance conditioning technique (Dewson, 1965), and an operant conditioning procedure (Gourevitch and Hack, 1966), it was found that the most appropriate method of audiometric assessment for the present purposes involved the use of the Preyer Reflex (Preyer, 1891). Evidence is already available which suggests that the Preyer Reflex is highly correlated with cochlear function. Herman and Clack (1963) have shown that the reflex is sensitive to both temporary and permanent threshold shifts. Also, Mikaelian and Ruben (1964) found in their study of the development of hearing in mice that the pinna response occurs at the fourteenth day of development when both the cochlear microphonic and eighth nerve potential appear. These findings are consistent with Hoshino's (1928) theory that the afferent origin of the reflex is in the cochlea. This, in combination with the fact that Kanamycin causes progressive destruction of the hair cells of the cochlea (Lundquist and Wersäll, 1966), leads to the
expectation that the presence or absence of the Preyer Reflex in response to various tones should indicate the extent of hearing loss in animals given Kanamycin.

Tones were generated by a Knight GH-688 sine wave generator and were led through an EICO 3070 amplifier. A photo-conductive electronic switch with a 40ms rise time brought the signal to a University 312 speaker. The speaker was mounted in a 2'x 2'x 2' sound treated box with an observation window on the front door. Inside the box there was a 6" x 12" electrified metal grid surrounded by four clear plexiglass walls extending from the grid floor to the chamber roof.

The sound field for each tone was measured by placing the microphone from a General Radio model 1551-C sound level meter in the box in approximately the same position occupied by the rat. Measurements taken in other nearby locations were found to be within ±5db of these readings.

The animal was placed in the box and allowed to explore for 30 seconds. Then a brief mild shock (0.2ma) was delivered to the grid. Immediately after this, the first tone in the series was presented. Twelve different frequencies were given, starting with 20KHz and progressing to 500Hz (see Figure 2). The threshold for each frequency was determined
by the method of descending limits, the first intensity level presented being one which elicited a response 100% of the time in normal animals. The intensity was reduced on each successive trial by one unit of a sixteen unit scale with an arbitrary reference point. The stimulus duration was 0.25 seconds for each tone and the time interval between presentations was approximately 2 seconds, provided the animal remained in the same position from trial to trial. Additional shocks, up to a limit of three, were given if the animal became restless and started to move about in the box. This procedure was continued until the thresholds for each frequency were obtained. The testing time for each animal was approximately 4-5 minutes.

This procedure differs in a number of ways from the procedure reported by Herman and Clack (1963). In their experiments the animals were restrained in a tubular device and no shock or other preparatory stimulation was given.

The purpose of the present procedure, in particular the shock, was to encourage a state of vigilance in the animal so that he was more likely to attend to sounds in the environment. Also, the shock ensured that the animal would remain in one position during the period of testing. The expectation was that
this technique might produce thresholds somewhat more sensitive than those previously obtained with the Preyer Reflex.

One other important difference involves the threshold criterion itself. In most experiments the tones are either presented randomly, or the method of ascending and descending limits is used. These are appropriate procedures when the concern is with the absolute auditory threshold. When the emphasis of the procedure is on quickly establishing a relative difference in responding between deaf and hearing animals, the present procedure of descending limits and non-random assignment of frequencies seems more appropriate and convenient. Also, the presentation of the loudest tones first had the effect, in the same way as the shock, of making the animal more attentive to the subsequent tones.

Results of Audiometric Assessment.

Deafened Rats A summary of the responses of the Kanamycin group is given in Table 1. Two of the eleven animals in this group did not show any pinna reflex to any of the tones presented. No animals in this group responded beyond the 6000Hz level. The finding that some of the deafened animals responded to low frequency sound is consistent with the literature dealing with the effect of Kanamycin on the hair cells of the
Table 1

Incidence of Preyer Reflex in the deafened group (n=11)

<table>
<thead>
<tr>
<th>Sound frequency (in Hertz)</th>
<th>Reflex present</th>
<th>Reflex absent</th>
<th>Sound level (in dB)</th>
</tr>
</thead>
<tbody>
<tr>
<td>500</td>
<td>9</td>
<td>2</td>
<td>105</td>
</tr>
<tr>
<td>1000</td>
<td>7</td>
<td>4</td>
<td>105</td>
</tr>
<tr>
<td>1500</td>
<td>2</td>
<td>9</td>
<td>95</td>
</tr>
<tr>
<td>6000</td>
<td>1</td>
<td>10</td>
<td>105</td>
</tr>
<tr>
<td>all other frequencies</td>
<td>0</td>
<td>11</td>
<td>105</td>
</tr>
</tbody>
</table>
cochlea. Lundquist and Wersäll (1966) showed that the
destruction of cells progressed from the basal to the apical
turn of the cochlea. It was therefore expected that in some
animals the degeneration would not proceed to the apical
turn of the cochlea—the area, according to the place-frequency
theory, which is important for low frequency hearing (von Bekéséy
and Rosenblith, 1965). The progressive nature of hair cell
destruction allows one to assume that the areas of the cochlea
which are important for frequencies higher than those generated
by the standard equipment in this experiment have been effectively
destroyed, so that no hearing at these frequencies remains. It
follows from this that for present purposes it is not necessary
to become involved in the rather complicated procedure of
presenting very high frequency sounds to the animals (rats can
apparently hear up to 100KHz (Crowley, 1965)).

The auditory threshold curves for the Tetracycline
and Ringer's Solution groups appear in Figure 2. There is no
appreciable difference between these two curves indicating
that the antibiotic per se does not affect the Preyer Reflex.
As can be seen in Figure 2 these curves are similar to the one
reported by Herman and Clack (1963) for the 500 to the 8000Hz
frequencies. For the frequencies above 9000Hz the present
curve is more sensitive—the largest threshold difference, 40db, being at 14KHz.

