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The Development of Directional Responses to Sounds

in the Rat (Rattus norvegicus) and Gerbil

(Meriones unguiculatus)

by

Marc Potash

A thesis submitted to

the Faculty of Graduate Studies

in partial fulfillment of the requirements for

the degree of Doctor of Philosophy

Department of Psychology

Carleton University

August, 1978

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The undersigned recommend to the Faculty
of Graduate Studies acceptance of the thesis
"The Development of Directional Responses to Sounds in the Rat
(Rattus norvegicus) and Gerbil (Meriones unguiculatus)"

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Abstract

The major purpose of Experiments I and II was to examine the tendency of gerbil (16-23 days of age) and rat (13-20 days of age) infants to approach auditory signals. Tests were conducted in a circular maze with a central start area and eight response areas around the periphery. Stimuli were played back over a loudspeaker placed behind one of the eight response areas. Signals included species calls and white noise at high and low intensities. Control conditions with blank tapes were also used. Both gerbils and rats showed a clear tendency to approach the low intensity playback of species vocalizations.

The aim of Experiments III and IV was to investigate the importance of binaural cues for localization by infants. Rat and gerbil pups were tested with either one ear blocked, both ears blocked or neither ear blocked. The effect of the ear plug(s) was to attenuate the sound approximately 7-10 dB. The results indicated that only the binaurally blocked and normal control subjects approached the sound source at above chance levels. The failure of subjects in the monaural group to approach the sound probably resulted from a disruption of binaural cues. The ability of infants to localize sounds and process binaural cues is discussed in relation to the onset of hearing and in terms of physiological responses that are present early in ontogeny.

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I. INTRODUCTION

The ability to localize a source of sound in space is evident in most, if not all, avian and mammalian species (Erulkar, 1972). The localization of sounds of brief duration is sometimes essential for the survival of a species (Erulkar, 1972). For example, accurate localization is vitally important when it is used to detect prey and/or to avoid predators. The localization of sounds is also of value when auditory cues are used to identify the location of group members (Winter, Ploog and Lotta, 1966). For example, certain animals that inhabit dense jungle areas (e.g., tapirs) or animals that have poor vision (e.g., night monkeys) depend on auditory cues to maintain contact within the group (Hunsaker and Hahn, 1965; Moynihan, cited in Erulkar, 1972). Other vocalizations may serve to signal the mother to retrieve her young (Allin and Banks, 1972) or the young to approach the parents (Beer, 1970). In addition, certain calls emitted by both mother and young may function to bring the two back together in a mutual approach effort (Bartholomew and Collias, 1962).

Masterton and Diamond (1973) have pointed out that 1) sounds occur as a result of movement and therefore signify the presence of a moving object; 2) an animal reacts differently to abrupt, brief sounds than it does to continuous sounds; and 3) an animal either approaches, avoids or orients to an abrupt sound, indicating

that the animal perceives its location. They concluded that "it is the detection, localization and identification of other animals (and, therefore, of brief sounds) that provides a primary source of selective pressure on animal auditory systems" (p. 421).

Jerison (1973) has also recognized the evolutionary significance of sound localization ability; according to his reconstruction of perceptual worlds, auditory mechanisms for encoding spatial information (i.e., localizing sounds) evolved when nocturnal reptiles first appeared approximately 200 million years ago.

Masterton, Heffner and Ravizza (1968) have suggested that the need to detect and localize brief sounds has had a major impact on the evolution of sensitivity to sounds. Specifically, Masterton et al. (1968) have argued that selective pressure for accurate localization led to an extension of mammals' ability to perceive high frequencies, especially in the case of animals with close-set ears. To understand the logic behind this argument, we need to distinguish between the two binaural cues that are relevant in localizing brief sounds in the azimuthal plane.¹ The first is the difference in the time of arrival of the sound at the two ears (Δt) and the second is the difference in the frequency-intensity spectra at the two ears (Δf_i).

If a sound originates from the midline, either in front of or behind the subject, the sound energy reaches the two ears at the same time. If a sound originates to one side of the midline, the sound arrives first at the ear nearest the sound source and later at the ear furthest from the source. The difference in the time of arrival is known as the binaural time difference.²

The frequency-intensity spectra of sound at each ear will be the same for a sound that emanates from the midline. The sound spectra will differ at the two ears for a sound that originates either to the left or right of midline. This spectral difference cue, as well as the time difference cue, results "from the longer and more indirect path traveled by the sound around the head to the far ear" (Masterton and Diamond, 1973, p. 422). The greater the difference in the spectrum reaching each ear, the more useful the cue in localizing a sound source. Because the head and pinnae attenuate high frequencies more than low frequencies, spectral differences vary directly as a function of frequency.³

The range of Δt cues available to animals with close-set ears is greatly limited (Masterton et al., 1968). When an animal is deprived of Δt cues, Δf_i cues provide the basis for localization. And, in order to maximize Δf_i cues, high frequency sensitivity is necessary (Masterton et al., 1968). This is precisely why Masterton et al. (1968) have argued that selective pressure for more accurate sound localization went hand in hand with pressure for high frequency sensitivity.

In fact, there is a high correlation between the availability of Δt cues and the upper frequency limit of hearing (Masterton, 1974). If a broad range of Δt cues is available to an animal, the upper limit of hearing is generally low. If only a restricted range of Δt cues is available, the animal usually has a high upper limit of hearing.

Questions concerning the ontogenetic course of localization behaviors become intriguing in light of the survival and social

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value of these behaviors during early development. For example:

Do the young of all species possess the ability to localize sounds?

Are the neurological structures necessary for localizing sounds

fully mature at birth, or, do these structures mature rapidly or

over an extended period following birth? What are the effects of

various prenatal and postnatal influences--such as an enriched or

restricted auditory environment--on the ability to localize sounds?

In the experiments to be described below, an attempt was made to

determine the time of onset of localization behavior and the

effects of restricting auditory input on this behavior in two

altricial species--the albino rat and the mongolian gerbil.

II. BINAURAL PROCESSING IN THE AUDITORY SYSTEM

II.1 Superior Olivary Complex

The superior olivary complex is the first central auditory structure to receive projections from both ears. Masterton (1974), as well as others (Masterton and Diamond, 1967; Goldberg and Brown, 1968), have argued that at least two of the superior olivary nuclei--the medial superior olives (MSO) and the lateral superior olives (LSO)--are important in coding binaural cues. Some of the anatomical, physiological, ablation-behavior and comparative evidence that supports this hypothesis is reviewed below.

Anatomical. Harrison and Feldman (1970) have noted that two major pathways of the auditory system pass through the superior olivary complex: one pathway ascends through the MSO and the other, via the LSO.⁴ However, the relative development of these two pathways varies from species to species; in any particular species one may see that both nuclei are highly developed or that only one of the two nuclei predominate (Harrison and Feldman, 1970; Sehmsdorff, 1966; Harrison and Irving, 1966). Which of the two nuclei is most advanced depends on which of the two chief binaural cues is most available to the animal (Masterton and Diamond, 1967). When Δt cues provide the basis for localization (e.g., man), the size of the MSO is large relative to the LSO, and when Δf cues are used to localize sounds, (e.g., hedgehog, bat), the LSO is more

pronounced than the MSO (Harrison and Feldman, 1970). When a wide range of both cues are available to the animal (e.g., cat, monkey), both nuclei are large (Harrison and Feldman, 1970).

