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DIRECTIONAL RESPONSES OF THE YOUNG
GUINEA PIG TO AUDITORY STIMULI

by

Maureen Clements

A thesis submitted to the Faculty of
Graduate Studies in partial fulfilment
of the requirements for the degree of
Doctor of Philosophy

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TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	i
LIST OF TABLES.....	iii
LIST OF FIGURES.....	v
ABSTRACT.....	1
INTRODUCTION.....	3
<u>EXPERIMENT I</u>	17
METHOD.....	17
RESULTS.....	22
<u>EXPERIMENT II</u>	29
METHOD.....	29
RESULTS.....	32
DISCUSSION.....	55
REFERENCES.....	64
APPENDIX A.....	68
APPENDIX B.....	75
APPENDIX C.....	77
APPENDIX D.....	90
GLOSSARY OF COMMON NAMES.....	97

LIST OF TABLES

1. Summary table of analysis of variance for the total number of responses, summed over the 4 testing sessions, made by each of the 3 groups.....	23
2. Summary table of analysis of variance for the total number of responses made by each of the five groups over the twenty one day testing period.....	34
3. Summary table of analysis of variance for number of correct initial responses.....	37
4. Summary table of analysis of variance for percentage of correct initial responses.....	39
5. Summary table of analysis of variance for number of correct responses made to speaker position.....	42
6. Summary table of analysis of variance for percentage of correct responses made to speaker position.....	44
7. Number of animals reaching criterion on the initial response, in each of the 5 conditions.....	45
8. Number of animals reaching criterion on the speaker position response, in each of the 5 conditions.....	46
9. Summary table of analysis of variance for proportion of correct initial responses that were Type 1.....	48
10. Summary table of analysis of variance for proportion of correct responses to the speaker position that were Type 1.....	49
11. Summary table of analysis of variance for initial responses towards or away from the ear block in groups 1-1, 0-1, 1-0.....	50
12. Summary table of analysis of variance for speaker position responses towards or away from the ear block in groups 1-1, 0-1, 1-0.....	51
13. Additional subjects retested three weeks after original testing.....	53

14. Additional subjects that wore ear plugs for 4 days and then were tested for 21 days, starting at day 11	54
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Appendix C

1. Summary table of analysis of variance for low intensity stimuli	85
2. Summary table of analysis of variance for high intensity stimuli	86

Appendix D

1. Mean percentage of total responses that were correct with the standard deviations and t tests for the first and final responses of all conditions	94
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LIST OF FIGURES

1. Frequency analysis of the auditory stimulus and background noise measured with a B and K octave band filter type 1613. x's indicate the sound pressure level with the stimulus on. Circles indicate the sound pressure level with the stimulus off.....	19
2. Sonagram of the auditory stimulus. Three seconds represents one revolution of the taped loop of guinea pig chirps.....	21
3. Mean total number of responses made by each of the 3 groups. The total number possible was 12 for each of the 3 conditions.....	24
4. Mean percentage of correct initial responses made by each of the 3 groups.....	25
5. Mean percentage of correct final responses made by each of the 3 groups.....	27
6. Mean total number of responses made by each of the 5 groups. The total number possible was 84 for each of the conditions.....	33
7. Mean number of correct initial responses made by each of the 5 groups over each block of 7 days.....	35
8. Mean percentage of correct initial responses made by each of the 5 groups over each block of 7 days.....	38
9. Mean number of correct speaker position responses made by each of the 5 groups over each block of 7 days.....	40
10. Mean percentage of correct speaker position responses made by each of the 5 groups over each block of 7 days.....	41
Appendix A	
1. Percentage of startle responses of young guinea pigs to loud hand claps.....	73
2. Percentage of startle responses of adult guinea pigs to loud hand claps.....	74

Appendix B

1. Sound pressure level for a series of pure tones measured with a 2 mm. probe tube inserted into the guinea pigs external meatus. x's show intensity with ear plugs in place. Open circles show intensity with ear plugs removed. Solid line indicates calibrations with the tip of the probe blocked 76

Appendix C

1. Percentage of total possible responses, summed over test sessions, that were approaches or withdrawals to low intensity stimuli for individual subjects 83
2. Percentage of total responses, summed over test sessions, that were approaches or withdrawals to high intensity stimuli for individual subjects 84

Appendix D

1. Total number of each type of first response, summed over subjects and days of testing, for each of the six conditions 93
2. Final response. Total number of final responses summed over days of testing and subjects, for each of the six conditions 95

ABSTRACT

Two experiments investigated 1) the auditory localization ability of young guinea pigs, 2) the effect of varying interaural intensity stimulation on this localization, 3) the effect of varying interaural intensity on subsequent localization. Interaural intensity stimulation was varied by blocking the animals ears with wax plugs. Localization ability was tested in a circular 8 choice apparatus. In the first experiment, 30 guinea pigs were divided into 3 groups as follows; 1) no ears blocked, 2) one ear blocked, 3) both ears blocked. The plugs were inserted 4 - 18 hours post nately. Testing started 4 hours after the ear blocking and continued once daily for 4 days. The results indicated that animals with no ears blocked and those with both ears blocked performed the localization task at above a chance level while those with one ear blocked performed at a chance level. The second experiment consisted of a pretest period of 11 days, during which the animals were raised under various conditions, followed by a test period of 21 days. Forty animals were divided among 5 conditions: 1) no ears blocked during either pretest or test periods (0-0), 2) both ear blocked during both the pretest and test periods (2-2), 3) one ear blocked during the pretest and test periods (1-1), 4) one ear blocked during the pretest period only (1-0), and 5) one ear blocked during the test period only (0-1). Initial ear blocking took place 4-8 hours postnatally and testing started when the animals were 11 days old. The results indicated that the animals in the 0-0 and 2-2 condition performed the localization significantly

better than did those in the 1-1, 1-0, and 0-1 conditions. The animals in the latter 3 conditions performed the task at essentially a chance level. The results were interpreted to mean that the neonate (1 - 4 days) and the juvenile (11 - 21 days) guinea pigs could localize the auditory stimulus though their performance in absolute terms was rather poor. The effect of blocking one ear was to disrupt the localization response in both age groups suggesting that these animals used interaural intensity cues to localize the auditory stimulus. There was no displacement of the directional response while the animals were wearing ear plugs or after the ear plugs were removed. Also in the animals wearing one ear plug there was no improvement in the accuracy of the response. Thus adaptation to the ear plugs and use of other cues by the animals were not evident. Further, when the ear blocks were removed after 11 days the response was still disrupted indicating that experience with normal interaural stimulation is essential for development of the localization response.

INTRODUCTION

The ability to localize the source of a sound is potentially of great value in the natural environment, providing a basis for directional responses even in the absence of visual, olfactory, or other cues. For example nocturnal animals or those whose habitat is in dense foliage may be unable to use visual cues for such functions as maintenance of contact with a species member, avoidance of a predator, or location of prey, and in many instances distance would preclude the use of olfactory cues. For example, an animal that lives in dense foliage, the South American Tapir, has a variety of vocalizations, some of which appear to function to maintain contact with other animals or to warn the others of the presence of a predator (Hunsaker and Hahn, 1965). Tapirs can be induced to approach an imitation of their vocalizations, indicating that they can localize a species member on the basis of auditory cues alone, though the authors suggest that vocalizations may more frequently serve to maintain distance in this solitary species.

Another species in which the call may serve to maintain the distance between members is the chipmunk. Dunford (1970) has suggested that the "chipping" vocalisation of chipmunks may serve to prevent the approach of other chipmunks to the calling one, and so help to maintain the chipmunks social spatial organization. In support of this hypothesis he showed that a recording of the "chipping" call played from near a pile of sunflower seeds, prevented the approach of chipmunks to the

pile of seeds while a similarly played recording of a bird calling did not interfere with an approach to the pile.

Auditory cues may be crucial in maintaining contact between mother and young. Bartholomew and Collias (1962) have suggested that in crowded Elephant Seal colonies, where mother and infant often become separated, they locate each other by means of vocalizations. Both mother and young have specific calls which among other functions apparently serve to inform the one of the position of the other. Thus the mother may approach a calling infant or vice versa, indicating that both mother and infant have the ability to use auditory cues to localize a stimulus. Further, Zepplius and Scheidt (in Noiret, 1969) have shown that mice quickly find and retrieve their young when the latter are emitting ultrasonic sounds but find the young only by chance when they are silent.

Auditory cues from another species member or from a predator may aid an animal to avoid the predator. The vocalizations of the Yellow-bellied Marmot apparently not only served to warn other species members (and even the members of another species, the Pikas) of the presence of a predator but also communicate the position of the predator. Waring (1966) observed that when a strange stimulus approached a colony of these marmots the animal nearest to the stimulus, and only that animal vocalized. When the stimulus moved nearer to another animal this animal now vocalized and the first one remained silent. Thus the observer was able to determine the position of the stimulus by determining the position of the vocalizing marmot and presumably the marmots

could also determine the position of the stimulus in the same manner.

An animal can also use auditory cues from a predator to locate and avoid the predator. Webster and Webster (1971) studied the ability of Kangaroo Rats to use auditory cues to avoid a Side-winder Rattlesnake. These rats have a very large middle ear volume which is correlated with unusually sensitive cochlear microphonic responses between 1000-3000 Hz. Reduction of this volume, by surgical methods, results in reduction of sensitivity to sounds between 1000-3000 Hz, which is the frequency of the prestrike sound of the rattlesnake. The investigators compared the ability of normal rats to avoid the snake, with that of surgically blinded rats, rats with the middle ear volume surgically reduced, rats with both operations, and control operated rats. Only the rats with both blinding and reduction of the middle ear volume were unable to avoid the snake, demonstrating that the rats could use either visual or auditory cues to accurately locate and avoid the predator. The manner in which the rats avoided the snake was first to approach it, then face it obliquely and finally leap backwards. Thus accurate localization and orientation are made first and the avoidance leap is relatively stereotyped. Further studies in which rats with middle ear volume reduced, control operated rats, and normal rats were released into a natural environment, demonstrated that a significant number of the rats with the middle ear volume reduced disappeared from the area. Presumably they were caught by predators of which the side-winder rattlesnake is the chief.

Further the greatest number of disappearances occurred on moonless nights when the rats with the middle ear damage would be unable to compensate by using vision to avoid the predators. These studies demonstrate that the Kangaroo Rat can use auditory cues to avoid a predator and does so under natural conditions.

Auditory cues can also be used to locate a prey. Payne and Drury (1958) demonstrated that the nocturnal Barn Owl could catch a mouse in a barn where all light was excluded. That the owl was using sound, rather than smell or heat, as a cue was demonstrated by the finding that the owl struck equally accurately at a piece of paper pulled across the floor. Further it was shown that when there were no leaves on the floor, and therefore the mouse made no noise, the owl did not strike at all. The technique that the owl used to catch the mouse was to orient to the first sound and strike on the second sound, thus in this case as opposed to that of the Kangaroo Rat, both the orientation and the directional response are accurate. Payne and Drury also demonstrated that the owl was using binaural cues to locate the mouse, since when one ear was stuffed with cotton the owl consistently landed to one side of the mouse and missed it. Payne (1962) suggests that it is most likely that the owl was using binaural intensity cues to localize the mouse since mapping of the response to sound at the eardrum of the owl indicated that if the owl orientated both horizontally and vertically so that all intensities in a complex sound were equal at each ear then the owl would be facing the source of

the sound directly.