This increased sensitivity in the higher frequency range may be attributable to the particular psychophysical procedure used in this experiment—i.e. the method of descending limits. Also, the strain difference may be a factor. However, part of the increase in sensitivity may be due to the present procedure of making the animal more vigilant to the sound environment through the use of shock. In addition, in the Herman and Clack (1963) situation the animal was physically restrained in a tubular device. This could have disrupted the integrity of the Preyer Reflex as a total adaptive response involving gross body re-orientation, and resulted in a decrease in sensitivity of the reflex.

Deaf Mice A sample audiogram for the 12 dn/+ mice is given in Figure 3. The genetically deaf mice did not show any evidence of hearing ability even to the loudest tones presented (110db).
Fig. 2  Mean auditory thresholds for rats administered Tetracycline and Ringer's Solution, compared to results reported by Herman and Clack (1963).
Fig. 3  Sample auditory threshold curve for dn/+ mouse.
Experiment 1

The purpose of the first experiment was to determine if rats who are experimentally deafened shortly after birth perform a simple visual discrimination differently than rats with normal hearing.

Method

Subjects. The male pups from 6 female hooded rats (Quebec Breeding Farm) were randomly assigned to receive either Kanamycin or Physiological Saline, according to the split-litter method. At 3-4 days of age subcutaneous injections of 400mg/Kg Kanamycin Sulfate (0.5gm/cc) and Physiological Saline were given every day at the same time for 20 successive days. For the first 10 days a Hamilton microlitre syringe with a 30 gauge needle was used, and for the next 10 days a 1cc disposable tuberculin syringe with a 26 gauge needle was used. Each mother and her litter were housed individually in a clear plexiglass cage and fed water and Purina rat chow on an ad-lib schedule.

Apparatus. The visual discrimination apparatus was similar to that used by Smith (1967). The box shown in
Figure 4 had 4 grid floors which could be independently electrified. The grids in areas 1 and 2 delivered 0.85mA of unscrambled shock whereas the grids in areas 3 and 4 delivered only 0.5mA of shock. There were two one-way doors, hinged at the top, which could be selectively locked with a steel rod.

The stimuli, which could be fastened to the doors, were two 4" x 4" cards, one of which was black and the other white. The box was fitted with a plexiglass top, and the lighting consisted of 4 overhead fluorescent lights. The box remained in the same position in the room throughout the testing session.

Procedure. At weaning the animals were separated from the mother and litter-mates were housed in groups of 3-4 animals per cage. From the 10th to the 30th day the animals were tested for hearing ability according to the procedure already described, and only those animals who during this time showed greater than a 100db loss were included in the deaf group. All animals in the saline group showed normal hearing ability. Each animal given Kanamycin was tested for vestibular dysfunction. Three animals were discarded because they did not show a 100db hearing loss, and one animal
was discarded because he showed some slight vestibular
dysfunction. Two animals in the Kanamycin group and three
animals in the saline group died, apparently from respiratory
disease, so that the final number in the Kanamycin group
was five and the number in the saline group was eight.

At 4-5 months of age the animals were taken
from their cages, marked for classification, and subjected
to one day of pretraining in the visual discrimination
apparatus. The animals were placed in the box and allowed
to explore for one minute. Then they were taught to escape
from the electrified area to the goal area. The animal
was shocked every 2 seconds for 1 second if it failed to leave
the start box within 5 seconds. The animal then had 25
seconds to escape from the choice point by either exit.
Both doors remained wide open during this time. If the
animal failed to escape within 25 seconds all areas were
electrified. A 30 second intertrial interval was given
throughout. When the animal made three successful avoidances
(-i.e. without shock) the door of its last exit was barred, and
the grid in front of it was electrified. The trials were
repeated until one correct response was made.

On the following day at the same time, training
began. Both the black and the white cards were put in place and the negative door, in this case the door with the black card, was locked and the entrance to this door was electrified. Shock was given for 1 second every 2 seconds if the animal failed to leave the start box in 5 seconds. A 1 second shock every 10 seconds was given if the animal failed to leave the choice area after 25 seconds.

The response which the animal had to learn was to go consistently to the door with the white stimulus card. Each subject was given 20 trials a day. The position of the correct stimulus card was varied in a fixed order according to Gellerman (1933). If an animal developed a position response, which was defined as five consecutive responses to the same side, that side was blocked until the animal made a correct response, after which the Gellerman series was resumed. A trial was counted as an error if the animal placed two feet in the electrified area in front of the negative stimulus. A position response was not counted as an error. The total number of trials and errors for each subject to reach a criterion of nine out of ten correct responses was recorded.
Results and Discussion

Since there was some doubt about the normality of the distributions of mean trial and error scores, the non-parametric Mann-Whitney U test (Ferguson, 1966, p. 360) was used. There was no significant difference between the groups in terms of number of trials to criterion ($U=11.5; p>.05$) or errors to criterion ($U=9.0; p>.05$). The means for trials and errors to criterion are shown in Table 2. It should be noted that there was a sizable difference between the means for errors, which did reach the .06 level of confidence (one-tailed test). Because of the somewhat small samples it was thought desirable to replicate the experiment to obtain more reliable evidence of any possible difference between the two groups. Also, a replication was desirable in order to control directly for any possible effects of the antibiotic per se.
Fig. 4 Visual discrimination apparatus
Table 2

Mean number of trials and errors to learn black-white discrimination for groups given Kanamycin (n=5) and Physiological Saline (n=8)

<table>
<thead>
<tr>
<th></th>
<th>Kanamycin</th>
<th>Physiological Saline</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trials</td>
<td>50.87</td>
<td>65.60</td>
</tr>
<tr>
<td>Errors</td>
<td>21.12</td>
<td>30.00</td>
</tr>
</tbody>
</table>
Experiment 2

This experiment was a replication of Experiment 1 with an added control for the effect of the antibiotic on the performance of the visual discrimination.