Comparative. Masterton, Thompson, Bechtold and Roberts (1975) have demonstrated the importance of the MSO for analyzing Δt cues in a comparative study of the cat, tree shrew, rat and hedgehog. The MSO varies greatly in size in these four species: the cat has a large MSO; the tree shrew, a moderate-sized MSO; the rat, a small MSO; and the hedgehog has no MSO at all. Masterton et al. (1975), after ruling out performance and sensitivity factors, found that an animal's ability to localize low frequency tones is directly related to the size of the MSO. The cat, with a large MSO, performed best on the localization task and the hedgehog, without an MSO, was unable to localize low frequencies. The rat and tree shrew were intermediate between these two species with the tree shrew, as expected, somewhat better than the rat. Each subject was also tested at high frequencies. Subjects had little difficulty in localizing at these frequencies since they all had moderate to large-sized LSOs (and thus, could presumably utilize Δt cues).

Physiology. Binaural interaction is inferred when stimulation of both ears leads to a greater or lesser probability of response than would be expected from a summation of each ear stimulated separately. Binaural interaction takes a number of forms (Galambos, Schwartzkopff and Rupert, 1959): 1) Stimulation of both ears results in a suppression of unit responding although a discharge is seen when only one of the ears is stimulated. 2) Some neurons respond to binaural stimulation but not to stimulation of either ear.

3) Binaural stimulation produces greater responsiveness than would be expected by summation of the discharges evoked by monaural stimulation of both ears. Goldberg and Brown (1968) have pointed out that 88% of all MSO neurons are binaural and Boudreau and Tsuchitani (1968) have observed that 83% of LSO cells are binaural.

Goldberg and Brown (1969, 1968) have described excitatory-inhibitory (EI) cells in the LSO and excitatory-excitatory (EE) cells in the MSO. The EI unit, which has an excitatory input from one ear and an inhibitory input from the other, corresponds to the first type of cell that Galambos et al. (1959) observed (see above).⁵ The EE unit, which receives an excitatory input from each ear, corresponds to the third type of cell described above.

A considerable number of MSO cells are sensitive to small binaural time differences and are important in localizing low frequency stimuli (Galambos et al., 1959; Moushegian, Rupert and Whitcomb, 1964a, 1964b). Moushegian et al. (1964a, 1964b) have found that the degree of response inhibition (or excitation) depends on the time of arrival of the sound stimulus at the two ears. At a particular delay--known as the characteristic delay--a neuron shows maximum (most favorable delay) or minimum (least favorable delay) responsiveness. These characteristic delay units vary in terms of 1) the interaural time delay required to produce maximum suppression (or excitation); 2) the length of the period of maximum suppression (or excitation) and 3) the number of points of maximum suppression (or excitation) (Galambos et al., 1959; Moushegian, Rupert and Langford, 1967).

Ablation. A number of ablation-behavior experiments have underscored the superior olives' part in the analysis of binaural cues (Masterton, Jane and Diamond, 1967; Casseday and Neff, 1975; Moore, Casseday and Neff, 1974; Neff, 1968). Masterton et al. (1967) have reported that a complete transection of the major afferent pathway to the SOC, the trapezoid body, results in an elevation of Δt thresholds on a lateralization task. The increased thresholds caused by the lesion made it impossible for the subjects (cats) to use temporal cues that occur in their natural habitat to localize sounds. Moore et al. (1974) have also observed a severe loss in cats' ability to localize sound after transection of the trapezoid body and have concluded that "the superior olivary complex plays a critical role in encoding cues for localization of sound" (p. 24).

II.2 Inferior Colliculus

A high proportion of inferior colliculi (IC) neurons are under binaural influence (Aitkin, Blake, Fryman and Bock, 1972; Bock and Webster, 1974; Stillman, 1972). Of these, most have been classified as either EE or EI cells or as cells that are sensitive to small time differences (Geisler, Rhode and Hazelton, 1969; Aitkin et al., 1972; Rose, Gross, Geisler and Hind, 1966; Benevento and Coleman, 1970). In addition to these common types of binaurally influenced units, Altman (1968) has observed IC neurons that are capable of detecting the direction of movement.⁶ These cells would not only be of value in localizing a sound source, but also in detecting the approach and withdrawal movements of that source (e.g., another animal).

Ablation. The effects of IC lesions on sound localization depend on the severity and placement of the lesion (Masterton, Jane and Diamond, 1968). Cats with lesions of nearly two-thirds of the apical region of the IC are able to lateralize sounds (Masterton et al., 1968). Bilateral transection of the brachium of the IC, which is deep enough to separate the forebrain auditory structures from the hindbrain structures, leaves a cat unable to use binaural cues to lateralize or localize sounds (Masterton et al., 1968; Strominger and Oesterreich, 1970). When bilateral transections of the brachium are more limited (i.e., do not destroy most of the adjacent tracts), animals can relearn to localize sounds, but only after a lengthy retraining period and never with the same accuracy as normal subjects (Casseday and Neff, 1975).

Function. Thompson (1975) and Leiman and Hafter (1972) have suggested that the function of the IC is sensorimotor--to use the binaural analysis from hindbrain centers to direct responses (head, pinna and eye movements) toward the sound source. Support for the IC's role in directing orientational responses comes from anatomical and ablation studies. First, projections from the IC terminate in the intermediate and deep layers of the superior colliculus, which in turn, have projections to cranial nerves that control head movements (XIth nerve), ear movements (VIIIth nerve) and eye movements (IIIrd, IVth and VIth nerves) (Thompson, 1975; Gordon, 1972). Wickelgren (1971) has observed that about one-half of the units in the deep layers of the superior colliculus respond to both auditory and visual stimuli and has suggested that

these cells are involved in following and orienting responses (e.g., controlling eye movements toward the stimulus). Second, since destruction of large portions of the IC does not result in impairments in sound localization, Masterton (1974) has suggested that the primary role of the IC is probably to direct eye and head movements toward the sound source.

II.3 Medial Geniculate Body

There have been relatively few reports on the binaural responsiveness of medial geniculate (MG) cells, although a large percentage of these cells are influenced by binaural stimulation (Aitkin and Dunlop, 1968). Aitkin and Dunlop (1968) have reported that unit responses to binaural stimulation range from facilitation (a response that is greater than the most effective monaural response) to occlusion (a response smaller than the least effective monaural excitatory response). Aitkin and Webster (1972) have also described neurons of low best frequency which are sensitive to interaural time differences.

II.4 Auditory Cortex

Physiology. EI units, which have been observed in all lower auditory centers, have also been identified in the auditory cortex (Benson and Teas, 1976; Brugge, Dubrovsky, Aitkin and Anderson, 1969; Hall and Goldstein, 1967). As noted previously, EI units are most sensitive to differences in interaural intensity. Thus, when the intensity to the inhibitory ear is raised, the number of spikes recorded from the EI unit is greatly reduced,

but when intensity is changed equally (either raised or lowered) at the two ears, there is little change in response. Brugge et al. (1969) have also described phase-sensitive cells (i.e., characteristic delay cells) in the auditory cortex that are extremely sensitive to small time differences in the arrival of the sound at the two ears but which are relatively insensitive to the stimulus frequency. In addition to these standard phase-sensitive units, Benson and Teas (1976) have described a type of unit that peaks at different intervals depending on the frequency of the stimulus tone. Hence, Benson and Teas have suggested speaking in terms of optimal delays, rather than characteristic delays, to describe a particular cell's output under a particular set of stimulus conditions.