Either monaural or binaural cues might be involved in the ability to localize a sound depending on factors such as species differences, stimulus configuration, etc. Studies with humans (Erulkar, 1972) indicated that when head movements are permitted, this species can localize both pure and complex sounds equally accurately both monaurally and binaurally. When head movements were not permitted, however, only complex sounds could be localized monaurally and there was a shift in the perceived position of the sound towards the unoccluded ear. Studies with cats indicated that while these animals could use monaural cues to make a location response when one cochlea had been destroyed (Neff, 1962) their performance was poorer than that of normal animals. Further they could only make an accurate response when a stimulus of relatively long duration was used as the cue and when the animal was free to make head and body movements.

Binaural localization of a sound depends on two stimulus parameters, intensity and time, which can be used as cues. Binaural utilization of intensity cues depends on the differences in intensity of the sound at each cochlea (Δi), due to the shadowing effect of the head. Thus, the sound is more intense at the cochlea nearer to its source. Because this cue depends on the shadowing effect of the head it is most effective at high frequencies.

The second stimulus parameter is the time at which the stimulus arrives at each cochlea. There are two aspects of

time which can be used as cues, one of which is the difference in time of onset of the stimulus at each cochlea. This cue depends for its effectiveness on the distance between the ears, thus, the wider the head is the greater the time difference (Δt) will be between the two cochlea and therefore the more easily discernable the cue. The other aspect of time which can be used as a cue is the difference in phase angle of the stimulus arriving at each cochlea. The utilization of this cue depends on the width of the head in relation to the size of the sound wave; that is to ensure an unambiguous cue the sound wave must be larger than the head. Thus this cue will be most effective at low frequencies, though the specific range of frequencies at which it is most effective will vary with head width (Licklider, 1951; Marler, 1955 & 1959; Masterton et al, 1969).

Three conditions are necessary for the utilization of these binaural cues by an organism. The first is that there must be some structures in the auditory pathways that are binaurally innervated; that is ones which receive an input from both ears. To preserve interaural differences these structures should be as near as possible to the input structures and have a minimum of synapses in the pathways leading to them. The second condition is that the cells of these structures must be able to respond to interaural input differences. The third condition is that the organism must be able to utilize the differential responding of these structures as cues to localize sound in space.

The first structures in the auditory pathways that are bilaterally innervated are some of the superior olivary nuclei. Harrison and Feldman (1970) suggest, for example, from anatomical evidence in the rat that the medial superior olivary nucleus and most probably the lateral trapezoid body nucleus are bilaterally innervated. They also suggest that the lateral superior olivary nucleus is bilaterally innervated via the medial trapezoid body nucleus. These structures are also well developed in species other than the rat, including the guinea pig (Harrison and Irving, 1966; Irving and Harrison, 1967). In addition in various species, for example in kangaroo rats (Stillman, 1971 & 1972), cats (Rosenzweig, 1954, Hind et al, 1963; Brugge et al, 1964, Moushegian et al, 1964a and b; Hall, 1965; Rose et al, 1966; Boudreau and Tsuchitani, 1970) and squirrel monkeys (Starr & Don, 1972), structures higher in the auditory pathways contain neurons which respond differentially to binaural stimulation and provide an anatomical basis for interaction between the ears.

That animals can use interaural differences as cues to make location responses has been demonstrated in studies by Masterson and Diamond (1964), Masterson et al (1966), and Don and Starr (1972). In these studies earphones were used on the animal so that the interaural cues could be varied independently. Masterson and Diamond (1964) and Masterson et al (1966) showed that cats can use Δt as a cue to make an avoidance response and Don and Starr (1972) showed that Squirrel Monkeys can use both Δt and Δi to make a localization response and

that this response generalizes to stimuli located in space. Other studies (Riss, 1959; Neff et al, 1956; Harrison and Beecher, 1969; Neff, 1962), using a sound source located at a distance from the animal, have shown that cats and rats can use the location of this stimulus as a cue for responding, either to approach it directly for food, or to signal or correct a response. Further it has been shown that cats can orient instantly to an auditory stimulus (Riss, 1959; Thompson and Welker, 1963).

Thus it appears that the ability to localize a sound in space has functional value for many species of animals and that the requisites for auditory localization are present in at least the adult members of some species. Few studies, however, have investigated auditory localization ability in the young organism or how this ability develops. Among the studies that have investigated auditory localization ability in the young organism is that of Wertheimer (1961). He observed that a human infant, within ten minutes of birth, made more eye movements towards than away from an auditory stimulus. This suggests that the neonate was able to localize the stimulus, since otherwise an equal number of movements would have been expected in either direction. Turkewitz et al (1966) also investigated the directional eye movements of human neonates in response to an auditory stimulus. They found that two day old babies showed a tendency to make eye movements towards the source of a low intensity stimulus and away from the source of a high intensity stimulus but that the effect was dependent on which ear was

stimulated. Thus, they had to postulate differential sensitivity at each ear to account for the results. Clements (Appendix C & D) demonstrated that neonate guinea pigs approached low intensity stimuli and withdrew from high intensity stimuli indicating an ability to localize an auditory stimulus. Further, the approaches towards a low intensity stimulus were made with a fair degree of accuracy.

Spigelman and Bryden (1967) investigated the development of auditory localization ability in rats. They showed that early blinded rats were more deficient than late blinded rats in localizing an auditory stimulus when tested as adults. They suggested that this deficiency was due to an impairment in organization of perceptual space implying that correlation of audition with vision is necessary for the development of auditory spatial concepts. Aronson and Rosenbloom (1971) demonstrated that in human infants correlation of auditory and visual space occurs as early as thirty days, since infants of this age were distressed when they observed their mothers speak to them from one position while the mother's voice came from another position.

While studies on the development of auditory localization ability are sparse those on the development of visual perceptual ability are plentiful and demonstrate that interaction with the environment is necessary for the development of many perceptual skills. Early studies (Hebb, 1937a & b; Hymovitch, 1952; Reisen, 1949; etc.) have tended to be very general ones in which animals were reared in darkness or blinded and later tested on

a wide variety of tasks, both visual and non-visual. The problem with these studies is that they change many aspects of the animals' environment at once and care needs to be taken in ascribing deficits as due to one or another factor. Once, however, it was demonstrated that experience did in some way influence perceptual ability, studies became more specific in examining the precise nature of this relationship.

A series of studies that demonstrates a very specific relationship between visually guided behaviour and experience is that of Held and Hein (Held and Hein, 1963 & 1964; Held, 1968; Hein and Diamond, 1971). Held and Hein hypothesized that deficiencies in visually guided behaviour, as a result of visual deprivation might be due to a lack of feedback from bodily movement in a patterned environment. Testing this hypothesis they found that kittens moving actively in a patterned environment showed normal visually guided behaviour while those which received passive exposure only, did not show these guided movements. Further, they (Hein and Diamond, 1971) demonstrated that if only one eye was exposed during activity in a patterned environment, only this eye could mediate visually guided behaviour. Also, kittens unable to see their paws while moving in a patterned environment, were unable to do visually guided tasks using their paws. When kittens were only able to view one paw with one eye at a time, the eye that had viewed a particular paw only was able to guide that paw for the behaviour.

The results of these experiments on the role of experience on perception indicate that visual experience is a necessary prerequisite for complex types of visual behaviour. Further, they indicate that experience must be specifically related to the task to be performed.

Some suggestion of the structure underlying visual perception and the way in which it changes with experience appears in a group of physiological studies. Hubel and Wiesel (Hubel, 1967) investigated the effects of deprivation of visual experience on the structure of the visual system of kittens. They showed that shortly after birth the visual system demonstrates considerable organization in that certain cells respond specifically to certain types of stimuli. The most effective type of stimuli for eliciting responses of single cells were rod shaped stimuli, and different orientations of the stimuli elicited responses from different cells. Visual restriction resulted in the loss of this responsiveness and they concluded that experience is required to maintain the organization present shortly after birth (Hubel and Wiesel, 1965 & 1970; Wiesel and Hubel, 1963). Further, they discovered that normal kittens have many cells in the cortex that can be driven by both eyes and showed that if a kitten is reared with one eye occluded the number of cells that can be driven by that eye is greatly reduced. Also kittens reared with an artificial squint or with monocular occlusion of both eyes alternately showed a reduction in the number of cells that could be driven binocularly. Behavioural tests of kittens reared with one eye occluded (Dews

and Wiesel, 1970) indicated that they were deficient in learning a pattern discrimination task with the occluded eye as opposed to the normal eye.

The specificity of the relationship between structure and experience is further demonstrated in some studies by Hirsch and Spinelli (1970), Blakemore and Cooper (1970), and Schlaer (1971). Hirsch and Spinelli (1970) showed that when a kitten was reared with a specific input (horizontal or vertical stripes) to each eye the cells in the cortex driven by a particular eye responded only to the specific stimulation that that eye had experienced. These investigators (Hirsch, 1972) succeeded in reviving some of their cats and after at least two weeks of unrestricted visual experience tested these animals behaviourally. They found small differences in discrimination learning between the two eyes which depended on the relationship between the experiential stimulation and testing stimulation of the two eyes. Further the experimental animals showed less interocular transfer than did the normal animals. However, the experimental animals did show a considerable amount of interocular equivalence. On remapping the cells of two of the animals, Hirsch found that there was some reorganization in the orientation to which the cells responded and particularly there were now a considerable number of cells which could be binocularly driven. Blakemore and Cooper (1970) reared kittens in darkness except for one hour visual experience each day. During this hour the kittens were placed in an environment in which the only patterned stimulation was either horizontal or

vertical stripes. In behavioural testing they found that the kittens orientated only to lines in the orientation which they had experienced and did not appear to see lines in the opposite orientation. Mapping of the orientation of the cells indicated a lack of responsiveness to orientations which the kittens had not experienced. These investigators suggested that the changes in orientation of the cell's responses was due to reorganization rather than degeneration of tissue as they were unable to find any 'silent' areas indicating dead cells. Schlaer (1972) also found a reorganization of cell functioning when he raised kittens with prisms that introduced a vertical disparity in front of their eyes. He found that after several months rearing with these prisms there was an abnormal optical disparity which tended to compensate for the disparity introduced by the prism. Abnormal visual input may also result in abnormal visual functioning in humans. Freeman (1972) found that humans with pronounced astigmatism showed sensitivity differences in resolution of vertical and horizontal grids. He suggests that this effect is a result of abnormal visual input that modifies the neural patterns of the brain in a similar fashion to that found in kittens.

In conclusion, these studies indicate that interaction with the environment is essential for the development of certain types of visual perception, and that this interaction affects both structure and function. It is possible that in a similar manner interaction with the environment is essential for auditory perception, in particular for the development of

auditory localization ability. The purpose of the present studies is to investigate the development of auditory localization ability in young guinea pigs.