Method

Subjects. The male pups from 6 female hooded rats were used as subjects in this experiment. All animals were subjected to the audiometric procedure described previously from day 10 to day 30, and also at the termination of the visual discrimination task. Only those animals who showed a hearing loss of 100db or greater were included in the deaf group.

Procedure. The procedure was essentially the same as that in Experiment 1 except that, in addition to the group given Kanamycin, there were two further groups, one given Tetracycline, and one given Ringer's Solution according to the method already described in the section dealing with the deafening procedure.

Thirty-four animals were available at the start of the experiment. At the time of testing, age 4-5 months,
there was a total of 21 animals remaining, n=8 in the Kanamycin group, n=7 in the Tetracycline group, and n=6 in the group given Ringer's Solution. One animal in the Kanamycin group was discarded because of vestibular dysfunction, and two animals were not used because they did not show the required degree of hearing loss, and the other animals died, apparently from respiratory disease.

The visual discrimination task was identical to that used in the previous experiment, with some minor modifications in the pretraining procedure. It was found that closing the doors gradually during the initial trials, before one of the doors was locked and the grid in front electrified, facilitated the pretraining procedure. This allowed the animal to become accustomed to pushing the doors open before he received any shock. When the animal successfully pushed one of the doors open from the closed position, the door was locked, and the area in front electrified, so that the animal had to go to the other door to escape. When this response was made without the animal receiving shock the pretraining was ended. The next day the training trials were begun as in the previous experiment.
Results and Discussion

The Kruskal-Wallis one-way analysis of variance for ranks (Ferguson, 1966, p. 362) indicated that there was no difference between mean number of trials to criterion \( (H=1.22; \ df=2; \ p>.05) \) or mean number of errors to criterion \( (H=.02; \ df=2; \ p>.05) \). The appropriate means are shown in Table 3. There is very little difference between both the mean number of trials and mean number of errors for the three groups. Neither deafness, nor the antibiotic, affected the animal's ability to perform a simple visual discrimination. These results confirm the main findings of the first experiment, namely that sensory compensation is not evident in the deaf group.

A comparison of the absolute number of trials and errors to criterion for this experiment and the previous one indicates that the modification in the training procedure used in the second experiment did result in a substantial reduction in these scores (Table 2 and Table 3). This raised the possibility that the difference in scores in the first experiment may have reflected a difference in learning strategies, rather than perceptual skill per se. In the first experiment, the animals spent more trials during the
training period learning how to escape the shock, push the
appropriate door, etc. In the second experiment the animals
had learned these skills during pretraining, and were more
ready to attend to the visual stimuli in the training period.
The possibility that sensorily deprived animals do develop
different learning strategies has already been studied by
Melzack (1968) in dogs. He found that when sensorily deprived
dogs had to learn a reversal problem they adopted very different
strategies, and took longer to learn the problem. In particular,
the dogs perseverated incorrect responses for an abnormal
length of time. In the light of this evidence and the results
of the two experiments reported here, it seemed desirable to
study the performance of deaf animals in a situation which
would directly assess a relevant aspect of problem solving—
specifically, reversal learning.
Table 3

Mean number of trials and errors to learn black-white discrimination for groups given Kanamycin (n=8), Tetracycline (n=7), and Ringer's Solution (n=6)

<table>
<thead>
<tr>
<th></th>
<th>Kanamycin</th>
<th>Tetracycline</th>
<th>Ringer's Solution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trials</td>
<td>39.25</td>
<td>42.10</td>
<td>43.60</td>
</tr>
<tr>
<td>Errors</td>
<td>16.25</td>
<td>19.28</td>
<td>16.50</td>
</tr>
</tbody>
</table>
Experiment 3

The purpose of this experiment was to compare the ability of deaf and hearing animals to perform a reversal learning task.

Method

Subjects. The subjects in this experiment were the same as those used in Experiment 2. However, there were 6 animals in the Kanamycin group, 6 in the Tetracycline group, and 5 in the Ringer's Solution group, due to the death of 4 animals. The animals were 6 months of age at the start of the experiment.

Procedure. Since all the animals had previously been exposed to the apparatus, pretraining was unnecessary. The correct response in this situation consisted of going to the door with the black stimulus card on it, rather than to the door with the white card, as in Experiment 2. Apart from this the procedure was exactly the same as in the second experiment.
Results and Discussion

The mean number of errors and trials to criterion are shown in Table 4. The Kruskal-Wallis one-way analysis of variance for ranks (Ferguson, 1966, p. 362) showed that neither the mean number of errors ($H=.84; df=2; p>.05$) nor trials ($H=2.65; df=2; p>.05$) to criterion were significantly different for the three groups.

Table 5 shows the mean number of position habit errors made by the three groups. The Kruskal-Wallis analysis of variance on these data showed that the difference between groups is not significant ($H=4.02; df=2; p>.05$).

These data then, indicate that deafness does not affect the conceptual ability involved in reversal learning, nor is it particularly associated with persistence of errors.
Table 4

Mean number of trials and errors to learn black-white reversal for groups given Kanamycin (n=6), Tetracycline (n=6), and Ringer's Solution (n=5)

<table>
<thead>
<tr>
<th></th>
<th>Kanamycin</th>
<th>Tetracycline</th>
<th>Ringer's Solution</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trials</td>
<td>82.33</td>
<td>93.33</td>
<td>99.60</td>
</tr>
<tr>
<td>Errors</td>
<td>44.16</td>
<td>51.16</td>
<td>50.20</td>
</tr>
</tbody>
</table>
Table 5

Mean number of position habit responses in black-white reversal learning situation for groups given Kanamycin (n=6), Tetracycline (n=6), and Ringer's Solution (n=5)

<table>
<thead>
<tr>
<th></th>
<th>Kanamycin</th>
<th>Tetracycline</th>
<th>Ringer's Solution</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>27.66</td>
<td>27.50</td>
<td>16.16</td>
</tr>
</tbody>
</table>
Experiment 4

To assess the generality of the findings of the previous experiments, it was desirable to study a different species of animal, and also to study animals who were congenitally deaf, rather than deafened by the action of a drug. The strain of mice described by Deol and Kocher (1958) serves both these purposes.