Ablation. The specific role of auditory cortex in detecting the location of a sound source remains elusive. In the past, a complete disruption of localization ability was reported for animals (including cats, monkeys, hedgehogs, bush-babies and men) that had undergone large bilateral lesions of auditory cortex areas (Masterton and Diamond, 1964; Neff, 1968, 1962; Neff, Fisher, Diamond and Yela, 1956; Riss, 1959). However, more recent evidence indicates that the ability of animals with lesions to localize sound is related to the response requirements of the task (Heffner, in press; Heffner and Masterton, 1975; Kelly and Glazier, 1978; Ravizza and Diamond, 1974; Ravizza and Masterton, 1972). Thus, deficits resulting from auditory cortex lesions are no longer described solely in sensory terms.

If the localization task requires the subject to locomote to the place from where a brief sound emanates, animals with lesions show a severe decrement in performance (Ravizza and Diamond, 1974). However, these animals have little difficulty in tracking the source of a continuous sound. Ravizza and Diamond (1974) have suggested that the inability of subjects with cortical lesions to localize a brief sound results from a disruption of "spatial organization", which, they maintained, encompasses knowing, remembering and approaching the locus of a sound source.

Heffner and Masterton (1975) have also observed that monkeys with auditory cortex lesions are unable to approach the source of a single click. However, animals with lesions are able to learn to indicate the location of a brief click. In the indication task, monkeys were trained to press a lever on the side (left or right) corresponding to the side where a click had been emitted. Animals with lesions were able to localize the source of a brief click as well as normals even at small angles of separation. On the second task, which required subjects to locomote to the sound source, monkeys with auditory cortex removed could approach the source of a click train, presumably by using cues gained by scanning, but were unable to approach the source of a single click. Since both the indication and locomotor tests had similar sensory and motivational requirements, Heffner and Masterton (1975) have suggested that the difference in performance on the two tasks

could be explained by the difference in motor requirements. Hence, they have argued that the deficit observed on the locomotor problem is "audiomotor" in nature.

In a recent paper, Heffner (in press) has shown that dogs with lesions in auditory cortex are able to make a spatial response to sounds which they could not localize. Thus, the poor localization performance in animals with cortical lesions cannot be explained in terms of attention or memory deficits. Rather, as Heffner has pointed out, the cortical impairment in sound localization is solely the result of an inability to respond on the basis of the locus of sounds.

Most early reports had indicated that animals with unilateral auditory cortex lesions were unimpaired on localization tasks (Masterton and Diamond, 1964; Neff et al., 1956). More recently, a number of deficits have been reported for complex sound localization problems following unilateral lesions of the primary auditory cortex (Cranford, 1975; Cranford, Ravizza, Diamond and Whitfield, 1971). Cats with unilateral lesions have difficulty attending to stimuli on the side contralateral to the lesion (Cranford, 1975). These data are consistent with other physiological evidence that indicates that the crossed (contralateral) neural pathway from cochlea to cortex has dominance over the uncrossed (ipsilateral) pathway (e.g., see Rosenzweig, 1961, 1954).

Neff and Casseday (1977) have demonstrated that cats with one cochlea destroyed (i.e., monaural animals) are unable, even with extensive training, to localize a sound source after unilateral ablation of the cortex contralateral to the intact ear but are able, after minimal training, to localize sounds following ablation of the cortex ipsilateral to the functional ear.⁷

In summary, it is apparent that all major parts of the central auditory system are involved in sound localization. Hindbrain structures are important in the analysis of binaural cues in the azimuthal plane; midbrain mechanisms are probably important in generating orienting movements toward the sound; and forebrain structures seem to be necessary in executing motor responses to sound.

III. DIRECTIONAL RESPONSES TO SOUND IN YOUNG ANIMALS

III.1 Schneirla's Hypothesis

Schneirla (1966, 1965, 1959, 1939) has proposed a motivational theory based on approach and withdrawal responses in animals. According to Schneirla (1965), "...biphasic mechanisms underlying directionally opposed orientative responses, governed first of all by quantitative properties of stimulation, are present in all animals from protozoans to primates" (p. 7).

Schneirla has argued that, regardless of phyletic level, an animal will approach a low intensity stimulus and withdraw from a high intensity stimulus. This hypothesis holds throughout ontogeny for the lower phyletic levels and only for the earlier stages of development on higher levels.

Schneirla has also suggested that qualitative differences in stimuli are less important than quantitative differences in eliciting approach or withdrawal behavior. With respect to the auditory modality, Schneirla has argued that a low intensity signal, irrespective of the type of sound, will tend to evoke approach reactions. In contrast, others (e.g., Gottlieb, 1965) have shown that some calls (e.g., species calls) are more likely to result in approach responses than others (e.g., non-species calls).

Schneirla pointed out that it was the effective intensity that was important in determining whether an approach or withdrawal response was made. Thus, the energy characteristics of the signal as well as the receptor system of the organism need to be considered. This raises a particularly interesting question for those involved in testing young animals, such as gerbil and rat pups, which do not begin to hear until sometime after the first postnatal week and whose hearing progressively increases in sensitivity over a period of several weeks: Are sounds perceived in the same way by young and adult animals? Possibly, a loud sound processed by a young animal with immature auditory structures might be perceived as a low intensity signal, whereas this same sound, presented to an adult animal with fully developed structures, might be perceived as a high intensity signal.

III.2 Sound Localization in Human Neonates

Leventhal and Lipsitt (1964) have demonstrated that young infants, 23-100 hours old, can distinguish between sounds to the left and right of midline. In their experiment, a 0.2 kHz tone (75 dB, no SPL cited) was presented from speakers that were placed about 1 foot from the subjects' right and left ears. The tone was presented from one speaker until the subject failed to respond (e.g., respiration rate, body movement) on three consecutive trials. At this time, the tone was presented to the opposite ear (test trial). Control subjects continued to receive the tone at the same ear. Leventhal and Lipsitt found that while only one control subject

responded on the test trial, the majority of experimental subjects again responded to the tone.

Bronshtein, Antonova, Kamenetskaya, Luppova and Sytova (1960) have briefly described results that indicate that newborns react to small Δ t differences. They then concluded that "spatial hearing is well developed in newborns and presents an example of inborn function of the human being" (p. 6). Unfortunately, information concerning experimental procedure (e.g., age of subjects, type of signal) was not included in the report.

Wertheimer (1961) presented a series of clicks (no sound specifications given) at the left or right ear of a newborn girl. The greatest majority of eye movements (18/22) were in the direction of the click. Wertheimer concluded that "within 40 minutes after birth, rudimentary directional auditory localization is possible..." (p. 134). Turkewitz, Birch, Moreau, Levy and Cornwall (1966) have shown that eye movements of infants (23-72 hours old) are predominantly in the direction toward the ear stimulated with a 200 msec white noise burst.

Although Aronson and Rosenbloom's (1971) primary interest was to determine whether infants "perceive within a common auditory-visual space", their data also provide evidence that infants (30-55 days old) can identify the locus of a sound source. In their study, the subject's mother was situated behind a transparent window in an adjoining room and stood two feet directly in front of her infant. Her voice was transmitted to the infant's room via loudspeakers. When the speakers were in balance (i.e., equal

intensities emanated from both speakers which were 90° to each side of the infant), the infants appeared calm and relaxed. When the sound was displaced to one side (by varying the intensity of the two speakers so that the sound would seem to emanate from one side, even though the mother remained directly in front of the infant), the infants showed signs of discomfort.