Three major questions were asked, (1) How well can young guinea pigs localize an auditory stimulus? Previously it was shown that neonate guinea pigs would approach some stimuli and withdraw from others, in a two choice situation, and that in an eight choice situation they localized an auditory stimulus with a fair degree of accuracy (Appendix C & D). In the present experiments it was proposed to confirm that neonates could localize an auditory stimulus in an eight choice situation and to investigate the localization ability of juvenile guinea pigs. (2) What cues do young guinea pigs use to localize an auditory stimulus? This question was investigated by comparing animals with one ear blocked with those with no ears blocked or with both ears blocked. If binaural cues are utilized to localize an auditory stimulus then guinea pigs with one ear blocked should show an impaired performance on the localization task and there might be a shift in the direction of the response. (3) What after effects does ear blocking have on localization ability? If the development of the auditory system is similar to that of the visual system and experience is important in determining the localization response there should be some change in the animals performance after the ear blocking.

EXPERIMENT I

In the first experiment the auditory localizing ability of neonate guinea pigs and the effects of ear blocking on this ability were investigated.

METHOD

Subjects and Treatments: Thirty young guinea pigs, born to multicoloured females, were randomly assigned to one of three experimental groups; (1) animals with no ears blocked, but wearing a plaster foundation for the ear blocks, (2) animals with both ears blocked, and (3) animals with either the left or right ear blocked. The ear plugs were fashioned out of wax ear plugs designed for human ears. They were inserted into the external meatus in two parts. The inner ear plug consisted of a small cylindrical piece of wax inserted directly into the external meatus. The outer ear plug, a mushroom shaped piece of wax, was then inserted with the stalk into the external meatus and the umbrella covering the entire external ear. Strips of elastoplast held the ear plugs in place (details of the blocking procedures are described in Appendix A). The ears were blocked when the animals were between 4 and 16 hours old and testing was begun 4 hours after the insertion of the ear plugs. At the conclusion of testing the ear plugs were removed and the ears were checked visually for any signs of infection and to see if the ear plugs had remained in place. No signs of infection were found in any of the animals. All the outer ear plugs were in place but the inner ones were fitted loosely into the external meatus.

Apparatus: The testing apparatus consisted of a cylinder 76.2 cms. in diameter and 50.8 cms. high. The wooden floor was divided into 8 equal sections by straight black lines. The walls were made of white Bristol board and lined with fibre glass covered with beige burlap. Eight openings, 12.7 x 12.7 cms., (one in each section) were cut in the walls. Gates of 2.5 cms. wire netting blocked the openings and these gates were fixed in position. A 20.3 cms. speaker, set in a Styrofoam block and covered with dark blue burlap, was positioned behind one of the gates. Seven identical Styrofoam blocks, covered with burlap to resemble the speaker, were placed behind the other gates. The position of the speaker on any one set of trials was randomly determined. A cylindrical wire start box, 22.9 cms. in diameter, was made of 2.5 cms. wire netting and covered with cheese cloth. This was placed in a start area marked in the center of the apparatus and could be raised at the start of a trial by means of a pulley. The entire apparatus could be viewed by an overhead mirror.

Details of stimulus: The auditory stimulus was a tape of young guinea pig chirps made into a continuous loop. The sound pressure level of the stimulus measured, with a 1 in. microphone in the start area was 47.5 db., re 0.0002 dyne/cm², on the A scale of a Brüel and Kjaer 2204 sound level meter. The background noise in the test situation was 30.5 db. A. Since the stimulus was obviously quite complex a further analysis was made to determine the frequency content of the taped chirps. The results of this analysis are shown in Figure 1. As can be seen the stimulus consisted mostly of frequencies between 500 and 2000 Hz. Noise in the test apparatus was mostly at lower frequencies.

Figure 1: Frequency analysis of the auditory stimulus and background noise measured with a B and K octave band filter type 1613. x's indicate the sound pressure level with the stimulus on. Circles indicate the sound pressure level with the stimulus off.

This general conclusion was confirmed by measurements with a Kay Sonagram. The Sonagram also provided a detailed breakdown and temporal analysis of frequency components over the 3 sec. period of each recorded chirp. The results of this analysis are shown in Figure 2. Note the temporal complexity and transient nature of the stimulus.

Procedure: Each of the animals was stroked while being carried to the apparatus in the experimenter's hand. This controlled handling was found previously to be important in getting the approach response. The animal was placed in the start box, the auditory stimulus turned on, and the start box raised. The animal was given 30 secs. to respond, after which it was returned to the home cage and the next subject was tested. This procedure was repeated until all subject had been tested once. The speaker position was then changed and each of the animals was tested again. In this manner each animal was tested three times daily.

On each trial the activity of the animal was scored on data sheets that corresponded to the floor of the apparatus. Several dependent measures were taken. The first was the type of initial response, which was defined as the response which first took the animal out of the start area and into a marked section of the apparatus. The second dependent measure was the final response and was defined as the position of the animal at the end of the 30 sec. testing period. The third measure was the total number of responses and was defined as the total number of trials on which an animal responded over the four days of testing.

On the initial and final responses there were five possible

Figure 2: Sonagram of the auditory stimulus. Three seconds represents one revolution of the taped loop of guinea pig chirps.

types of response, which were related to the position of the speaker. A response taking the animal into the section with the speaker was a type 1 response, a response taking it into the sections on either side of the speaker was a type 2 response. Responses to sections at a 90 degree angle to the speaker were type 3 and those to the next sections were type 4. Responses directly away from the speaker were type 5. The probability of a type 1 or a type 5 response was $1/8$ while that of a type 2, 3, or 4 was $1/4$. For the purpose of analysis, type 1 and type 2 responses were called correct and type 3, 4, and 5 incorrect. Thus the probability of a correct response was $3/8$ and an incorrect one $5/8$.

RESULTS

Total number of responses: Figure 3 shows the mean number of responses made by each of the 3 groups. As can be seen from this figure the group with no ear plugs made more responses than either of the other two groups. The summary table of the analysis of variance is shown in Table 1. The effect of ear blocking was statistically significant and multiple comparison tests, using the Neuman-Keuls procedure, indicated that the group with no ear blocks made more responses than either of the other two groups, and that these two groups did not differ statistically from each other.

Initial response: Because of the difference in over all responsiveness between the groups, accuracy of localization was assessed in the form of percentages. Figure 4 shows the mean percent correct initial responses for each of the 3 groups. Single sample t

Figure 3: Mean total number of responses made by each of the 3 groups. The total number possible was 12 for each of the 3 conditions.

TABLE 1

SUMMARY TABLE OF ANALYSIS OF VARIANCE FOR THE
TOTAL NUMBER OF RESPONSES, SUMMED OVER THE 4
TESTING SESSIONS, MADE BY EACH OF THE 3 GROUPS

Source of Variance	df	MS	F	P
Ear Blocking	2	41.234	3.69	< .05
Error	27	10.404

Figure 4: Mean percentage of correct initial responses made by each of the 3 groups.

tests, comparing the observed versus the expected percentage of correct responses, indicated that both the group with no ears blocked and the group with both ears blocked made significantly greater percentages of correct responses than could have been expected by chance ($t = 4.04$, $p < .01$; $t = 2.79$, $p < .05$ respectively). This indicated that these groups could localise the auditory stimulus. The group with one ear blocked did not differ statistically from chance on this measure, ($t = .25$, $p > .05$) indicating that this group could not localise the stimulus well.

Final response: Again the data were assessed in the form of percentages. Figure 5 shows the mean percent correct final responses made by each of the 3 groups. Single sample t tests indicated that the group with no ear plugs made more correct final responses than could have been expected on a chance basis ($t = 4.24$, $p < .01$) indicating that this group tended to spend more time near the source of the stimulus during the 30 sec. test period. The other two groups did not differ statistically from chance on this measure ($t = 1$, $p > .05$; $t = 1.71$, $p > .05$ respectively), indicating that they did not spend time near the stimulus source.

Type 1 versus type 2 responses: For the two groups with above chance performance it was of additional interest to determine how frequently responses were type 1 as opposed to type 2. This measure permits comparison of the groups with respect to the accuracy of their responses. The mean percentage of type 1 initial responses for the groups with both ears blocked was 35.0% and that for the group with no ears blocked was 31.79%. The results of a t test for the difference between means indicated that these two groups did not differ statistically ($t = 0.3$, $p > .05$).

Figure 5: Mean percentage of correct final responses made by each of the 3 groups.

Thus no differences in accuracy were apparent.

Displacement of response: To determine whether the single ear plug resulted in a displacement of the response in the group with one ear plug, a comparison was made between the number of responses toward and away from the side with the ear plug.

Since any given response could be towards the side with the ear block, away from it, or to a neutral position, responses towards or away from the ear block were statistically independent and were analysed as correlated samples. The mean number of responses towards the ear plug was 3.2 and the mean number away from it was 2.7. A t test for correlated samples failed to indicate any significant difference between these values ($t = 1.22$, $p > .05$). Thus there was no indication of any displacement of the response.

EXPERIMENT II

The results of Experiment I indicated that neonatal guinea pigs can localize a sound and that a single ear plug disrupts their performance. The second experiment investigated the localization ability of juvenile guinea pigs (11 to 31 days) and the effects of ear plugs on their performance. It also investigated the effect of neonatal ear blocking on juvenile performance.

METHOD

Subjects: Forty young guinea pigs, 4 - 8 hours old, were randomly assigned to 1 of 5 treatments. The experiment consisted of a pre-test period of 11 days and a test period of 21 days following the pre-test period. The treatment conditions of one ear blocked or no ears blocked were varied in all possible combinations during these periods. There was also a control group with both ears blocked. The treatment groups were as follows: (0-0) no ears blocked during either pretesting or testing, (1-1) one ear blocked during both pretesting and testing, (1-0) one ear blocked during pretesting only, (0-1) one ear blocked during testing only, (2-2) both ears blocked during both pretesting and testing. The ear plugs and/or the plaster foundation, as described in the previous experiment, were put on the animals at the time that they were assigned to treatment conditions. The plugs were changed every 5 days to ensure that they remained in place, to allow for head growth, and to check for infection. Following testing the external ear canals of the animals were examined with an otoscope for signs of infection. One

1. from the 2-2 condition, was found to have an ear infection at this time and was discarded. It was replaced by the next animal to be born. The animals were reared in opaque polythene cages until day 4, when they were placed, with their mothers, in a nursing pen with other litters. The young animals were weaned on day 6 and placed with other young animals in a pen adjacent to the one in which their mothers were kept. They were placed on water deprivation on day 10, and received one hour of access to water per day following testing. Testing started on day 11. During rearing the animals received cabbage daily.

Four additional conditions were added. Two of these conditions consisted of three subjects from the 0-0 condition and 3 subjects from the 1-0 condition, that had their ear plugs removed at the conclusion of testing. These animals were retested for a period of 2 weeks, 3 weeks after the first testing period ended. The other two conditions consisted of 2 subjects from the one ear plug condition and 2 subjects from the no ear plugs condition of Experiment 1. The one ear plug animals had their ear plugs removed on day 4 and all these animals were tested, starting on day 11, for 3 weeks.

Apparatus: The apparatus was the one used in the previous experiment, with the addition of goal boxes and provision for reinforcement in the form of cabbage. The 8 goal boxes were 18 x 18 x 23 cm. Bristol board boxes, open at one end. The closed end of the boxes was covered with dark blue burlap. The body of the boxes was covered with fibreglass insulation and lined with dark blue terry towelling. A goal box was placed behind each of the gates in the apparatus. These gates could be opened remotely by

a series of pulleys. The auditory stimulus was the recording of chirps used in Experiment 1 and it could be turned on remotely. The speaker was the one used in the previous experiment. The responses of the animals were viewed by means of a television camera and monitored from another room.