Method

Subjects. The subjects in this experiment were 11 dn/dn (deaf) and 12 dn/+ (hearing) litter-mates. In the dn/dn group there were 7 females and 4 males and in the dn/+ group there were 4 females and 8 males. Females were used in this experiment to facilitate the formation of groups according to the split-litter method. The males and females were housed in separate plexiglass cages, 3-6 in a cage, and fed on an ad-lib diet of water and Purina chow. Two to three times a week the mice were handled and allowed to run about on the feeding stand for 3-5 minutes. All the animals were tested in the audiometric apparatus from 10 days after birth to 30 days, and were also tested at the
termination of the visual testing period. The dn/+ animals showed normal hearing ability and the dn/dn animals showed no response to any of the tones presented.

Procedure. At 4-5 months of age the animals were tested in the visual discrimination apparatus. The pretraining and training procedures were identical to that used for the rats in Experiment 2.

Results and Discussion

The mean number of errors and trials to criterion are presented in Table 6. The t tests (Winer, 1962, p. 32) for differences between the mean errors (t=.75; df=21; p>.05) and mean number of trials to criterion (t=.07; df=21; p>.05) were not significant. These findings are consistent with those of Experiment 2, and they suggest that deafness in mice does not affect their ability to perform a simple black-white discrimination.
Table 6

Mean number of trials and errors to learn black-white discrimination for deaf (n=11) and hearing (n=12) mice

<table>
<thead>
<tr>
<th></th>
<th>Deaf</th>
<th>Hearing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trials</td>
<td>20.65</td>
<td>24.83</td>
</tr>
<tr>
<td>Errors</td>
<td>5.81</td>
<td>7.00</td>
</tr>
</tbody>
</table>
Experiment 5

All the evidence gathered up to this stage indicated that deafness does not affect black-white discrimination. There remained the possibility that on a more complex perceptual task, differences between deaf and hearing groups would occur. The following experiment on pattern perception was carried out in order to test this possibility. The dwindling population of rats, due to respiratory illness, necessitated that the remaining experiments use mice as subjects.

Method

Subjects. The subjects used in Experiment 4 were also used in this experiment. There were 10 animals in the deaf group and 12 in the hearing group. Testing in the visual apparatus was carried out when the mice were 5-6 months of age.

Procedure. The procedure used was the same as that in Experiment 4 except that the discriminanda in this experiment were vertical and horizontal stripes on cardboard cards (4" x 4"). The cards were equated for black and white area by slightly reducing the width of the vertical stripes.
(this equated them for brightness and luminous flux, Smith, 1967). The positive stimulus in this situation was the vertical striped card.

Results and Discussion

The means are shown in Table 7. The t test (Winer, 1962, p. 32) for differences in mean number of trials to criterion (t=.50; df=20; p>.05) and errors to criterion (t=.80; df=20; p>.05) were not significant. These results indicate that even on more complex perceptual tasks there is no difference between deaf and hearing animals.
Table 7

Mean number of trials and errors to learn pattern discrimination for deaf (n=10) and hearing (n=12) mice

<table>
<thead>
<tr>
<th></th>
<th>Deaf</th>
<th>Hearing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trials</td>
<td>53.11</td>
<td>59.00</td>
</tr>
<tr>
<td>Errors</td>
<td>18.60</td>
<td>23.00</td>
</tr>
</tbody>
</table>
Experiment 6

Since the weight of the evidence thus far did not support the presence of any sensory compensation on the part of deaf animals, it was decided to examine some of the assumptions upon which the hypothesis of compensation is based. Krech et al. (1963) and Gyllensten et al. (1966) suggest that sensorily deprived animals would engage in more exploratory behavior and thus encourage sensory compensation. This notion is consistent with the results described by Glickman (1958), and Zucker and Bindra (1961). The question examined by this experiment is whether or not congenitally deaf mice in fact engage in more exploratory behavior than mice with normal hearing.

Method

Subjects. The subjects from Experiment 5 were used in this study. They were 6-7 months old at the time of testing. There were 10 animals in the deaf group and 12 in the hearing group.

Apparatus. The test apparatus consisted of a wooden box 2' x 2' x 2' with plexiglass walls. The floor of the
box was divided into thirty-six 4" squares. Illumination was provided by 4 overhead fluorescent lights, and the box remained in one position throughout the testing session.

Procedure. All subjects were placed in the apparatus in the same initial position for one three minute trial on three successive days, at the same time each day. The measures taken were those suggested by Glickman (1958); number of squares crossed (walking), number of rears, number of grooms, and number of boluses (amount of defecation). An animal who placed his shoulders and forepaws in a square was considered to have entered it.

Results and Discussion

The means for walking, rearing, grooming, and defecation for the three day period, for deaf and hearing groups, are shown in Table 8. The two-way analyses of variance for unequal n's (Winer, 1962, p. 375) for walking, rearing, grooming, and defecation are shown in Tables 9, 10, 11, and 12 respectively, and graphs plotting these means as a function of days are shown in Figures 5, 6, 7, and 8 respectively.

Walking. The F value (2.44; df=2, 40) for the interaction between groups and days for walking scores was
significant below the .10 level. Inspection of Figure 5 shows that the greatest difference in walking scores between the two groups appeared on day 3. The deaf group showed a drop in mean number of squares crossed on the third day, while the hearing group maintained the same level of performance as on the two previous days. All the other F values in Table 9 did not reach significance.

**Rearing.** Table 10 shows that both days (F=2.46; df=2,40; p < .10), and the interaction of groups with days (F=2.71; df=2,40; p < .10), had some effect on performance. Figure 6 shows that the interaction is due to the constant level of performance over the three days shown by the hearing group, as opposed to the decrease in number of rears on the third day shown by the deaf group. All other F values in this Table did not reach significance.