III.3 Directional Responding in Infrahuman Neonates

There have been several investigations of approach behavior to sound in the young of avian (Evans, 1970; Beer, 1970, 1969; Gottlieb, 1965) and mammalian species (Clements and Kelly, 1978; Clements and Kelly, 1978, in press). Gottlieb has observed that Peking ducklings (10-21 hours after hatching) approach the calls of their own species much more often than calls of other species. Studies with laughing gull chicks (16-23 days of age) have shown that these birds orient toward and approach the vocalizations of their own parents but do not respond to the vocalizations of other parents (Beer, 1970, 1969).

Clements and Kelly (1978) tested newborn guinea pigs (1-4 days old) and older animals (11-31 days old) in a circular eight choice apparatus with a central start area. They found that subjects ^{in both age} groups responded in the direction of guinea pig vocalizations and were capable of processing binaural cues. In another study, (Clements and Kelly, 1978, in press), kittens between 4-32 days of age were required to approach an auditory stimulus (comprised of kitten calls) for a milk reward. The test apparatus was a straight alley with a center start area and goal boxes at both ends. Beginning around the middle of the third week, the kittens responded to the side with sound at well above chance levels.

IV. IMPORTANCE OF EARLY SENSORY STIMULATION

During the past decade, considerable interest has focused on the effect of sensory stimulation on the development of behavior and neural mechanisms (Ganz, 1975; Gottlieb, 1973). Various enrichment or deprivation conditions, introduced during sensitive or critical periods of development, have been shown to have a profound impact on behavior and on the differentiation of neural structures. While there is some evidence that restricted input during the early months will modify the growth of auditory structures (see e.g. Clopton and Silverman, 1977), the deleterious effects of deprivation on developing sensory systems are best known for the visual modality.

IV.1 Visual System

Hubel and Wiesel (1970, 1965a, 1965b, 1963) have conducted a series of elegant experiments on the electrophysiological and behavioral maturation of the visual system in normally reared and deprived cats. Single cell recordings of cortical units in very young kittens (8-16 days of age) to visual stimuli have indicated that these cells respond very much like adult cells in terms of

- 1) the percentage of units that are driven by both eyes (80%);
- 2) the types of cells (e.g., simple and complex) that are encountered; and 3) the preferred orientation displayed by different cells⁸ (Hubel and Wiesel, 1963). On the basis of these results and other findings which have indicated that cell responses are

unaffected by any type of visual deprivation during the first two weeks of life, Hubel and Wiesel (1963) have suggested that binocular connections in the cortex are established at birth (or shortly thereafter). Barlow and Pettigrew (1971) and Pettigrew (1974) have also found that visual cortex neurons in young kittens can be driven by binocular stimuli but have shown that these inexperienced units do not display other adult characteristics (e.g., orientational selectivity). According to Pettigrew (1974), Hubel and Wiesel (1963) have confused orientational selectivity with directional selectivity. Pettigrew (1974) has shown that most neurons in kittens respond equally to either a spot or a bar that is moved through the receptive field whereas units in adult cats respond more vigorously to the bar. (Both stimuli were moved in the same direction and at the same speed.) Thus, Pettigrew (1974) has concluded that visual experience is necessary for the development of orientational selectivity.

A number of researchers have discussed the severe and frequently permanent deficits in visual cortex cells that result from exposure to unusual environments (e.g., Hirsch and Spinelli, 1970; Blakemore and Cooper, 1970). Hirsch and Spinelli (1970) raised cats from birth with one eye viewing horizontal stripes and the other eye, vertical stripes. After eight hours of daily exposure from about the third to the tenth week (the cats were housed in a dark room at other times), single unit recordings from the visual cortex were made. Hirsch and Spinelli found that the majority of units were monocularly driven and that units with horizontal

fields were only activated by the eye exposed to the horizontal lines and, correspondingly, units with vertical fields by the eye exposed to vertical stripes. Blakemore and Cooper (1970) demonstrated a similar change in feature detector units after raising kittens in a dark room (from the second week to the fifth month), except for a daily five hour exposure to either vertical or horizontal stripes. Their physiological recordings indicated that the majority of units were binocularly driven (as is normally the case) but that the orientations of cells were abnormal. Most units had preferred orientations within 45° of the striped pattern that the subject had experienced. Prior to the physiological recordings, (but following a period of acclimation in a normal environment), the animals were tested on a number of behavioral tasks. These tests indicated that the animals were "virtually blind for contours perpendicular to the orientation they had experienced" (Blakemore and Cooper, 1970, p. 478).

Held and Hein (1963) have examined the effects of self-produced movements on visually guided behaviors. Kittens were raised in a dark room from birth to about twelve months of age. At this time, the kittens were tested in pairs in a specially constructed gondola apparatus. One of the kittens--the active kitten--was free to walk around in any direction; the other (passive) kitten was placed in a restraining device which was mechanically linked to the active kitten. The passive cat was denied any of its own locomotor movement, but the device in which it sat was put in motion by the movement of the active cat. The

head movements of both cats were unrestrained and thus, they both received an equivalent amount of visual stimulation. Held and Hein reported that cats given the passive experience were retarded in certain visually guided behaviors (e.g., paw placement, avoidance of visual cliff, blink to an approaching stimulus), whereas subjects given the active exposure behaved like normally reared subjects. Held and Hein (1963) concluded "that self-produced movement with its concurrent visual feedback is necessary for the development of visually-guided behavior" (p. 875). Ganz (1975) has raised serious objections to this interpretation. Since the passive cats recovered after 48 hours of normal experience, Ganz argued that the temporary deficit in performance was caused by a disruption of innately determined behavior. After reviewing some of the evidence that indicates that "visual placing is innate in kittens" (p. 206), Ganz suggested that visual-motor experiences are necessary to "sustain and nurture normal, visually guided behavior" (p. 206), but are not necessary for the development of these behaviors.

Hubel and Wiesel (1970) have described the physiological effects and Dews and Wiesel (1970) have provided an account of the behavioral effects that result from monocular deprivation at various ages and for various durations. Simply put, there is a sensitive period in development during which time monocular deprivation produces severe deficits. For physiological responses, this period starts around the fourth week of life and continues to about the third month, but the susceptibility to deprivation is greatest during the first

30 days of this period.⁹ In fact, Hubel and Wiesel (1970) have reported that monocular eye closure that lasts for only 3-4 days during the fourth and fifth weeks after birth results in a drastic decline in the number of binocularly driven cells. Furthermore, for kittens deprived of sight in one eye during the susceptible period, "there is very limited recovery in the cortical physiology" (Hubel and Wiesel, 1970, p. 419) over a five year period. In contrast, closure of one eye in an adult cat for an extended period (up to one year) has no effect.

There are also pronounced behavioral deficits following monocular deprivation. The period of susceptibility lasts until four months of age (with maximum sensitivity during the second month), after which time deprivation has little effect on cats' ability to respond on a number of visual tasks (Dews and Wiesel, 1970). The period of vulnerability begins by at least the first month and possibly, even before this time. Dews and Wiesel have also found that the longer the duration of the deprivation, the more severe the behavioral deficit. For example, if closure only lasted up to the sixth week, the only deficit was a lowering of visual acuity; if the closure lasted up to the 16th week, deprived animals showed no indication of paw placement or pattern discrimination and appeared behaviorally blind. Dews and Wiesel have also noted that visual control of behavior improved if the suture was reversed (i.e., placed over the previously normal eye), and this was the case whether the reverse suturing occurred immediately following the original deprivation condition or more than one year

later (both eyes were open during the intervening year). However, this reverse suture procedure did not result in an increase in the number of cells driven by the deprived eye.