Unlike the previous experiment this one involved the use of reinforcement in goal boxes. To avoid the possibility of introducing non-auditory cues associated with smell or sight of the reinforcement all goal boxes were baited in the same fashion and incorrect choices were prevented by locking the goal box gates. Procedure: Starting on day 11 of age each animal received 4 trials per day for 21 days. On each daily session the speaker was placed behind one of the goal boxes and the gate leading to this goal box was unlocked so that it could be raised by the experimenter when the animal reached it. The position of the speaker was determined randomly on any one trial. The animal was placed in the start box and the auditory stimulus was turned on. Five seconds later the start box was raised and the animal was given 60 secs. to make a correct response. If it had not done so in this time it was guided to the correct goal box. The auditory stimulus was turned off 10 secs. after the animal entered the goal box. Each animal remained in the goal box for 60 secs. on days 1 and 2 of testing and 30 secs. on all subsequent days. After this period the animal was returned to the pen. The speaker position was then changed and the next subject was tested. This procedure was repeated until all animals had been tested 4 times.

Dependent measures were total responses and initial responses,

as in the previous experiment, and the speaker position response, determined by the first speaker position that the animal touched. The responses were termed correct or not correct as in the previous experiment. Two measures of performance were used; the number of days to a criterion of 9 out of 12 correct responses over 3 days, and the number of correct trials in each block of 7 days. In addition, for the animals wearing one ear plug it was noted whether the response was towards or away from the side with the ear plug.

RESULTS

Total number of responses: In the previous experiment there was a difference in the total number of responses made by each group so this measure was calculated for the present experiment also to investigate if there was any difference in responsiveness between the groups. The means are shown in Figure 6. As can be seen in this figure there was almost no differences between the groups. The slightly lower score in the 1-0 condition is a function of lack of responsiveness of one subject. Analysis of variance (Table 2) indicated that the effect of treatments was not significant.

Initial response: The number of correct initial responses made by each animal was summed over each block of 7 days and the data was analysed in this form. Figure 7 shows the mean number of correct responses made by each group on each of the seven days. As can be seen from this figure the 0-0 and 2-2 groups made more correct responses than any of the other three groups, the latter of which performed essentially at a chance level. The results of

Figure 6: Mean total number of responses made by each of the 5 groups. The total number possible was 84 for each of the conditions.

TABLE 2

SUMMARY TABLE OF ANALYSIS OF VARIANCE FOR THE TOTAL
NUMBER OF RESPONSES MADE BY EACH OF THE FIVE GROUPS
OVER THE TWENTY ONE DAY TESTING PERIOD

Source of Variance	df	MS	F	P
Ear blocking	4	24.69	.71	ns
Error	35	34.70

Figure 7: Mean number of correct initial responses made by each of the 5 groups over each block of 7 days.

the analysis of variance, with the mean number of correct responses for the main effects of experimental treatment and days are shown in Table 3. As can be seen from this table the main effect of ear blocking was statistically significant. Multiple comparisons on this effect, using Tukey's HSD test, indicated that groups 0-0 and 2-2 made significantly more correct responses than did groups 1-1, 0-1, and 1-0. Group 0-0 did not differ from group 2-2, and groups 1-1, 0-1, and 1-0 did not differ from each other. The main effect of days was also significant indicating that there was an improvement in the number of correct responses over blocks of days. The interaction was not statistically significant.

Since a few subjects did not respond on all trials, the possibility was considered that lack of responsiveness contributed to the differences in correct responses even though the difference in total number of responses was not significant. Therefore, the percentage of the total responses that were correct was calculated for each subject and the data was analysed again in this form. As can be seen from Figure 8 and Table 4 the results are very similar to those in the analysis of the original data. Both main effects are significant and conclusions regarding individual means are the same.

Speaker position response: The number of correct speaker position responses made by each animal was summed over each block of 7 days and the data was analysed in this form. Figure 9 shows the mean number of correct responses made by each group on each of the 7 days. As can be seen from this figure the 0-0 and 2-2 groups made more correct responses than any of the other three

TABLE 3

SUMMARY TABLE OF ANALYSIS OF VARIANCE
FOR NUMBER OF CORRECT INITIAL RESPONSES

Source of Variance	df	MS	F	P
Between Subjects				
Ear blocking	4	225.32	45.14	< .01
Error	35	4.9917		
Within Subjects				
Days	2 (1, 35)*	26.908	4.24	< .02 < .05*
D x EB interaction	8	6.2208	.98	ns
Error	70	6.3488		

* df and P for Geisser-Greenhouse conservative F test.

Figure 3: Mean percentage of correct initial responses made by each of the 5 groups over each block of 7 days.

TABLE 4
SUMMARY TABLE OF ANALYSIS OF VARIANCE FOR
PERCENTAGE OF CORRECT INITIAL RESPONSES

Source of Variance	df	MS	F	P
Between Subjects				
Ear blocking	4	2711.1	54.03	<.01
Error	35	50.182		
Within Subjects				
Days	2 (1, 35)*	378.78	5.00	<.01 <.05*
D x EB interaction	8	69.975	.92	ns
Error	70	75.772		

* df and P for Geisser-Greenhouse conservative F test (Kirk, 1968).

Figure 9: Mean number of correct speaker position responses made by each of the 5 groups over each block of 7 days.

groups, which performed essentially at a chance level. The results of the analysis of variance, with the mean number of correct responses for the main effects of experimental treatment and days are shown in Table 5. As can be seen from this table the main effect of ear blocking was statistically significant. Multiple comparisons on this effect, using Tukey's HSD test, indicated that groups 0-0 and 2-2 made significantly more correct responses than did groups 1-1, 0-1, and 1-0. Group 0-0 did not differ from group 2-2 and groups 1-1, 0-1, and 1-0 did not differ from each other. The main effect of days was also significant indicating that there was an improvement in the number of correct responses over blocks of days. The interaction was not significant.

Again, in case the lack of responsiveness contributed to the differences between the groups the percentage of total responses that were correct was calculated for each subject and the data analysed in this form. As can be seen from Figure 10 and Table 6 the results are very similar to those in the analysis of the original data. Both main effects are significant and conclusions regarding individual means are the same.

Number of subjects reaching criterion: The number of subjects in each of the 5 conditions that reached criterion on the initial response is shown in Table 7 and on the speaker position response in Table 8. As can be seen from these Tables all subjects in the 0-0 and 2-2 conditions reached criterion on both measures indicating that all these subjects could localize the stimulus. In contrast no subjects in the 0-0 or 1-0 conditions reached criterion on either measure. Also only 1 out of 8 subjects in the 1-1

TABLE 5

SUMMARY TABLE OF ANALYSIS OF VARIANCE FOR
NUMBER OF CORRECT RESPONSES MADE TO SPEAKER
POSITION

Source of Variance	df	MS	F	P
Between Subjects				
Ear blocking	4	161.80	23.20	< .01
Error	35	6.9738		
Within Subjects				
Days	2 (1, 35)*	40.408	6.39	< .01 < .05*
D x EB interaction	8	8.6479	1.37	ns
Error	70	12.470		

* df and P for Geisser-Greenhouse conservative F test.

Figure 10: Mean percentage of correct speaker position responses made by each of the 5 groups over each block of 7 days.

TABLE 6
 SUMMARY TABLE OF ANALYSIS OF VARIANCE FOR
 PERCENTAGE OF CORRECT RESPONSES MADE TO
 SPEAKER POSITION

Source of Variance	df	MS	F	P
Between Subjects				
Ear blocking	4	1953.6	23.36	< .01
Error	35	83.618		
Within Subjects				
Days	2 (1, 35)*	499.73	6.27	< .01 < .05*
D x EB interaction	8	99.87	1.25	ns
Error	70	79.709		

* df and P for Geisser-Greenhouse conservative F test.

TABLE 7

NUMBER OF ANIMALS REACHING CRITERION,
ON THE INITIAL RESPONSE, IN
EACH OF THE 5 CONDITIONS

Conditions	Number of Animals Reaching Criterion	Number of Animals Not Reaching Criterion
0-0	8	0
2-2	8	0
1-1	1	7
0-1	0	8
1-0	0	8

TABLE 8

NUMBER OF ANIMALS REACHING CRITERION,
ON THE SPEAKER POSITION RESPONSE, IN EACH
OF THE 5 CONDITIONS

Conditions	Number of Animals Reaching Criterion	Number of Animals Not Reaching Criterion
0-0	8	0
2-2	8	0
1-1	2	6
0-1	0	8
1-0	0	8

condition reached criterion on the initial response. Using the Fisher Test the 1-1 group differs significantly from the 0-0 and the 2-2 groups ($p < .01$) but does not differ from the 0-1 and 1-0 groups. Two out of 8 subjects in the 1-1 group reached criterion on the speaker position responses. Again this differs significantly from the 0-0 and the 2-2 groups ($p < .01$) but not from the 0-1 or 1-0 groups.

Proportion of correct responses that were Type 1: To see if there was any difference in the accuracy in responding between the groups the proportion of correct responses that were Type 1 as opposed to Type 2 was calculated for each subject. Table 9 shows the results of the analysis of variance for the initial response on this measure and Table 10 shows the results for the speaker position responses. As can be seen from these tables none of the main effects of treatment or days or the interaction were significant on either response. These results indicate that there was no detectable difference in accuracy between the groups and that none of the groups improved in accuracy over the treatment period.

Displacement of response: The number of responses made by each subject towards or away from the side with the ear plug was calculated for each subject in the 1-1, 0-1, and 1-0 groups. Since any given response could be towards the side with the ear block, away from it, or to a neutral position, responses towards or away from the ear plug were statistically independent and were analysed as a repeated measure. The results of the analysis of variance for the initial response are shown in Table 11 and for the speaker position response in Table 12. As can be seen from these tables none of the main effects or interaction were stat-

TABLE 9
 SUMMARY TABLE OF ANALYSIS OF VARIANCE FOR
 PROPORTION OF CORRECT INITIAL RESPONSES
 THAT WERE TYPE 1

Source of Variance	df	MS	F	P
Between Subjects				
Ear blocking	4	524.94	2.39	ns
Error	35	219.51		
Within Subjects				
Days	2	287.76	1.44	ns
D x EB interaction	8	129.74	.65	ns
Error	70	199.28		

TABLE 10

SUMMARY TABLE OF ANALYSIS OF VARIANCE FOR
PROPORTION OF CORRECT RESPONSES TO THE
SPEAKER POSITION THAT WERE TYPE 1

Source of Variance	df	MS	F	P
Between Subjects				
Ear blocking	4	230.78	1.00	ns
Error	35	230.71		
Within Subjects				
Days	2	338.41	1.50	ns
D x EB interaction	8	105.77	.47	ns
Error	70	225.92		

TABLE 11

SUMMARY TABLE OF ANALYSIS OF VARIANCE FOR
INITIAL RESPONSES TOWARDS OR AWAY FROM
THE EAR BLOCK IN GROUPS 1-1, 0-1, 1-0

Source of Variance	df	MS	F	P
Between Subjects Groups	2	6.7708	1.09	ns
Error	21	6.2331		
Within Subjects Days	2	5.6875	1.43	ns
G x D interaction	4	2.3333	.59	ns
Error	42	3.9831		
T or A	1	.17361	.02	ns
G x T or A interaction	2	7.1319	.65	ns
Error	21	10.971		
D x T or A interaction	2	38.799	2.49	ns
G x D x T or A interaction	4	10.068	.65	ns
Error	42	15.59		

TABLE 12^s

SUMMARY TABLE OF ANALYSIS OF VARIANCE FOR SPEAKER
 POSITION RESPONSES TOWARDS OR AWAY FROM THE
 EAR BLOCK IN GROUPS 1-1, 0-1, 1-0

Source of Variance	df	MS	F	P
Between Subjects				
Groups	2	10.715	2.17	ns
Error	21	4.9315		
Within Subjects				
Days	2	4.1736	.81	ns
G x D interaction	4	1.2153	.24	ns
Error	42	5.1458		
T or A	1	.17361	.02	ns
G x T or A inter- action	2	9.0486	1.00	ns
Error	21	9.0268		
D x T or A inter- action	2	34.174	2.11	ns
G x D T or A inter- action	4	3.3611	.21	ns
Error	42	16.211		

istically significant. Thus the results show no indication of any displacement of the response in any direction by any of the groups. Also there was no evidence of change on this measure over days.