**Grooming.** The analysis of variance for differences in grooming scores is presented in Table 11. The difference between the deaf and hearing groups is highly significant (F=17.78; df=1,20; p < .001). None of the other F values are significant. Figure 7 presents the mean grooming scores for deaf and hearing groups over the three days of testing. The Scheffé test (Ferguson, 1966, p. 296) for differences between
individual means showed that on all three days the deaf group groomed more than the hearing group \( (p < .01) \).

**Defecation.** Table 12 summarizes the analysis of variance for defecation scores for the two groups. None of the F values reached significance.

The main difference between the groups is evidently in terms of grooming; the deaf mice appear to groom much more than the hearing mice (Figure 7). Also, there appears to be a tendency, significant at the .10 level, for the deaf groups to show a different pattern of rearing over the three days than the hearing group. Finally, the hearing group appears to show more walking than the deaf group, especially on the third day, but the overall difference between walking scores for the two groups is significant only at the .10 level, and should be interpreted with caution.
Table 8

Mean walking, rearing, grooming, and defecation scores for deaf (n=10) and hearing (n=12) mice raised in normal environment. Age of testing—6-7 months; test period—3 minutes per day for 3 successive days

<table>
<thead>
<tr>
<th></th>
<th>Deaf</th>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Day 1</td>
<td>Day 2</td>
<td>Day 3</td>
<td>Day 1</td>
</tr>
<tr>
<td>Walking</td>
<td>54.90</td>
<td>53.60</td>
<td>40.50</td>
<td>52.83</td>
</tr>
<tr>
<td>Rearing</td>
<td>17.30</td>
<td>11.60</td>
<td>8.50</td>
<td>8.66</td>
</tr>
<tr>
<td>Grooming</td>
<td>4.50</td>
<td>3.10</td>
<td>3.20</td>
<td>1.41</td>
</tr>
<tr>
<td>Defecation</td>
<td>2.00</td>
<td>2.40</td>
<td>2.10</td>
<td>2.08</td>
</tr>
</tbody>
</table>
Fig. 5  Mean number of squares crossed for deaf and hearing mice raised in normal environment. Age of testing, 6-7 months.
Fig. 6  Mean number of rears for deaf and hearing mice raised in normal environment. Age of testing, 6-7 months.
Fig. 7  Mean number of grooms for deaf and hearing mice raised in normal environment. Age of testing, 6-7 months.
Fig. 8  Mean number of boluses for deaf and hearing mice raised in normal environment. Age of testing, 6-7 months.
Experiment 7

The results reported thus far indicate that while there is some difference in exploratory behavior between deaf and hearing mice, there is no clear evidence for a difference in perceptual ability. However, there still exists the possibility that the occurrence of sensory compensation is contingent on the experience of an enriched early environment, as suggested by Krech et al. (1963). The animals in the experiments already reported, even though they received repeated handling during development and were allowed to explore on the feeding-stand at various intervals, may in fact constitute a somewhat deprived group, especially if visual stimulation is considered. The object of the present experiment was to provide both deaf and hearing groups with an enriched early environment and to determine the effects of this experience on performance. Previous research (Rosenzweig et al., 1969) has indicated that even fairly short exposure to an enriched environment in early life can lead to changes in brain weight and chemistry. Could enrichment of this type result in sensory compensation?
Method

Subjects. Nine deaf (dn/dn) and nine hearing (dn/+), male litter-mate pairs of mice were used as subjects in this study.

Apparatus. The apparatus consisted of a 2.5' x 2.5' x 2.5' box which was filled with various black and white toys, tunnels, and barriers. One wall of the box was black and the other was white, and on each of these walls stripes of the opposite colour were placed at various angles. The other two walls were natural wood colour. The free environment box had no top, and ordinary room lighting was used.

Procedure. The mice were placed in the enriched environment for 1/2 hour periods on 30 consecutive days following weaning, and after this time were handled in the same way as the animals in Experiments 5 and 6. Nine animals were placed in the box at one time.

At 4-5 months of age the animals were individually tested for their ability to discriminate vertical and horizontal stripes according to the procedure previously described in Experiment 5.
Results and Discussion

The mean number of trials and errors to criterion are presented in Table 13. The t tests for differences between mean number of trials ($t=.56; \text{df}=16; p>.05$) and errors ($t=.80; \text{df}=16; p>.05$) were not significant. There was no difference between the deaf and hearing groups in ability to learn the horizontal-vertical pattern discrimination.
Table 13

Mean number of trials and errors to learn pattern discrimination for deaf (n=9) and hearing (n=9) mice raised in an enriched environment

<table>
<thead>
<tr>
<th></th>
<th>Deaf</th>
<th>Hearing</th>
</tr>
</thead>
<tbody>
<tr>
<td>Trials</td>
<td>51.66</td>
<td>53.77</td>
</tr>
<tr>
<td>Errors</td>
<td>19.55</td>
<td>21.22</td>
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</tbody>
</table>
Experiment 8

In the final experiment an attempt was made to assess the effect of an enriched early environment on the exploratory behavior of deaf and hearing mice. Also, the question of whether exploratory activity would change as a function of age was examined. This latter problem was of interest because of the finding of Gyllensten et al. (1966) that visually deprived mice showed a different type of anatomical growth in the auditory cortex at 2 months of age than was shown at 4 months of age.

Method

Subjects. The mice used in this experiment were the same as those used in Experiment 7. There were 9 animals in the deaf group and 9 animals in the hearing group. The mice were tested at 2 months of age and again at 5-6 months of age.

Procedure. The procedure used to measure exploration was identical to that used in Experiment 6.
Results and Discussion

**Exploration at age 2 months.** The means for walking, rearing, grooming, and defecation are shown in Table 14 and are represented graphically in Figures 9, 10, 11, and 12. The two-way analysis of variance (Winer, 1962, p. 375) for walking scores shown in Table 15 indicated that only the days effect reached significance (F=3.80; df=2,32; p<.05).