Blakemore and Van Sluyters (1974) have suggested that the critical period concept is as applicable to the facilitating effects of reverse suturing as it is to the debilitating effects of monocular deprivation. In their study, cats were monocularly deprived for periods ranging from 5-14 weeks, after which the lid of the originally deprived eye was re-opened and the lid of the non-deprived eye sutured shut. If the reverse suturing occurred at five weeks of age, all neurons in the cortex were driven by the originally deprived eye. (Compare this to the case when monocular deprivation lasts to five weeks of age, there is no reverse closure, and all neurons are driven by the non-deprived eye.) If the reverse suture operation was performed during the 6th-14th weeks, neurons were found that were dominated by each eye. And if reverse suturing occurred at 14 weeks or later, there was little effect on ocular dominance, all cells being driven by the originally open eye. Thus, the limited time during the sensitive period when monocular deprivation has its maximum effects (4th-8th weeks) is also the time when reverse suturing can maximally cancel the effects of this deprivation. Blakemore and Van Sluyters (1974) have concluded that the sensitive period "is a period of true neuronal plasticity, during which time connexions can be broken and re-made...reverse suturing in the sensitive period causes total re-establishment of the effectiveness of the deprived eye" (p. 212).

Van Hof-Van Duin (1976b) has noted that cats show differential recovery from monocular and binocular deprivation. For binocular deprivation, even of fairly long duration (e.g., until the first year after birth), there is almost complete behavioral recovery (Van Hof-Van Duin, 1976a), although the longer the duration of the deprivation, the longer the recovery time that is required (Fantz, 1965). For monocular deprivation of long duration (e.g., until the seventh month after birth), behavioral impairments have been observed for the deprived eye on a number of visuomotor tasks (e.g., visual cliff, visually guided reaching), even after reverse suturing, but few deficits have been observed for simple pattern discriminations (Van Hof-Van Duin, 1976b). While others have reported a marked recovery in animals following monocular deprivation, Van Hof-Van Duin has suggested that the success rate varies with the novelty of the task. She argued, for example, that improved performance of subjects that have undergone repeated testing in the same apparatus reflects acclimation to the task (e.g., learning where the obstacles are) and not improvement in visual acuity. Van Hof-Van Duin (1976b) has found that visual deficits that are masked in a familiar environment reappear quite markedly when the animal is placed in a novel environment.

IV.2 Auditory System: General

Reports on the effects of auditory deprivation are meager in comparison to the extensive research on visual deprivation. This, to some extent, reflects a bias by experimenters who consider

the visual modality to be more important than the auditory. However, in some ways this bias is inconsistent with the facts that the cat, which is often used as the subject in visual experiments, is predominantly an auditory animal (Jane, Masterton and Diamond, 1965) and that auditory deprivation in humans may easily result in deficits of great importance to language and learning (Wiley, 1971).

While there are several studies on the effects of enriched or deprived conditions on auditory development, there are few investigations of whether or when the critical period occurs during development. From the limited research that has been conducted (Batkin, Groth, Watson and Ansberry, 1970; Batkin and Ansberry, 1964; Clopton and Silverman, 1976; Clopton and Winfield, 1976; Gauron and Becker, 1959; Gottlieb, 1975, 1971; Stein and Shuckman, 1973; Tees, 1967a, 1967b), there is near unanimous agreement that a restriction of early auditory experience has a debilitating effect on most auditory-related behaviors.

Gauron and Becker (1959) deprived some rats of auditory cues (by ear blocking) from the 11th to the 26th days after birth and other rats of visual cues (by dark rearing) from the 16th to the 26th day. They found that the auditory deprived animals lost in a competition for food task against visually deprived animals when a buzzer was used to signal the trial but performed better than the visually deprived subjects when a light was the signal.

Stein and Shuckman (1973) ear plugged rats at 13 days of age and maintained this treatment over a one month period. At the end of this time, rats were trained on a lever press response

using electrical stimulation of the cortex as a discriminative stimulus. Early auditory restriction resulted in significant retardation in learning when stimulation of the auditory rather than the visual cortex served as the discriminative stimulus. In contrast, animals initially deprived of auditory stimulation at 40 days of age and tested 45 days later learned the task with equal facility when either the auditory or visual cortex was stimulated. These data seem to point to a sensitive period somewhere between 13 and 40 days; during this period, auditory input might be necessary for the maintenance of normal auditory function.

The results from a series of experiments conducted by Gottlieb (1975, 1971) quite clearly indicate a short-term deficit in certain perceptual tasks as a result of auditory deprivation. Gottlieb's procedure was to isolate young ducklings in a sound attenuated chamber (to prevent subjects from hearing conspecific vocalizations) and to devocalize the ducklings (to prevent subjects from hearing self-vocalizations, which begin during the embryonic stage) four days prior to hatching. Ducklings that were deprived of auditory input showed a deficit in responding to the high frequency component (>0.825 kHz) of the maternal call.

Tees (1967a, 1967b) has investigated the importance of auditory stimulation in learning a number of auditory pattern discriminations. Deprived animals were raised from birth to 60 days in sound-resistant lockers and, in addition, had their ears plugged. Control subjects were raised in standard laboratory colony cages and hence, were exposed to naturally occurring

sounds. Tees found that deprived rats performed significantly worse than normally reared rats on pattern and duration discriminations but performed as well as normals on frequency and intensity discriminations. Tees (1967b) suggested that the capacity to perform frequency and intensity discriminations has an innate basis whereas the ability to perform duration and pattern discriminations requires some experience with patterned auditory stimulation.

Batkin and his colleagues (1969, 1964) have looked at behavioral and electrophysiological changes that occur following auditory deprivation. In a brief initial report (Batkin and Ansberry, 1964), they found that guinea pigs that were raised in a sound attenuated room for several months after birth showed marked insensitivity to sounds and did not display the Preyer reflex (a reflexive twitch of the pinna to sound). In a more detailed report, Batkin et al. (1969) measured auditory thresholds by means of cortical evoked potentials in normally reared and sound deprived rats. Immediately after birth, the experimental rats were placed in a sound attenuated room inside the crater wall of an extinct volcano for eight months. (Ambient noise level for frequencies between 0.2-20.0 kHz remained below 15-dB SPL.) Pure tones at six levels (0.5, 1.0, 2.0, 4.0, 8.0 and 10.0 kHz) and of varying intensities (from 30-75 dB) were used to assess auditory thresholds in experimental and non-deprived control subjects. The results indicated that the animals deprived of auditory stimulation had elevated thresholds at each frequency.

Following this initial testing, the deprived and control subjects were exposed to ambient noise for three weeks. This treatment had little effect on control subjects. However, experimental animals showed a significant increase in sensitivity following the exposure period and attained thresholds that were, on average, equivalent to those of the control animals.