Additional groups:

Animals retested after 3 weeks: These animals showed some signs of being able to localize sounds. As can be seen from Table 13 all 3 subjects in group 0-0 reached criterion. Also all made at least 16 correct responses on one block of seven days, which is significant at the .05 level, using the chi square test. Thus these animals were still able to do the task when retested after 3 weeks. Two of the 1-0 animals achieved the same level of performance indicating that these 2 subjects could also do the task. The performance of the third animal did not reach statistical significance, but it only falls slightly below this and would possibly have reached it in a few further days of testing. It appears, therefore, that six weeks after the ear plugs were removed two guinea pigs were able to perform the localization task.

Animals with ear blocks from days 1 - 4 and tested from day 11 - 31: Four days of ear blocking failed to produce severe impairment in these animals. As can be seen from Table 14 both subjects in these 2 groups reached the criterion and also reached a performance level of at least 16 correct responses over 7 days. Thus it appears from the evidence that is available that 4 days of ear blocking had no disruptive effect on the auditory localization task.

TABLE 13
 ADDITIONAL SUBJECTS RETESTED THREE
 WEEKS AFTER ORIGINAL TESTING

Subjects		Number of Correct Responses Day 1-7	Responses Day 8-14	Days to Criterion
Group 0-0	s1	11	17	13
	s2	11	17	14
	s3	21	19	3
Group 1-0	s1	13	20	10
	s2	10	15	-
	s3	16	14	6

TABLE 14

ADDITIONAL SUBJECTS THAT WORE EAR PLUGS
FOR 4 DAYS AND THEN WERE TESTED FOR
21 DAYS, STARTING AT DAY 11

Subjects		Number of Correct Responses			Days to Criterion
		day 1-7	day 8-14	day 15-21	
Group 0-0	s1	18	16	17	5
	s2	18	13	20	3
Group 1-0	s1	17	17	14	6
	s2	18	17	15	5

DISCUSSION

Ability to localize

Both the neonate (1 - 4 days) and the juvenile (11 - 31 days) guinea pigs without ear plugs demonstrated their ability to localize an auditory stimulus. Performance levels were well above chance for both age groups. In addition all animals in the juvenile group reached criterion. On the other hand in absolute terms the performance of both the neonates and juveniles was poorer than expected. Typically animals in either age group performed at between a 50% and 60% level when chance was 37.5% and 100% was possible. The performance of the juveniles improved slightly over the 21 days of testing, with the greatest improvement occurring from the first block of seven days to the second. There was no improvement in the precision of the response, however, as evidenced by the lack of increase in the proportion of type 1 to type 2 responses over the testing period. One possible reason for this rather poor performance is that guinea pigs do not have good localizing ability and the 60% level was the limit that they could achieve.

It is possible that the guinea pig in its natural habitat does not need very good auditory localization ability. This animal lives in open grassland, interspersed with thorn bushes (King, 1956; Rood, 1972) in which conspecifics can be localized relatively easily by cues other than auditory ones. Rood (1972) suggested that olfactory and visual cues are most important in location of species members, and though auditory cues may play some part in this he did not observe any overt directional responses to these. Further, though vocalizations may warn conspec-

ifics of danger, the typical response of the guinea pig to such vocalizations is to freeze in an attend posture, rather than to run away from the danger. Thus there may have been no environmental pressure for the guinea pig to develop good auditory localization ability.

On the other hand the reason for the poor localization in this situation may be that the task was a difficult one. For example in the case of the neonates there was no deliberate reinforcement in the test situation. Furthermore in the case of the juveniles there was a low probability of immediate reinforcement. It should be noted here that in our training procedure the probability of a correct response was $3/8$ while the probability of being reinforced immediately was $1/8$. In addition the behaviour of the guinea pigs was stereotyped in a way that led to considerable delay of reinforcement, viz., they would orient to the auditory stimulus in the start box but once this was opened they would leave it in whatever direction they were facing. If this response did not take them to the goal box they would turn in a random direction and try each goal box in turn. Thus while their response might be correct the animal might experience a long delay between a correct response and reinforcement.

Effects of ear blocks

Both the neonate and the juvenile guinea pigs with one ear blocked were unable to localize the auditory stimulus. This finding suggests that the normal guinea pigs were using binaural cues to localize the stimulus and that disruption of these cues led to a disruption of the response. There are three known ways in which the ear plugs could affect binaural cues: (1) by increasing the

time taken for the sound to reach the ear, (2) by excluding sound totally from the ear, and (3) by reducing the intensity of the sound at the ear. It is unlikely the ear plug would appreciably affect the time taken for the sound to reach the ear. Also it would appear that the ear plug did not exclude sound totally from the ear since both the neonate and juvenile guinea pigs with both ears blocked performed at above a chance level. Further, there was no difference in the proportion of correct responses that were type 1 as opposed to type 2 between the groups wearing two ear plugs and those not wearing ear plugs. This indicated that all these animals could localize the stimulus with similar accuracy and that the ear plugs per se did not substantially affect their localization ability. Evidence that the effect of the ear plug was to reduce the intensity of the sound at the ear comes from two observations. First, guinea pigs wearing two ear plugs showed no startle response to a sound which clearly elicited such a response in guinea pigs without ear plugs (Appendix A). Second, measurements of sound pressure level taken with a probe tube positioned inside the meatus indicated a substantial drop when an outer ear plug was fitted securely in place (Appendix B). Thus it is reasonable to believe that the deficient performance of the animals wearing one ear plug was due to disruption of binaural intensity cues and the normal animals were using these cues to localize the stimulus. If other cues such as Δt were available the animals were very inefficient in using them in our test situation.

The result that young guinea pigs, with one ear blocked, were deficient in localizing an auditory stimulus is consistent

with Payne and Drury's (1958) finding that an owl with one ear blocked could not accurately localize an auditory stimulus. Payne (1962) also suggests that the owl normally used binaural intensity cues to localize the stimulus. Furthermore, a recent finding of Don and Starr (1972) indicated that squirrel monkeys could use intensity differences between the two ears (Δi) to localize a stimulus and that the necessary Δi that can be used as a cue need be very small. At a Δi of 2 db. the monkeys performed as though the stimulus was to one side of them, at above a chance level, and at a Δi of 6-10 db. their performance was at an 85% level, when chance was 50%. This is constant with human psychophysical data (Licklider, 1951). Thus it is likely that in guinea pigs the Δi produced by the ear plugs was sufficient to disrupt binaural intensity cues.

That the juvenile guinea pigs, even after 31 days of experience with disparate binaural intensity cues, showed no evidence of ability to localize the auditory stimulus suggests that this species only used intensity cues to localize the stimulus. Thus seemingly, in the absence of normal binaural intensity input these animals are unable to utilize other cues, such as time. On the other hand in a different situation, such as with a stimulus that differed from the present one along such dimensions as frequency, complexity or intensity, a different result might have occurred. For example, Butler and Naunton (1967) showed that humans depended on intensity cues to localize a low intensity auditory stimulus but that they could use other cues, such as time, to localize a high intensity stimulus. Thus, it is possible that had a high intensity stimulus been used in place of the low

intensity one in these experiments no disruption of the response would have occurred. Different cues for social localization are used by humans for high and low frequency stimuli (Licklider, 1951).

It was considered possible that the guinea pigs might attempt to make the intensity of the stimulus equal at each ear by turning the blocked ear towards the sound and, therefore, that their responses might be displaced towards the side without the ear block. Alternately there might be a shift in the perceived position of the stimulus, similar to that shown by humans (Erulkar, 1972) which would also result in displacement of the response towards the side without the ear block. The results, however, did not support this hypothesis in that there was no difference in the number of responses made towards or away from the ear block in either the neonatal or juvenile guinea pigs.

One manner in which disparate intensity cues might affect the localizing response is that the Δ created by the ear plugs, in this situation, was too great to allow any localization of the stimulus however inaccurate. For example, this Δ might result in a sound that had no apparent location, even a displaced one. Under these conditions no consistent displacement of the response would occur as a function of ear blocking. No displacement was seen. Also one would expect a lack of improvement or adaptation of response after prolonged experience with one ear blocked, since there would be no basis for a correlation or correspondence between auditory and visual (or other) spatial cues. In our testing situation there was no evidence of adaptation to the ear plug over 21 days of testing.

To account for the lack of accuracy on the localization task, by the guinea pigs with one ear blocked, the possibility

was considered that motivation or emotional factors were involved. For example it is possible that the reduction of stimulus intensity, occasioned by the ear plugs might account for the performance deficit. That both groups of neonates wearing ear plugs made less total responses and were less accurate on the final response suggests that motivation in these groups was indeed less than in the groups not wearing ear plugs. If, however, the lack of motivation was responsible for the inaccurate initial response of the neonates wearing one ear plug then the animals wearing two ear plugs should have shown a similar lack of accuracy on this response, since the stimulus intensity must have been at least as low, and was probably lower, for these animals. That this latter group of neonates did not show a performance deficit on the initial response suggests that any reduction of motivation did not affect the accuracy of this measure and that the performance deficit of the animals with one ear plug was due to an inability to localize the auditory stimulus. A similar situation occurs with the juvenile guinea pigs. That is if the ear plugs affected motivation then the animals with two ear plugs should be at least as much affected as those with one ear plug. This did not occur. Furthermore since some of the juvenile animals did not respond on all trials one would have expected different results when the data was analysed in its original form and in the form of percentages. Both data analyses gave identical results; i.e., that there was no difference between the groups of animals with no ear plugs and those with two ear plugs, and that the performance of both groups was superior to all the animals that wore one ear plug.