Similar analyses of variance for rearing (Table 16), grooming (Table 17), and defecation (Table 18) scores showed that there were no significant (.05 level) differences between the deaf and hearing groups on these measures. These data indicate then, that there are no differences between the deaf and hearing groups in any exploration measures at 2 months of age.

**Exploration at age 5-6 months.** The means for walking, rearing, grooming, and defecation scores for the deaf and hearing groups are shown in Table 19, and are represented graphically in Figures 13, 14, 15, and 16 respectively. The two-way analysis of variance for walking scores (Table 20) showed that there was a significant difference between the two groups in terms of number of squares crossed (F=6.86; df=1,16;
p < .05). All other factors were not significant. Figure 13 shows that the hearing group walked more than the deaf group, especially on days one and two.

Table 21 presents the analysis of variance for rearing scores. None of the F values in this analysis reached significance (p < .05 level). Inspection of Table 19 and Figure 14 shows that, at least on the third day, the deaf group showed substantially more rearing. In fact, the overall difference between groups did reach the .10 level of confidence (F = 3.48; df = 1, 16; p < .10). All other factors were not significant.

The analysis of variance for grooming scores (Table 22) showed a reliable difference between the deaf and hearing groups (F = 8.71; df = 1, 16; p < .05). Also, the days effect (F = 6.49; df = 2, 32; p < .05) and the interaction of days with groups (F = 6.50; df = 2, 32; p < .05) were significant. Figure 15 shows that on all days, especially the third day, the deaf group showed more grooming than the hearing group. The Scheffé test (Ferguson, 1966, p. 296) for differences between means, showed that on the third day the difference between means for the groups was significant (p < .01).

The analysis of variance for defecation scores
is shown in Table 23. This analysis indicated that there were no dependable differences between any of the factors.

To summarize, the analyses presented indicate that the hearing mice show more walking than the deaf mice. On the other hand, the deaf group groom more, and show a tendency to rear more than the hearing group. There were no differences in terms of defecation for the two groups.

These results, and the results of the first part of this experiment, show that there is a difference in exploratory behavior at 5-6 months of age, as opposed to 2 months of age. At 2 months of age there were no apparent differences between groups on any of the exploration measures (see Table 14). Also, providing an enriched environment for the mice in this study yielded results which were generally consistent with the results of Experiment 6 in which no enriched experience was given. In the previous experiment the deaf and hearing groups were not different in terms of walking scores, although there was a tendency for the deaf group to walk less on the third day, whereas in this experiment the hearing group clearly walked more than the deaf group, especially on days one and two. In both experiments the deaf
group groomed more than the hearing group, and there was also a tendency for the deaf groups in both experiments to show a different pattern of rearing than the hearing groups. In both experiments (6 and 8) there was no difference in defecation scores for deaf and hearing groups.
Table 14

Mean walking, rearing, grooming, and defecation scores for deaf (n=9) and hearing (n=9) mice given enriched experience. Age of testing--2 months; test period--3 minutes per day for 3 successive days

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</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Day 1</td>
<td>Day 2</td>
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<tr>
<td>Walking</td>
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<tr>
<td>Rearing</td>
<td>15.66</td>
<td>17.66</td>
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<tr>
<td>Grooming</td>
<td>2.22</td>
<td>2.55</td>
</tr>
<tr>
<td>Defecation</td>
<td>1.55</td>
<td>1.77</td>
</tr>
</tbody>
</table>
Fig. 9  Mean number of squares crossed for deaf and hearing mice raised in enriched environment. Age of testing, 2 months.
Fig. 10  Mean number of rears for deaf and hearing mice raised in enriched environment. Age of testing, 2 months.
Fig. 11 Mean number of grooms for deaf and hearing mice raised in enriched environment. Age of testing, 2 months.
Fig. 12  Mean number of boluses for deaf and hearing mice raised in enriched environment. Age of testing, 2 months.
Table 19

Mean walking, rearing, grooming, and defecation scores for deaf (n=9) and hearing (n=9) mice given enriched experience. Age of testing--5-6 months; test period--3 minutes per day for 3 successive days

<table>
<thead>
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<th>Deaf</th>
<th></th>
<th>Hearing</th>
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<tr>
<td></td>
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<td>Day 2</td>
<td>Day 3</td>
<td></td>
<td>Day 1</td>
<td>Day 2</td>
</tr>
<tr>
<td>Walking</td>
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<tr>
<td>Rearing</td>
<td>8.77</td>
<td>12.11</td>
<td>21.11</td>
<td></td>
<td>8.55</td>
<td>7.66</td>
</tr>
<tr>
<td>Grooming</td>
<td>5.44</td>
<td>6.22</td>
<td>11.44</td>
<td></td>
<td>2.88</td>
<td>2.88</td>
</tr>
<tr>
<td>Defecation</td>
<td>1.88</td>
<td>2.22</td>
<td>2.77</td>
<td></td>
<td>1.22</td>
<td>2.55</td>
</tr>
</tbody>
</table>
Fig. 13  Mean number of squares crossed for deaf and hearing mice raised in enriched environment. Age of testing, 5-6 months.
Fig. 14  Mean number of rears for deaf and hearing mice raised in enriched environment. Age of testing, 5-6 months.
Fig. 15  Mean number of grooms for deaf and hearing mice raised in enriched environment. Age of testing, 5-6 months.
Fig. 16 Mean number of boluses for deaf and hearing mice raised in enriched environment. Age of testing, 5-6 months.
General Discussion

The experiments with deafened rats and with congenitally deaf mice indicate that early auditory deprivation does not affect their visual ability as measured by performance on a simple black-white, and a more complex pattern discrimination task. Also, providing deaf mice with an enriched early environment does not affect their visual perceptual ability. Deaf mice raised in a normal laboratory environment show a different pattern of exploratory behavior than similarly raised hearing mice when tested at five months of age. This difference in exploratory behavior is even more striking when enriched early experience is provided. Deaf mice walk less, but show more grooming, and a marked tendency to rear more than mice with normal hearing ability. However, when tested at two months of age, deaf and hearing mice raised in an enriched environment show no different patterns of exploratory behavior.