Clopton and his colleagues (1976, 1977) have also examined electrophysiological changes that occur following auditory deprivation. Clopton and Silverman (1976) recorded the latency of single units in the inferior colliculi of rats deprived of auditory input to one ear. (Ligation of one auditory meatus was performed at ten days after birth and this closure condition continued for two months.) For units with high best frequencies,¹⁰ the latencies observed to clicks to the deprived ear were two to three times longer than those of comparable best frequency units stimulated at the non-deprived ear. For units with low best frequencies (<10 kHz), all units from the deprived and non-deprived ear showed normal latencies to a click stimulus.

Clopton and Winfield (1976) exposed young rats during the first four months of life to either an ascending or descending tone sweep. Following this period, they found that collicular units responded significantly more to the pattern that subjects had experienced than to the other pattern.

IV.3 Auditory System: Directional Responding

Since many cells of the various structures of the ascending auditory system are binaurally influenced, it is likely that disruption of binaural cues would have marked effects on directional

responding. One would anticipate that if the normal balance of auditory input to the two ears was altered, an impairment in binaural processing would result (e.g., blocking one ear would presumably interfere with the analysis of binaural cues). The evidence pertaining to this question supports this hypothesis.

In an interesting series of tests, Payne and Drury (1958) assessed a barn owl's ability to localize sound. An owl and a mouse were placed in a completely darkened barn. The floor of the barn was covered with dry oak leaves to ensure that the mouse's movements could be heard. On 13 out of 17 trials, the owl successfully struck the mouse and missed by only inches on the other trials. Payne and Drury ruled out odor cues by substituting a wad of paper (which was dragged through the leaves by a string) and found that the owl's accuracy remained the same. However, when one ear was plugged with cotton, the owl missed his target (a mouse again) by a good 18 inches. Although this study has serious methodological limitations (e.g., only one owl tested on a few trials in the monaural condition), the findings clearly suggest that cues from both ears are necessary for accurate localization.

A more systematic attempt to understand the role of binaural input has been undertaken by Clements and Kelly (1978), Silverman and Clopton (1977), and Feng, Gerhardt and Capranica (1976). Clements and Kelly (1978) have examined the effects of monaural and binaural ear blocking on approach behavior in guinea pigs. Newborn guinea pigs (1-4 days of age) that had both ears blocked

approached the sound source (guinea pig vocalizations) and, indeed, responded no differently than the normal, no-plugged animals (see p. 18). (The effect of ear blocking was to lower the intensity of the sound stimulus by about 10 dB. In the case of binaural blocking, it is assumed that the degree of attenuation was the same at both ears.) However, subjects with one ear plugged showed no tendency to respond toward the species call.

Clements and Kelly (1978) employed similar testing procedures to assess the effects of ear blocking in older guinea pigs (11-31 days old). For two of the groups--both ears blocked and only one ear blocked--the subjects were raised from birth and tested between days 11-31 with the blocks in place. Another group was raised with one ear blocked for the first 11 days after birth but tested without the blocks and a fourth group was reared without the blocks for the first 11 days but was tested with one ear blocked. Once again, the results indicated that binaurally blocked subjects approached the sound source more often than would be expected by chance, but monaurally blocked subjects did not. Ear blocking during the first 11 days seemed to result in at least a temporary disruption of approach behavior, even though neither ear was plugged during testing. Further, normal binaural input during the first 11 days did not improve performance if plugs were inserted during testing. Clements and Kelly (1978) concluded that "binaural cues play an important role in the ability of (guinea pig) infants to localize sounds" (p. 41) and suggested that disruption of normal binaural input during infancy might lead to impairments in localization behavior at later ages.

Feng, Gerhardt and Capranica (1976) have shown that under normal conditions, female treefrogs can accurately localize a male mating call but if one ear is blocked, subjects fail to orient toward this same call. They concluded that input from both ears was necessary for treefrogs to localize sounds.

Clopton and Silverman (1977) have studied the effects of monaural and binaural sound deprivation on the responsiveness of single unit activity in the inferior colliculi. In their study, rats were deprived of sound by either unilateral or bilateral ligation of the external auditory meatus(es) at 10, 30 or 60 days after birth. Deprivation was continued for the next three months in all groups. The number of units that were inhibited by the ipsilateral (click) stimulus was used as the measure of binaural interaction. (IC units are excited by contralateral stimulation and inhibited by ipsilateral stimulation.) Clopton and Silverman (1977) have reported that 1) rats that were monaurally deprived from ten days of age showed a marked loss of binaural interaction (i.e., absence of ipsilateral inhibition of unit activity); 2) this effect was less if begun at 30 days; 3) there was no effect of monaural deprivation if ligation occurred at 60 days; and 4) rats that were binaurally deprived from the tenth day to the third month had normal binaural activity. Clopton and Silverman (1977) have concluded that "the critical period for experiential validation of binaural interaction is between 10 days after birth and 60 days after birth" (p. 1275).

Summary. It is evident that the visual and auditory modalities have certain functional features in common. First, and most obvious, both systems

receive input from two external receptors.. The majority of units along the visual pathway respond to binocular stimulation and the majority of units along the auditory pathway are binaurally responsive. And in both systems, there is a critical period early in development during which time environmental events have their greatest impact. For example, during this sensitive period, monocular deprivation results in impairments in visuomotor behavior (Van Hof-Van Duin, 1976b) and a decrease in the number of neurons that respond to binocular stimulation (Wiesel and Hubel, 1965a) and similarly, monaural deprivation results in impairments in audiomotor behavior (Clements and Kelly, 1978) and a decrease in the number of neurons that respond to binaural stimulation (Silverman and Clopton, 1977).

V. EXPERIMENT I

The major aims of the first two experiments were to determine whether directional responses to sound occur early in ontogeny in gerbil and rat infants and to examine the relative potency of various stimuli (species vocalizations, white noise) of high and low intensity in eliciting approach behavior.

The intensity levels were chosen to provide a test of Schneirla's biphasic (approach-withdrawal) motivational theory (see p. 15).

Much of the evidence we have of directional responding during the early stages of development comes from observations of avian species (see p. 18) and the guinea pig, a precocial mammal (see p. 18 and p. 31). Thus, a demonstration of approach responses to sound in the young of altricial species would be of considerable importance if we wish to talk in general terms of sound localization ability in young mammals.

V.1 Method

Subjects. Forty-eight mongolian gerbil pups (Meriones unguiculatus), 16-23 days of age, were used in this experiment.

Twelve pregnant gerbils were purchased from High Oak Ranch (Goodwood, Ontario) and housed separately in breeding cages (12" x 14" x 7" high) on their arrival at the laboratory. The offspring of these gerbils were used as subjects. Both mother and pups remained

in the breeding cages for the duration of the experiment. All animals were provided food and water ad lib throughout the experiment.

Recording and Playback of Stimuli. Three sound stimuli were used in the present study. Frequency analyses of the auditory signals are included in Appendix 1. One call was recorded from four 11-day-old gerbils while they were huddled in their cage near their mother. Because huddling activity represents a typical social situation for gerbils at this age (Kaplan and Hyland, 1972), the vocalizations recorded during this activity will be referred to as a social call. [However, no additional meaning (e.g., biological significance) should be attached to this label.] Since other work (e.g., Gottlieb, 1965) has shown that species calls are effective in eliciting approach responses, it was felt that a species call might be equally effective in the present case. This assumption was borne out by pilot data which indicated that gerbils approached this stimulus (see Appendix 2).

A one-half inch Brüel-Kjaer microphone (Type 4133) was used to record the signal on an Ampex PR-500 instrumentation recorder. The tape of the call was made into a continuous loop on an Ampex FR-1300 instrumentation recorder. A sonogram (Kay Model B/65 Sonograph) of a portion of this call is shown in Figure 1. Note the rapidly descending frequency sweeps that characterize this vocalization.