Post blocking effect

The juvenile guinea pigs in the 1-0 condition were unable to perform the localization task even after 21 days of post blocking training, indicating that the disruptive effect of the ear plugs remained for a considerable period after the plugs had been removed. One factor that might have accounted for this was that some obstruction remained in the ears after blocking. Otoscopic examination after testing, however, failed to show any obstruction, although performance was still at a chance level. Another factor to be considered was that lack of experience with normal binaural intensity cues disrupted subsequent ability to use these cues. On the one hand, one might expect that experience with a consistently biased Δi (either left or right) would simply result in a shift of the apparent location of the sound source but that the apparent location would correlate in some fashion with the actual location in space. Under these conditions one might expect to find a shift in the direction of the responses following unilateral ear blocking. However, no such shift was found. A second possibility is that the Δi bias was sufficiently large that the neural correlates of Δi did not provide cues for the identification of any location in space, shifted or otherwise. Under these conditions there would be no basis for a correlation between auditory and other spatial cues and no directional responses could possibly develop. This idea is consistent with what was actually found.

In any case the disruption of directional responding was not permanent. When the 3 animals in the 1-0 condition were

retested after 6 weeks normal binaural experience, 2 animals were clearly capable of localizing the stimulus. It should be noted that these animals were tested daily for the first 3 weeks of this period and during that time showed no improvement in performance. During the second 3 week period the animals were not tested and thus the response could have developed any time during this period. In contrast in the neonate the response was established by 8 hours postnatally. Thus it requires a considerably longer period after ear blocking to establish the response. It is possible that a longer period of wearing the ear plugs would have resulted in a more permanent disruption of the response which even an extended period of normal experience could not have overcome.

The 2 animals that wore ear plugs for only 4 days did not show any disruptive effects. This suggests that the length of time of wearing the ear plugs is an important variable. On the other hand, since the precise time of ear plugging in these animals is not known (the ear plugs were placed somewhere in the 4 to 18 hour post natal period) it is possible that the ear plugs were placed at a later age in these animals. Any such delay could allow time for establishment of the response.

It is of interest to establish if the ear blocking would have a disruptive effect at a later age. In an attempt to do this observations were made of animals with ears blocked from day 11 to day 22. Out of 6 animals, 3 in the 1-0 condition and 3 in the 0-0 condition, however, only 1, in the 1-0 condition, performed the task. It was not possible, therefore, under our conditions to establish if the 1-0 animals showed any disruptive effect of the ear plugs.

Further, it would be of interest to establish if the ear blocks had their effect through disruption of an established response or through prevention of the development of a response. Our evidence on this point is only suggestive. Experiment 1 demonstrated that the localization response is present 8 to 16 hours after birth. It is possible, however, that in such an early developing animal as the guinea pig the localization response is present even earlier than this time, and prior to the placement of the ear plugs in Experiment 2 (4 to 8 hours post nately). That 4 to 8 hours experience with normal stimulation could be sufficient for developing the response is suggested by Blakemore and Mitchell's (1973) study on the visual system. In this study they found that one hour's exposure of visually restricted kittens to patterned visual stimulation was sufficient to modify the neural responses of the visual cortex. On the other hand it is possible that the localization response in our guinea pigs is not present prior to the placement of the ear plugs. Further research is needed to clarify this issue.

Conclusion

In conclusion these experiments demonstrate that both neonate and juvenile guinea pigs can localize an auditory stimulus. The results suggested that binaural intensity cues were used to do this. Further, it was demonstrated that experience with normal auditory stimulation is essential for the development of this response.

REFERENCES

- Aronson, E., and S. Rosenbloom. 1971. Space perception in early infancy: Perception within a common auditory-visual space. Science, 172, 1161-1163.
- Bartholomew, G.A. and H.E. Collias. 1962. The role of vocalizations in the social behaviour of the Northern Elephant Seal. Animal Behaviour, 10, 7-14.
- Blakemore, C. and G.F. Cooper. 1970. Development of the brain depends on the visual environment. Nature, 228, 477-478.
- Blakemore, C. and D.B. Mitchell. 1973. Environmental modification of the visual cortex and the neural basis of learning and memory. Nature, 241, 467-468.
- Boudreau, J.C. and Tsuchitani, C. 1970. Cat superior olive S-segment cell discharge to tonal stimulation. In Contributions to Sensory Physiology. Ed. W.D. Neff. Vol. 4, New York: Academic Press.
- Brugge, J.F., N. Dubrovsky, and J.E. Rose. 1964. Some discharge characteristics of single neurons in cats' auditory cortex. Science, 146, 433-434.
- Butler, R.A. and R.F. Naunton. 1967. The effect of stimulus sensation level on the directional hearing of unilaterally deafened persons. The Journal of Auditory Research, 7, 15-23.
- Dews, D.P. and P.W. Weisel. 1970. Consequences of monocular deprivation on visual behaviour in kittens. Journal of Physiology, 206, 437-455.
- Don, M. and A. Starr. 1972. Lateralization of performance of squirrel monkey (*Sciurus sciurus*) to binaural click signals. Journal of Neurophysiology, 35, 493-500.
- Dunford, G. 1970. Behavioural aspects of spatial organization in the chipmunk, *Tamias striatus*. Behaviour, 36, 215-231.
- Erulkar, S.D. 1972. Comparative aspects of spatial localization of sound. Physiological Reviews, 52, 237-360.
- Freeman, R.D., D.B. Mitchell, and M. Milodot. 1972. A neural effect of partial visual deprivation in humans. Science, 175, 1384-1386.

- Hall, J.L. 1965. Binaural interaction in the accessory superior olivary nucleus of the cat. Journal of the Acoustical Society of America, 37, 814-823.
- Harrison, J.M. and R. Irving. 1966. Visual and non-visual systems in mammals. Science, 154, 738-743.
- Harrison, J.M. and M.D. Beecher. 1969. Control of responding by the location of an auditory stimulus: Role of rise time of the stimulus. Journal of the Experimental Analysis of Behaviour, 12, 217-227.
- Harrison, J.M. and M.L. Feldman. 1970. Anatomical aspects of the cochlear nucleus and superior olivary complex. In Contributions to Sensory Physiology. Ed. W.D. Neff, Vol. 4. New York: Academic Press.
- Hebb, D.O. 1937a. The innate organization of visual activity: I Perception of figures by rats reared in total darkness: Journal of Genetic Psychology, 24, 101-126.
- Hebb, D.O. 1937b. The innate organization of visual activity: II Transfer of response in the discrimination of brightness and size by rats reared in total darkness. Journal of Comparative Psychology, 24, 277-299.
- Hein, A. and R.M. Diamond, 1971. Contrasting development of visually triggered and guided movements in kittens with respect to interocular and interlimb equivalence. Journal of Comparative and Physiological Psychology, 76, 219-224.
- Held, R. 1968. Dissociation of visual functions by deprivation and rearrangement. Psychologische Forschung, 31, 338-348.
- Held, R. and A. Hein. 1963. Movement, induced stimulation in the development of visually guided behaviour. Journal of Comparative and Physiological Psychology, 56, 872-876.
- Held, R. and A. Hein. 1964. On the modifiability of form perception. In models for the Perception of Speech and Visual Form. Eds. Walther-Dunn, Cambridge M.I.T. press.
- Hind, J.E., J.M. Goldberg, D.D. Greenwood, and J.E. Rose. 1963. Some discharge characteristics of simple neurons in the inferior colliculus of the cat: II Timing of discharges and observations on binaural stimulation. Journal of Neurophysiology, 26, 77-86.
- Hirsch, H.V.B. 1972. Visual perception in cats after environmental surgery. Experimental Brain Research, 15, 405-423.
- Hirsch, H.V.B. and D.N. Spinelli. 1970. Visual experience -- modifies distribution of horizontally and vertically orientated receptive fields in cats. Science, 168, 869-871.

- Hubel, D.H. 1967. Effects of distortion on sensory input on the visual system of kittens. The Physiologist, 17-45.
- Hubel, D.H. and T.M. Weisel. 1965. Binocular interaction in the striate cortex of kittens reared with an artificial squint. Journal of Neurophysiology, 28, 1041-1059.
- Hubel, D.H. and T.M. Weisel. 1970. The period of susceptibility to the physiological effects of unilateral eye closure in kittens. Journal of Physiology, 202, 419-436.
- Hunsaker, D. and T.C. Hahn. 1965. Vocalization of the South American Tapir, Tapirus terrestris. Animal Behaviour, 13, 69-74.
- Hymovitch, B. 1952. The effects of environmental variations on problem solving in rats. Journal of Comparative and Physiological Psychology, 54, 313-321.
- Irving, R. and J.M. Harrison. 1967. The superior olivary complex and audition: A comparative study. Journal of Comparative Neurology, 130, 77-86.
- King, J.A. 1956. Social relations of the domestic guinea pig living under semi-natural conditions. Ecology, 37, 221-228.
- Kirk, R.E., 1968. Experimental design: Procedures for the behavioural sciences. Brooks/Cole Pub. Co., California.
- Licklider, J.C.R. 1951. Basis correlates of the auditory stimulus. In Handbook of Experimental Psychology. Ed. S.S. Stevens, New York: John Wiley & Sons, Inc.
- Marler, P. 1955. Characteristics of some animal calls, Nature, 176, 6-8.
- Marler, P. 1959. Developments in the study of animal communications. In Darwin's Biological Work, Ed. P.R. Bell, Cambridge: Cambridge University Press.
- Masterson, R.B. and I.T. Diamond. 1964. Effects of auditory cortex ablation on discrimination of small binaural time differences. Journal of Neurophysiology, 27, 15-36.
- Masterson, R.B., J.A. Jane, and I.T. Diamond. 1966. Role of brainstem auditory structures in sound localisation: I Trapezoid body, superior olive, and lateral lemniscus. Journal of Neurophysiology, 30, 341-259.
- Masterson, R.B., H. Heffner, and R. Ravizza. 1969. The evolution of human hearing. Journal of the Acoustical Society of America, 45, 966-985.
- Moushegian, G., A. Rupert, and M.A. Whitcomb. 1964a. Brainstem neuronal response patterns to monaural and binaural tones. Journal of Neurophysiology, 27, 1174-1191.

- Moushegian, G., A. Rupert, and M.A. Whitcomb. 1964b. Medial superior-olivary-unit response patterns to monaural and binaural clicks. Journal of the Acoustical Society of America, 36, 196-202.
- Neff, W. 1962. Neural structures concerned in localization of sound in space. Psychologische Beiträge, 6, 492-500.
- Neff, W., J.F. Fisher, I.T. Diamond, and M. Yela. 1956. Role of auditory cortex in discrimination requiring localization of sound in space. Journal of Neurophysiology, 19, 500-512.
- Noiret, E. 1969. Ultra sonic distress calls of mouse pups as function of their age. Animal Behaviour, 17, 340-349.
- Payne, R.S. 1962. How the barn owl locates prey by hearing. In: The Living Bird: First Annual of the Cornell Laboratory of Ornithology. Ithaca, New York: Cornell University Press, 151-159.
- Payne, R.S., and W.H. Drury. 1958. Marksman of the darkness. Natural History, 67, 316-323.
- Riesen, A.H. 1949. The development of visual perception in man and chimpanzee. Science, 106, 107-108.
- Riss, W. 1959. Effect of bilateral temporal cortical ablation on discrimination of sound direction. Journal of Neurophysiology, 22, 374-384.
- Rood, J.P. 1972. Ecological and behavioural comparisons of three genera of Argentine caviés. Animal Behaviour Monographs, 5, Part 1.
- Rose, J.E., N.B. Gross, C.D. Geisler, and J.E. Hind. 1966. Some neural mechanisms in the inferior colliculus of the cat which may be relevant to localization of a sound source. Journal of Neurophysiology, 29, 288-314.
- Rosenzweig, M.R. 1954. Cortical correlates of auditory localization and of related perceptual phenomena. Journal of Comparative and Physiological Psychology, 47, 269-273.
- Shlaer, R. 1971. Shift in binocular disparity causes compensatory change in the cortical structure of kittens. Science, 173, 638-641.
- Spigelman, M.N., and M.P. Bryden. 1967. Effects of early and late blindness on auditory spatial learning in the rat. Neuro-Psychologica, 5, 267-274.
- Starr, A., and L. Don. 1972. Responses of Squirrel Monkey (Samiri sciureus) medial geniculate units to binaural click stimuli. Journal of Neurophysiology, 35, 501-517.