The results of the experiments on perceptual ability do not confirm the expectation, based on the studies of Krech et al. (1963), Rosenzweig et al. (1969), and Gyllensten et al. (1966), that animals with sensory loss would show an increase in the ability to perform certain perceptual tasks. The main evidence for sensory compensation offered by Krech,
Rosenzweig, Gyllensten, and associates was based on the observation of anatomical and chemical changes in the visual and somesthetic cortices of animals after early blinding. It is of course possible that the intersensory effects which they observed are specific to vision and somesthesis. In fact, in the Rosenzweig et al. (1969) study with rats and mice the main cortical changes were seen in the somesthetic area. But Gyllensten et al. (1966) in their study, did set the stage for a relation between audition and vision when they observed morphological alterations in the auditory cortex of visually deprived mice. However, they did not report on the effects of auditory deprivation on the visual cortex, and it is possible that different effects occur when the deprivation is in the auditory modality.

In the MacNeil and Zubec (1967) study on the effects of visual deprivation on anatomical growth and chemical activity in the auditory cortex, results were found which are consistent with the findings of the present experiments. They found no evidence of changes in anatomical growth or chemical activity in the auditory cortex after blinding. In spite of the fact that MacNeil and Zubec attribute their lack of confirmation of Krech and Rosenzweig's results to various
methodological considerations, their evidence, in conjunction with the results of the present experiments, seriously weakens the sensory compensation hypothesis. A tentative conclusion is that the anatomical, chemical, and physiological findings reported by Krech, Rosenzweig et al. (1963), Rosenzweig et al. (1969), and Gyllensten et al. (1966) do not reflect changes in perceptual ability, at least for the particular perceptual tasks studied in the present experiments.

The experiments on exploratory behavior reported here are not directly comparable to the work of Glickman (1958). In his study animals were blinded at maturity while in the present study only animals with congenital sensory loss were used. However, Zucker and Bindra (1961) did study the exploratory behavior of animals who were sensorily deprived early in development (age 23 days). They found no difference in exploratory behavior between the deprived and the control groups when the sensory deprivation occurred in infancy and the testing was at maturity. These results are somewhat different from those of Experiment 6 (normal environment condition) of the present report. There was a tendency in Experiment 6 for the hearing animals to walk more and rear less than deaf animals, and there was a clear difference between
groups in grooming behavior. This suggests that for animals raised in a normal environment auditory deprivation has a different effect on exploratory behavior than does visual or tactile deprivation.

Zucker and Bindra (1961) did not study the effect of enriched experience on exploratory behavior, but their "Young-Young" condition in which animals were deprived and tested early in development can be compared to the first part of Experiment 8, in which deaf and hearing animals were tested for exploration at age two months. The deaf animals in Experiment 8 showed no difference from the hearing group in any of the measures taken. This is consistent with Zucker and Bindra's finding that animals who had either their eyes enucleated, or vibrissae removed, were not different from control animals. The animals who had both enucleation and removal of the vibrissae in their experiment, however, showed an increase in walking and rearing. The hypothesis put forward by Zucker and Bindra that deprivation in one modality is not sufficient to produce a change in exploration in infancy is confirmed by the results of the first part of Experiment 8.

When deprivation is in infancy and the testing
at maturity however, the two experiments yield different results. Zucker and Bindra found that blinding or removal of the vibrissae in infancy did not lead to a change in exploratory behavior at maturity. In contrast to this the deaf animals (age 5 months) in the second part of Experiment 8 showed less walking but more grooming and a tendency to rear more than the hearing animals. The difference in findings may be due to the provision of enriched experience in Experiment 8. However, the fact that the deaf animals in Experiment 6 (normal environment conditions) showed the same general behavior pattern suggests that this is not the important factor. Another possibility is that the age of onset of deprivation is the critical variable. In the present experiment the sensory loss was congenital, while in Zucker and Bindra's experiment the deprivation took place at 23 days. The other important difference between the two experiments is the modality of deprivation. It may be that auditory deprivation, especially in conjunction with enriched early experience, leads to a different pattern of exploratory behavior than does visual or tactile deprivation.

When animals walk, they are actively exploring the environment. The primary purpose of this activity may be
to gain olfactory and tactile information about the environment through sniffing and use of the vibrissae. Rearing, on the other hand, appears to be more related to visual exploration of the environment. The significance of the grooming response is somewhat unclear. Obviously the main purpose of grooming is to keep the animal's coat clean, but grooming behavior in a novel environment could be a reflection of level of anxiety. However, the analysis of defecation scores, in which a lack of difference between groups was seen, does not substantiate this interpretation. Another possibility is that animals groom in order to receive tactual stimulation. If this interpretation is correct, the results from the experiments on exploratory behavior suggest that deaf compared to hearing animals engage not only in compensatory visual exploration (rearing), but also display more activity (grooming) which results in increased tactual stimulation. The apparent reduction in walking in deaf animals may not be a reflection of decreased overall exploration, but may indicate that deaf animals engage in a different pattern of exploratory behavior than hearing animals. It should also be remembered that the more time an animal spends grooming and rearing, the less time he has available for walking.

The hypothesis that deaf animals tend to
stimulate themselves more tactually would be consistent with Schultz's (1965) notion that sensorily deprived animals need to receive more stimulation via the unaffected modalities in order to maintain an optimal level of arousal. Increased visual exploration by deaf animals would also be expected on the basis of this theory. It remains unclear however why deaf animals choose grooming and rearing as opposed to walking as a way of obtaining stimulation and information from the environment. Perhaps the information about the environment from sniffing and use of the vibrissae is not as useful to the deaf animal as visual information. Since the deaf animal cannot be alerted by auditory cues in the environment, more time may be spent rearing and engaging in visual search behavior in order to perceive any signs of danger.