During playback, the signal was passed from the Ampex FR-1300 recorder through an attenuator (Hewlett Packard, Model 350D) and Epitek amplifier (Model 1240) and was transduced by a Kef speaker (Model T27).

Figure 1. Sonogram of segment of gerbil social call.

In selecting the equipment for the transmission and transduction of the signal, great care was taken to ensure that the high frequency content of the sound would be preserved since gerbils can hear in the ultrasonic range (Finck, Schneck and Hartman, 1972; Finck and Sofouglu, 1966). Tests in our laboratory have shown that all components in the sound system have a flat frequency response up to at least 40.0 kHz.

The second stimulus, a white noise signal, was chosen for two reasons: 1) it represented a "biologically neutral" sound which contains an expansive range of frequencies and 2) previous observations in our laboratory had indicated that gerbils approached this signal. The white noise was produced by a Grason Stadler Noise Generator (Model 4556) and fed through a one/second switch while being recorded on an Ampex FR-1300 recorder. The resulting signal was heard as alternating one second segments of white noise and silence.

A third signal consisted of all the noise present in the sound system. While the major purpose of this study was to provide evidence of approach behavior and not to identify specific sounds that would motivate approach behavior, it was, nonetheless, of importance to ensure that approach responses, if observed, were to a particular stimulus (or stimuli) and not to transient noises in the sound system. To rule out the possibility that the subjects were responding to noise in either the recorder and/or amplifier, an unrecorded section of the tape (i.e., one that contained no signal) was played back to the animals in the test apparatus.

Test Apparatus. The test apparatus is depicted in Figure 2. The floor of the test maze was a circular piece of wood, 36 inches in diameter, painted gray and divided into eight equal pie-shaped segments. The boundaries of these segments were clearly delineated by white lines. The sides of the apparatus were constructed of wire mesh and extended 17 inches from the floor. A cotton cloth material was affixed along the outside of the wire mesh to restrict subjects' vision of objects outside the apparatus.

Outside the maze, but directly centered behind each of the eight segments, were wooden speaker mounts. Both the base and vertical wood pieces that comprise these mounts were 6" x 8" x 1/2" thick. The Kef speaker was placed in one of these wooden blocks. The others, mock speakers, were placed to control for possible visual cues. To control for possible tactile or olfactory gradients, the position of the Kef speaker was randomly determined on each trial.

A circular start area, 7 inches in diameter, was located in the center of the apparatus and was painted white. A cylinder-shaped cage, consisting of a clear circular Plexiglass rim (6" in diameter) and 5" long steel bars (1/8" in diameter and spaced about 1/4" apart) inserted in the rim, could be placed over the start area. This start gate was used to restrain the animal in the maze until the sound stimulus was turned on. The experimenter, who was located in an adjacent room, controlled the operation of the start gate by means of a pulley hookup.

One other white circular line, 24" in diameter, was painted on the floor. This outside circle was used as a guide to locate the subject as it moved toward the periphery.

Figure 2. A cutaway view of the test apparatus.

Four room dividers, 2" x 72" x 48", high surrounded the maze and were used to cut down on reflected sound in the test apparatus.

A Sony video camera (type 3200), mounted on a tripod and equipped with a wide angle lens (Sony, VEL-08) was set up alongside the maze. The subjects' movements in the maze were observed by the experimenter on an Electrohome video monitor.

Procedure. Eight subjects were randomly assigned to one of four experimental or two control groups. Two of the experimental groups were exposed to the social call; another two, to the white noise signal; and the two control groups to the noise which was present in the sound system. One of the two groups at each stimulus level heard a high intensity signal and the other, a low intensity signal.

Testing began when pups were 16 days of age. Each subject was tested individually and given three trials/day on each of eight days (postnatal days 16-23). Pilot data had indicated that approach responses were strongest over this period.

On days 12-15, all subjects received three practice trials/day. Because subjects at this age did not locomote very well (Kaplan and Hyland, 1972) and were not yet sensitive to a number of frequencies (Finck, Schneck and Hartman, 1972), they seldom approached the sound source. However, pilot testing had shown that subjects became familiarized with the test apparatus and procedure during this practice period (see Appendix 3).

Prior to the start of a trial, a pup was placed in a separate holding bucket (6 1/2" x 10 1/2" x 5" high) and brought

to the room adjoining the test chamber. To initiate a trial, the pup was placed in the start area with the start cage lowered and the sound off. (On every trial, the subject was placed in the cage facing the same direction.) Following five seconds, the sound was turned on. After a further eight seconds, the start gate was raised and the movement of the subject was recorded.

Subjects' movements were scored on data sheets which contained a miniature facsimile of the floor plan of the maze (see Appendix 4). In addition, latency data were collected on a) initial responses (i.e., how fast the animal left the start area) and b) final responses (i.e., how fast the animal crossed the outer circle). The four-paw criterion was used to determine both initial and final responses.

Initial and final responses were scored as follows:

- a) no response--subject remained in start area (for initial)
--subject did not cross outer line (for final)
- b) direct approach--subject approached segment where speaker was positioned
- c) indirect approach--subject approached one of the segments adjacent to where speaker was positioned
- d) direct avoidance--subject approached segment directly opposite to where speaker was positioned
- e) indirect avoidance--subject approached one of the segments adjacent to segment directly opposite to where speaker was positioned
- f) neutral response--subject approached one of the two segments which represented neither approach nor avoidance responses (i.e., the two segments not included in categories b-e)

Assuming the Kef speaker was behind segment 3 in Figure 2, a direct approach would have been to segment 3; an indirect approach

would have been either to segments 2 or 4; a direct avoidance would have been to segment 7; an indirect avoidance would have been either to segments 6 or 8; and a neutral response would have been either to segments 1 or 5.

A subject that did not respond within 82 seconds was removed to the holding bucket to await the next trial (or, if it was the last trial, the animal was placed back in its home cage). If a subject crossed the outside line prior to 82 seconds, the sound was terminated and the subject was removed to the holding bucket until the start of the next trial. The intertrial interval was between 10-15 minutes.

It should be noted that the only reinforcement for the subject in the test situation was that provided by approaching the auditory signal or being removed from the maze.

V.2 Results

Initially, a 3 (Sound) x 2 (Intensity) multivariate analysis of variance was computed which included: 1) two measures of general responsiveness - number of crossings over the initial line (irrespective of direction) and number of crossings over the final line (irrespective of direction); 2) two latency measures-latency to initial response and latency to final response; 3) two general approach measures - percent initial direct plus indirect (D+I) approach responses and percent final D+I approach responses; and 4) two more precise measures of approach - percent initial direct approach responses and percent final direct approach responses.¹¹ The multivariate F's for the Sound effect ($F=5.50$, $df=16/70$, $p<.001$),

Intensity effect ($F=3.51$, $df=8/35$, $p<.005$) and the Sound X Intensity interaction ($F=1.86$, $df=16/70$, $p<.05$) were all statistically significant. Corresponding Wilkes Lambda values for the Sound ($U=0.19$, $df=2/42$, $p<.05$), Intensity ($U=0.55$, $df=1/42$, $p<.05$), and interaction ($U=0.49$, $df=2/42$, $p<.05$) effects were also significant.