- Stillman, R.D. 1971. Characteristic delay neurons in the inferior colliculus of the Kangaroo Rat. Experimental Neurology, 32, 404-412.
- Stillman, R.D. 1972. Responses to high-frequency inferior colliculus neurons to interaural intensity differences. Experimental Neurology, 36, 118-126.
- Tees, R.C. 1968. Effects of early auditory restriction in the rat on adult pattern discrimination. Journal of Comparative and Physiological Psychology, 63, 389-393.
- Thompson, R.F., and W.I. Welker. 1963. Role of auditory cortex in reflex head orientation by cats to auditory stimuli. Journal of Comparative and Physiological Psychology, 56, 996-1002.
- Turkewitz, G., H.G. Birch, T. Moreau, L. Levy, and A.C. Cornwell. 1966. Effect of intensity of auditory stimulation on directional eye movements in the human neonate. Animal Behaviour, 14, 93-101.
- Waring, G.H. 1966. Sounds and communications of the Yellow-Bellied Marmot (Marmota flaviventris). Animal Behaviour, 14, 177-183.
- Webster, D.B., and M. Webster. 1971. Adaptive value of hearing and vision in kangaroo rat predator avoidance. Brain, Behaviour and Evolution, 4, 310-322.
- Wertheimer, M. 1961. Psychomotor co-ordination of auditory and visual space at birth. Science, 134, 1692.
- Wiesel, T.N., and D.H. Hubel. 1963. Comparison of the effects of unilateral and bilateral eye closure on cortical unit responses in kittens. Journal of Neurophysiology, 26, 1003-1017.

APPENDIX A

. A technique for blocking the ears of guinea pigs.

The purpose of the present experiment was to determine if the described technique of ear blocking was an effective method for excluding sound from, or at least attenuating it at, the ears of guinea pigs.

METHOD

Subjects: The subjects were two young and two adult guinea pigs. The two young multicoloured guinea pigs were born in the laboratory to females obtained pregnant from High Oaks Ranch, Goodrich, Ontario. The young experimental subject, which had both ears blocked, was three days old at the start of testing and the control subject, which did not have either ear blocked, was five days old. The two albino males were obtained from the same source as the females and were approximately three months old. One was an experimental subject with both ears blocked and the other a control without either ear blocked.

Apparatus and Procedure:

Ear blocking: The hair was clipped short on the heads of the two experimental animals. An elastoplast foundation was then put in place so that the elastoplast retaining the ear plugs in place could be stuck to it. Thus the latter plaster could be removed and the ear plugs changed relatively easily. The foundation was put in place as follows: A half in. strip of plaster was placed parallel to the body, from half way between the nose and the top of the head to the neck. Another piece of plaster, one half in. wide, was placed under the throat from below one ear to

to below the other ear. These were then held in place with diagonal strips, quarter in. wide in the case of the young guinea pig and one third in. for the adult. The diagonal strips went completely around the head, going in front of one ear and behind the other ear. Two further strips, one quarter in. and one third in. wide for the infant and adult respectively, went around the head on top of the diagonal strips, one in front of the ears and one behind the ears. This completed the plaster foundation.

The ear plugs were put in place in two stages. First a small piece of a human wax ear plug, about one eighth in. in diameter for the infant and a little larger for the adult, was molded into a long narrow strip. The end of this was placed in the ear canal and the projecting end was molded flat to cover the opening of the canal, with a Q-tip. This was done for both ears. Next the outer ear plug was put in place. This consisted of half of a human ear plug for the infants and a whole one for the adults. The wax was molded into a mushroom shape, with a short stalk. The stalk was placed in the outer ear so that the umbrella part covered the entire ear. A piece of surgical gauze was placed over it and then a half in. wide piece of plaster was placed over the gauze, going from the top of the head to under the throat. This procedure was repeated for the second ear. A strip of plaster half in. for the infants and one in. for the adults, was placed along the top of the head. The ear plugs, gauze, and plaster were then held in place by more strips of plaster placed identically to the last four strips in the foundation.

Testing: The experimental animals, with or without ear plugs and the control animals without the ear plugs were placed each

in a separate polythene box on top of a table. The experimenter then clapped her hands as loudly as possible under the table and observed the subjects for a startle response. Responses were counted as startle responses if the guinea pigs emitted a slight twitch of the body. The times of testing, conditions of testing and the results are seen in Figures 1 and 2.

RESULTS

As can be seen from Figures 1 and 2, on no occasion did the experimental animals exhibit a startle response while wearing ear plugs, and they always exhibited such a response while not wearing ear plugs. The adult control always exhibited a startle response while the young one exhibited this response until the evening of day three. On the morning of day four this animal appeared to be dying so it was not tested. In the evening of this day it was dead. No reason was found for its death. No trace of infection or irritation was found in either of the subjects, either as a function of the ear plugs or the plaster.

DISCUSSION

It would appear from the results that this technique of ear blocking is effective at least in attenuating sound at the ear, to the extent that animals wearing ear plugs never exhibited a startle response. That this was not due to habituation was demonstrated by the fact that the control animals always exhibited such a response and also by the fact that the experimental animals exhibited such a response when they were not wearing ear plugs. There appeared to be no ill effects of either the ear plugs or the plaster as the ears and skin of both animals ap-

peared to be healthy when the ear plugs and plaster were removed.

* control subject ill. Dead on evening of day 4.

Figure 1. Percentage of startle responses of young guinea pigs to loud hand claps.

Figure 2. Percentage of startle responses of adult guinea pigs to loud hand claps.

The effectiveness of the ear plugs in reducing intensity of sound was measured using a B and K probe tube and a 3134 1/2 in. microphone. The length of the probe was 240 mm. No attempt was made to calibrate the system since our main interest was in relative sound pressure levels. The intensity of the sound at the ear of the guinea pig was measured by placing the probe just inside the external meatus of a dead 3 week old guinea pig. The intensity at the tip of the probe was measured with and without the ear plug in the ear. To do this an ear plug was formed around the plug. This ear plug could then be slid up and down the probe. The intensity of the sound was measured alternately with the ear plug in each position. Figure 1 shows the results of these measurements for pure tones of different frequencies. At least 3 measurements were taken at each frequency shown in the figure. The open circles represent the intensity of sound without the ear plugs in the ear. The crosses represent the intensity of the sound with the ear plugs held tightly in the ear. The solid line represents the intensity of the sound when the probe was blocked off with a finger. These values reflect the level at which sound is transmitted through the sides rather than the tip of the probe. As can be seen from the figure the decrease in intensity as a function of the ear plugs varies from at least 10 d.b. to 30 d.b. and the lower intensity is close to the limits of the measuring technique. A greater drop in intensity might have occurred but could not be measured with our procedure. Thus the ear plugs effectively reduce the intensity of the sound.

Figure 1: Sound pressure level for a series of pure tones measured with a 2 mm. probe tube inserted into the guinea pigs internal meatus. x's show intensity with ear plugs in place. o's show intensity with plugs removed. Solid line indicates calibrations with the tip of the probe blocked.

APPENDIX C

Approach-Withdrawal Responses of Young
Guinea Pigs to Auditory Stimuli

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and

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ABSTRACT

Young guinea pigs were tested for approach or withdrawal responses to auditory stimuli of different intensities. The stimuli were guinea pig chirps, guinea pig distress call, guinea pig maternal call, and clicks at 4 per sec. Both low and high intensity stimuli were used. The animals were first tested at age 11 hours and then every 24 hours thereafter until day 5. Two further tests were given on days 13 and 18. The results showed that more approach responses than withdrawal responses were made to the low intensity stimuli and more withdrawal responses than approach responses to the high intensity stimuli, which was interpreted as consistent with Schneirla's biphasic theory.

In newborn precocial animals the ability to localize the source of a sound may be an important factor in maintaining proximity to the parent and thereby in ensuring the survival of the neonate. Newborn precocial organisms have the motor ability to respond actively to the environment shortly after birth and therefore may become separated from the parent. In many environmental situations the use of non auditory cues, i.e. visual or olfactory ones, may be precluded and auditory cues may be essential in regaining contact with the parent. For example Bartholomew and Collias (1962) have suggested that due to crowding in elephant seal colonies the mother and infant often become separated and that they locate each other by means of vocalizations.

While many studies (Riss, 1959; Harrison and Beecher, 1969; Don and Starr, 1972; etc.) have indicated that adult organisms can localize the source of an auditory stimulus few have demonstrated that the young one can do so. Wertheimer (1961) demonstrated that a human infant made more eye movements towards the source of an auditory stimulus than away from it and Turkewitz et al (1966) demonstrated that human infants 23 hours after birth made, in general, more eye movements towards a low intensity auditory stimulus than away from it and more eye movements away from a high intensity stimulus than towards it. These studies suggest that the infants could localize the source of the stimulus since if they had not been able to, an equal number of eye movements would have been expected in either direction.

Schneirla (1965) has suggested in his biphasic theory of motivation that the neonate will approach low intensity stimuli

and withdraw from high intensity stimuli. This response in the neonate is a forced response and is determined directly by the stimulus intensity. Thus if when the neonate moves in the presence of a low intensity sound this movement results in an increased stimulus intensity the response will be repeated, and this responding will continue until the intensity of the stimulus reaching the receptors is optimized. In this manner the neonate will be led directly to the source of a low intensity stimulus. In a similar fashion the neonate will decrease the distance between its receptors and a high intensity sound.

On the basis of Schneirla's suggestion it was hypothesized that neonate organisms with adequate motor and sensory ability should be able to localize the source of an auditory stimulus and the purpose of the experiment was to investigate the responses of a precocial organism, the guinea pig, to sounds of different intensity.

The animal was placed in the center of the box, and the sound was presented at one of the two speakers. After approximately ten secs., the sound was turned off at the first speaker and on at the second one. This procedure was repeated with the location of the stimulus alternating from right to left, until five presentations of each stimulus had occurred. Each time a speaker was turned on constituted one trial. Each animal received each of the seven stimuli at each testing session on which that stimulus was presented. The animals were returned to their home cage between different stimuli. Order of presentation of the stimuli was varied among testing sessions.