In spite of the fact that deaf animals may engage in more visual exploration, the experiments on visual perception indicate that this compensatory activity does not lead to an increase in the ability to make simple and complex visual discriminations, even when enriched early experience is given. This may be attributable to the fact that in the early stages of development (2 months), a time which is critical for the occurrence of perceptual learning, there is
no evidence for compensatory exploratory activity of any type. Also, at 5-6 months of age in both the enrichment (Experiment 8) and non-enrichment (Experiment 6) conditions, the most pronounced difference between the deaf and hearing animals was in terms of grooming. This activity, while it may add to the general arousal level of the organism, could not be expected to result in increased visual perceptual ability.

As far as the case of deafness in children is concerned, the evidence presented (based on animal studies) weakens the suggestion that sensory compensation occurs as a result of auditory deprivation. On the other hand, the present study does not support the view that deafness leads to a deficit in visual perception (Mykelbust and Brutten, 1953; Doehring, 1960a). Also, the theoretical view advanced by Bartley (1958) in which intersensory facilitation is considered to be a necessary prerequisite for normal perceptual development is not supported by the present experiments. A reasonable, if tentative, hypothesis in the light of this evidence is that the reading, writing, and general academic problems shown by deaf children are due mainly to their lack of speech development and to the type of educational and social experience which they
receive, rather than to any deficit in visual perceptual ability or basic cognitive ability. The results of Experiment 3 on reversal learning do present some evidence which is consistent with Furth's (1968) contention that deafness does not alter basic cognitive development.

The findings of the experiments on exploratory behavior suggest that deafness can affect the way a deaf organism deals with the environment. It would be of interest to find out whether such a notion could be confirmed with deaf children. Perhaps deaf children need to receive more tactual stimulation from the environment in order to maintain an optimal level of arousal. Perhaps deafness causes children to use their intact senses in a unique way in order to obtain useful information about the environment. If this is the case, then it would be advantageous to provide the deaf child with an environment which would capitalize on his natural behavior tendencies.
Summary

The effect of early auditory deprivation on visual perceptual ability and exploratory behavior was studied. Rats deafened by an ototoxic drug were not different from hearing animals in their ability to learn a brightness and a pattern discrimination. Experiments comparing the performance of congenitally deaf and normally hearing mice raised in both a normal and enriched environment yielded similar results. Deaf mice raised in a normal environment showed a different pattern of exploratory behavior than similarly raised hearing mice when tested at maturity. This difference in exploratory behavior was even more striking when enriched early experience was provided. At two months of age deaf and hearing mice raised in an enriched environment showed no difference in their pattern of exploratory behavior. The results of the experiments on perceptual ability were interpreted as weakening the sensory compensation hypothesis. Also, it was suggested that deaf animals use their intact senses in a unique way to obtain information and stimulation from the environment. The implications of these findings for research with deaf children were discussed.
Table 9

Analysis of variance for mean walking scores for deaf and hearing mice at 6-7 months of age, raised in a normal environment

<table>
<thead>
<tr>
<th>Source</th>
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<th>F</th>
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<tr>
<td><strong>Between Subjects</strong></td>
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<td>Subj. within groups</td>
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<td><strong>Within Subjects</strong></td>
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<tr>
<td>Conditions (B)</td>
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<td>.06</td>
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<td>A x B</td>
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<td>972.82</td>
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<td>B x Subj. within groups</td>
<td>40</td>
<td>398.36</td>
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</table>
Table 10

Analysis of variance for mean rearing scores for deaf and hearing mice at 6-7 months of age, raised in a normal environment

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>MS</th>
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<td><strong>Between Subjects</strong></td>
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<tr>
<td>Between groups (A)</td>
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<tr>
<td>Subj. within groups</td>
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<td><strong>Within Subjects</strong></td>
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<tr>
<td>Conditions (B)</td>
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<td>A x B</td>
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<td>B x Subj. within groups</td>
<td>40</td>
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</table>
Table 11

Analysis of variance for mean grooming scores for deaf and hearing mice at 6-7 months of age, raised in a normal environment

<table>
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<td><strong>Within Subjects</strong></td>
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<td>Conditions (B)</td>
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<td>A x B</td>
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<td>B x Subj. within groups</td>
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### Table 12

Analysis of variance for mean defecation scores for deaf and hearing mice at 6-7 months of age, raised in a normal environment

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<td>B x Subj. within groups</td>
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Table 15

Analysis of variance for mean walking scores for deaf and hearing mice at 2 months of age, raised in an enriched environment.

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<td><strong>Within Subjects</strong></td>
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<tr>
<td>Conditions (B)</td>
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<td>917.38</td>
<td>3.80</td>
<td>.05</td>
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<td>A x B</td>
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<td>192.46</td>
<td>.79</td>
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<tr>
<td>B x Subj. within groups</td>
<td>32</td>
<td>241.03</td>
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Analysis of variance for mean rearing scores for deaf and hearing mice at 2 months of age, raised in an enriched environment

<table>
<thead>
<tr>
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Table 17

Analysis of variance for mean grooming scores for deaf and hearing mice at 2 months of age, raised in an enriched environment

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Table 18

Analysis of variance for mean defecation scores for deaf and hearing mice at 2 months of age, raised in an enriched environment

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Table 20

Analysis of variance for mean walking scores for deaf and hearing mice at 5-6 months of age, raised in an enriched environment

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Table 21

Analysis of variance for mean rearing scores for deaf and hearing mice at 5-6 months of age, raised in an enriched environment

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Table 22

Analysis of variance for mean grooming scores for deaf and hearing mice at 5–6 months of age, raised in an enriched environment

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Table 23

Analysis of variance for mean defecation scores for deaf and hearing mice at 5-6 months of age, raised in an enriched environment

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