On each trial the animal was scored for an approach response, a withdrawal response or no response. An approach response consisted of any response that decreased the distance between the animal's head and the stimulus source, such as, a movement directly up to the speaker, a short movement towards the speaker or a complete turn of the body towards the speaker. Conversely a withdrawal response consisted of any response that increased the distance between the source of the sound and the animal's head. Although it was possible for an animal to make a response which was neither an approach nor a withdrawal response, this occurred so rarely that these responses were categorized as no responses for the purpose of data analysis.

Method

Subjects and apparatus: The subjects were four young multi-coloured guinea pigs from a single litter. The mother was obtained from High Oaks Ranch, Goodrich, Ontario, when she was 14 days from term. The young were reared in an opaque polythene cage until the conclusion of testing. The guinea pigs were first tested at 11 hours post-natally, then every 24 hours until day eight. Two further tests were given on days 13 and 18.

The testing apparatus was a cardboard box (35 cm x 56 cm x 13 cm) with fine wire covering a 25 cm x 8 cm opening at each end. The floor was covered with litter. A tape recorder was used to play the recordings of the auditory stimuli, which were delivered to the animals through speakers placed at either end of the testing box.

Procedure: The auditory stimuli were tape recordings of (a) clicks, at a rate of four per sec.; (b) guinea pig maternal call; (c) chirping sounds made by a litter of guinea pigs; (d) and distress call of an infant guinea pig. The guinea pig vocalizations were recorded from an earlier litter. The maternal call and chirps were recorded while the entire litter was in its home cage and the distress call were played at both high and low intensities. The recordings were not exactly equated with respect to stimulus intensity. Thus the terms "high" or "low" refer to the relative intensity within a stimulus. It was not possible to play the chirps at a high intensity as the recording was a very low intensity one, the low intensity clicks and maternal call and the distress call at session two, while the high intensity maternal call was first presented at session four.

Results

Figure 1 shows the percentage of total possible responses that were approach or withdrawal responses to the low intensity stimuli for each subject. As can be seen from these figures all subjects made more approach than withdrawal responses to each of the low intensity stimuli. Similarly, Figure 2 shows the individual responses to high intensity stimuli. In general the high intensity stimuli elicited more approach than withdrawal responses, the one exception being the high intensity maternal call which varied with subjects.

Separate analyses of variance of responses to low and high intensity stimuli were made using the Geisser-Greenhouse conservative f test. These analyses indicated that in both cases the main effect of type of response was statistically significant

Figure 1: Percentage of total possible responses, summed over test sessions, that were approach or withdrawals to low intensity stimuli for individual subjects

Figure 2: Percentage of total responses, summed over test sessions, that were approaches or withdrawals to high intensity stimuli for individual subjects

TABLE 1

Summary table of analysis of variance for low intensity stimuli.

Source	df	df conservative test	MS	F	P
Type of response	1	1,3	10989.03	152.99	<.01
Type of stimuli	3	1,3	600.87	8.37	>.05
Interaction	3	1,3	542.36	7.55	>.05
Residual	21	-	71.83		

TABLE 2

Summary table of analysis of variance for high intensity stimuli.

Source	df	df conservative test	MS	F	P
Type of response	1	1,2	2016.66	22.10	<.05**
Type of stimuli	2	1,2	542.79	5.95	>.05
Interaction	2	1,2	506.55	5.51	>.05
Residual	15	-	91.26		

(Tables 1 and 2), with more approach responses being made to the low intensity stimuli and more withdrawal responses being made to the high intensity stimuli. In neither case was the main effect of type of stimuli or the interaction statistically significant.

Discussion

That the young animal approaches low intensity stimuli and withdraws from high intensity stimuli is consistent with Schneirla's (1965) hypothesis. All the subjects made a greater percentage of approach responses than withdrawal responses to each of the low intensity stimuli. Also all subjects made a greater percentage of withdrawal responses than approach responses to the high intensity clicks and distress call but the percentage of approach and withdrawal responses made to the high intensity maternal call varied with subjects. This exception may have been due to the fact that it was judged to be less intense than the other high intensity calls, that this stimulus was first presented on day four when responsiveness had declined, or that it was responded to on a qualitatively different basis.

By responding differentially to the high and low intensity stimuli, the young guinea pigs indicated that they were able to localize the source of the sounds. If they had not been able to localize the sound, an equal number of responses would have been expected to each of the stimuli. As, however, the speakers were large in relation to the testing box and there were only two speakers, it was not possible to assess the accuracy of localization.

The different types of stimuli did not differ statistically in the percentage of responses they elicited but one cannot rule out the possibility that stimulus quality is an important variable. Increased numbers of observations might have revealed a difference. Furthermore, in order to draw a sound conclusion about the effects of qualitatively different stimuli it is necessary to exclude stimulus intensity as a confounded variable. This latter condition is not met by our procedure.

Responses to all stimuli declined over the testing period and by the tenth session very few responses were made. This decline may have been due to such factors as habituation or extinction.

In conclusion young guinea pigs approach low intensity stimuli and withdraw from high intensity stimuli. This finding is consistent with Schneirla's hypothesis that young animals show directional responses on the basis of an intensity dimension. These results further imply that young organisms have an ability to localize the source of a sound very early in their development which could have important functions or consequences, for example in maintenance of parent-offspring relations.

- Bartholomew, G.A. and W.E. Collias, 1962. The role of vocalizations in the social behaviour of the northern elephant seal. Animal Behaviour, 10, 7-14.
- Don, M. and A. Starr, 1972. Lateralization of performance of Squirrel monkey (Samiri sciureus) to binaural click signals. Journal of Neurophysiology, 35, 493-500.
- Harrison, J.M. and Beecher, M.D., 1969. Control of responding by the location of an auditory stimulus: Role of rise time of the stimulus. Journal of the Experimental Analysis of Behaviour, 12, 217-227.
- Riss, W., 1959. Effect of bilateral temporal cortical ablation on discrimination of sound direction. Journal of Neurophysiology, 22, 374-384.
- Turkewitz, G., H.G. Birch, T. Moreau, L. Levy, and A.C. Cornwell. 1966. Effect of intensity of auditory stimulation on directional eye movements in the human neonate. Animal Behaviour, 14, 93-101.
- Schneirla, T.C., 1965. Aspects of stimulation and organisation in approach/withdrawal processes underlying vertebrate behavioural development. In Advances in the Study of Behaviour. Vol. 1, Eds. Lehman, Hinde, Shaw. New York: Academic Press, 1-71.
- Wertheimer, M., 1961. Psychomotor co-ordination of auditory and visual space at birth. Science, 134, 1962.

APPENDIX D

The purpose of this experiment was to determine how accurately young guinea pigs can localize a sound source, and under what conditions the sound can be localized. In a previous experiment (Appendix C) it was found that young guinea pigs could localize a sound source in that more approach responses were made to low intensity stimuli and more withdrawal responses to high intensity stimuli. If the guinea pigs had not been able to localize sound, an equal number of responses would have been expected to both types of stimuli. In this experiment the ability of the guinea pigs to localize sound was tested in an eight choice situation which allowed evaluation of the accuracy of their responses.

Method

Subjects: Seventeen newborn guinea pigs, from four litters, were randomly assigned to an experimental group 1 ($N = 9$) and a control group ($N = 8$). A further seven animals, from two litters, were assigned to an additional experimental group (experimental group 2). The litters were composed of both multi-coloured and albino young. In experimental group 1 and in the control group the animals were first tested between 8 and 16 hours of age, and thereafter every 24 hours until day 4. In experimental group 2 the animals were tested on days 5 through 8. All litters were born and raised, until the conclusion of testing, in opaque polythene cages. The pregnant multicoloured females were obtained from High Oaks Ranch, Goodrich, Ontario.

Procedure: The apparatus and testing procedure were identical to that described in Experiment 1 except each animal was tested 6 times daily. Also the stimulus conditions in this study included tests with single chirps as well as trains of chirps.

Results

The number of each type of response made by all subjects over the four days of testing, are plotted against chance for each of the six experimental conditions in Figure 1 and Figure 2. Figure 1 shows the number of each type of first response and Figure 2 shows the number of each type of final response. For the purpose of data analysis the responses made by each subject over the four days of testing were grouped into two categories of correct or incorrect. Type 1 and type 2 responses were counted as correct and types 3, 4, and 5 as incorrect. Because of the number of times that no response was made, the percentage of total responses that were correct was calculated for each subject and single sample t tests were used to test if the percentage of correct responses differed from chance.

First response: As can be seen from Figure 1 and Table 1 the only condition in which the percentage of correct responses differed from chance was response of the 1-4 day old guinea pigs exposed to the train of chirps.

Final response: As can be seen from Figure 2 and Table 1 the only condition in which the percentage of correct final responses differed from chance was the 1-4 day old guinea pigs exposed to the train of chirps.

Figure 1: Total number of each type of first response, summed over subjects and days of testing, for each of the six conditions.

TABLE 1

Mean percentage of total responses that were correct with the standard deviations and t tests for the first and final responses of all conditions.

		<u>train of chirps</u>		<u>single chirp</u>	
		first response	final response	first response	final response
Experimental group 1	$\bar{X}$ *	69.44	71.97	30.37	29.13
	s	13.02	15.47	10.84	10.05
	t	7.36**	6.68**	-1.93	-2.26
Experimental group 2	$\bar{X}$	49.37	50.8	38.9	34.86
	s	36.70	40.78	23.3	21.25
	t	.86	.82	.14	-.28
Control group	$\bar{X}$	29.58	30.21	37.3	36.34
	s	14.92	16.78	17.37	12.73
	t	-1.5	-1.23	-.03	-.26

* Mean percent of responses that would have been expected to be correct on a chance basis would have been 37.5%.

** Statistically significant beyond the .01 level.

Figure 2: Final response. Total number of final responses, summed over days of testing and subjects, for each of the six conditions.

Discussion

The 1-4 day old guinea pigs made a greater percentage of responses towards the sound source, either directly towards it or to each side of it, than could have been expected on a chance basis alone, indicating that they were able to locate the source of the sound with a fair degree of accuracy. This conclusion, however, is only applicable when the stimulus was the train of chirps as the animals gave no indication that they were able to localize the single chirp since the percentage of responses towards this stimulus did not differ from what would have been expected on a chance basis. That the young guinea pigs did not appear to be able to localize the single chirp suggests that they needed a continuous sound to be able to locate its source. It is possible, however, that the animals were able to localize the single chirp but in the present experiment there was no motivation for them to approach the source of the sound once the sound had ended. Thus the deficit in responding to the single chirp might represent a motivational rather than a perceptual deficit.

GLOSSARY OF COMMON NAMES

Barn Owl	<u>Tyto alba</u>
Chipmunk	<u>Tamias striatus</u>
Domestic Cat	<u>Felis domesticus</u>
Guinea Pig	<u>Cavia porcellus</u>
Human	<u>Homo sapiens</u>
Kangaroo Rat	<u>Dipodomys merriami</u>
Laboratory Rat	<u>Rattus norvegicus</u>
Northern Elephant Seal	<u>Mirounga angustisatris</u>
Side-winder Rattle Snake	<u>Scrotalus cerastes</u>
South American Tapir	<u>Tapirus terrestris</u>
Squirrel Monkey	<u>Samiri sciureus</u>
Yellow Bellied Marmot	<u>Marmota flaviventris</u>