The means and standard deviations for the number of initial and final responses are given in Table 1. With number of initial or final responses as the dependent measure, neither the Intensity effect nor the interaction effect was significant, but the main effect of Sound was statistically significant (see Table 2). Newman-Keuls' comparisons ($p<.05$) indicated that, for both the number of initial and final responses, the white noise and control groups did not differ but that both these groups had significantly fewer responses than the "social call" group. Thus, a species social call appears to have facilitated responding in gerbils, at least in the apparatus used in this experiment. It should be noted, however, that for initial responses, subjects in all groups showed a fairly high rate of response and that the difference between the social group and the other groups, while statistically significant, was not large.

The latency data are summarized in Table 3. A 3 (Sound) x 2 (Intensity) analysis of mean latency for initial and final responses indicated a significant main effect of Sound, but neither the main effect of Intensity nor the interaction effect was significant (see Table 2). Newman-Keuls' tests ($p<.05$) revealed that subjects

TABLE 1

MEANS AND STANDARD DEVIATIONS FOR THE NUMBER OF INITIAL
AND FINAL RESPONSES (EXPERIMENT I)

Sound	Intensity	Initial		Final	
		M	SD	M	SD
Social	Low	23.62	0.74	21.50	2.73
Social	High	23.88	0.35	20.12	2.59
White Noise	Low	22.62	1.18	17.50	2.56
White Noise	High	23.12	1.36	16.50	3.74
Control	Low	22.75	1.28	19.62	3.42
Control	High	22.12	1.13	17.25	2.76

Note: Mean maximum number of responses was 24. (Subjects were run for 3 trials/day over 8 days.)

TABLE 2

SUMMARY TABLE OF ANALYSES OF VARIANCE FOR INITIAL AND FINAL RESPONSES (EXPERIMENT I)

Dependent Variable	Source of Variance	df	Initial			SIG	df	Final			SIG
			MS	F				MS	F		
Number of responses	Sound	2	7.14	6.27		p<.01	2	59.31	6.59		p<.01
	Intensity	1	0.02	0.02		ns	1	30.08	3.34		ns
	Interaction	2	1.39	1.22		ns	2	2.02	0.22		ns
	Within Cell	42	1.13				42	9.00			
Latency	Sound	2	58.66	4.44		p<.05	2	230.27	6.47		p<.01
	Intensity	1	20.93	1.59		ns	1	9.45	0.27		ns
	Interaction	2	1.10	0.08		ns	2	0.94	0.42		ns
	Within Cell	42	13.20				42	5.59			
Percent D+I	Sound	2	1902.10	24.66		p<.001	2	1059.60	10.56		p<.001
	Intensity	1	180.19	2.34		ns	1	1150.50	11.47		p<.01
	Interaction	2	397.94	5.16		p<.01	2	613.52	6.11		p<.01
	Within Cell	42	77.14				42	100.35			
Percent direct	Sound	2	682.75	8.93		p<.001	2	290.33	3.63		p<.05
	Intensity	1	20.02	0.26		ns	1	432.00	5.41		p<.05
	Interaction	2	42.33	0.55		ns	2	302.25	3.78		p<.05
	Within Cell	42	76.45				42	79.87			

TABLE 3

MEANS AND STANDARD DEVIATIONS FOR LATENCY TO INITIAL
AND FINAL RESPONSES (EXPERIMENT I)

Sound	Intensity	Initial Latency (in secs.)		Final Latency (in secs.)	
		M	SD	M	SD
Social	Low	8.31	3.05	19.45	5.45
Social	High	9.19	4.16	22.09	9.16
White Noise	Low	11.61	2.78	28.92	6.80
White Noise	High	13.51	5.45	27.74	4.20
Control	Low	9.75	2.36	24.45	3.29
Control	High	10.94	3.11	25.69	5.02

responded over the initial line more rapidly to the social call than to the white noise and that subjects in the control group did not differ from subjects in either of the two sound groups. For final responses, subjects that heard the social call crossed over the final line significantly faster than either subjects that heard the white noise or control noise and subjects in the latter two groups did not differ (Newman-Keuls, $p < .05$).

For each of the six groups, single-sample t tests (Hayes, 1963) were computed to assess whether initial or final approach behavior was above what could have been expected by chance. For the D+I approach measure, the level of approach expected by chance alone was 37.5%, since three of the eight segments in the circular maze were scored as representing an approach response. For the direct approach measure, the chance level was 12.5%, since only one of the eight segments was scored as representing direct approach. For D+I approach, the low intensity social group as well as the low and high intensity white noise groups showed above chance performance for initial responses. In addition, the low intensity social group performed at an above chance basis for final responses (see Table 4). For direct approach, only subjects in the low intensity social call group exhibited more responses toward the speaker than could have been expected on a chance basis, and this was the case for both initial and final responses (see Table 4).

The mean percent D+I initial and final responses are presented in Figures 3 and 4. For initial response, the analysis

TABLE 4

VALUES FOR SINGLE SAMPLE t TESTS USED TO DETERMINE ABOVE
CHANCE D+I AND DIRECT APPROACH BEHAVIOR (EXPERIMENT I)

t values for D+I approach		
Group	Initial	Final
Social Low	16.63*	17.88*
Social High	2.16	1.14
White Noise Low	3.74*	2.27
White Noise High	4.15*	0.84
Control Low	1.32	0.63
Control High	0.00	0.10

t values for direct approach		
Group	Initial	Final
Social Low	4.40*	5.33*
Social High	2.35	0.19
White Noise Low	1.42	1.89
White Noise High	1.84	0.39
Control Low	1.11	0.42
Control High	0.05	0.76

* $p < .01$

** $p < .05$

FIGURE 3. Mean percentage of initial D+I approach responses made by each of the six groups (Experiment I). Note: 37.5% represents chance level of approach responding.

FIGURE 4. Mean percentage of final D+I approach responses made by each of the six groups (Experiment I). Note: 37.5% represents chance level of approach responding.

of mean percent D+I approach indicated a significant Sound X Intensity effect and a significant Sound effect, but the Intensity effect was not significant (see Table 2). While the low and high intensity white noise groups and the low intensity social call group all showed above chance approach performance (see above) Newman-Keuls' comparisons ($p < .05$) indicated that subjects in the low intensity social group made a higher percentage of approach responses than subjects in the white noise groups and that the latter two groups did not differ. For final response, the analysis of mean percent D+I approach indicated significant main effects of Sound and Intensity and a significant Sound X Intensity interaction (see Table 2). Newman-Keuls' comparisons ($p < .05$) indicated that the low intensity social group had significantly more final D+I approaches than the other groups and that the other three experimental and two control groups did not differ.

The analysis of mean percent direct approach for initial responses indicated a statistically significant effect of Sound; however, the Intensity effect and interaction effect were not significant (see Table 2). The analysis of mean percent direct final responses indicated that both main effects and the interaction effect were significant (see Table 2). These results can largely be attributed to the high percentage of direct responding by subjects in the low intensity social group, which was the only group to show above chance performance.

V.3 Discussion

Gerbil pups that were exposed to a species social call crossed over the initial and final lines more often and more quickly than pups who were exposed to either the white noise or control signals. Although the differences between sound groups on response rate and latency were not large, the species call did serve to push initial responding up near the 100 percent level and to shorten initial response latencies by about two seconds and final response latencies by almost five seconds. These results are in accord with Gottlieb's (1965) findings for an avian species. Gottlieb reported that Peking ducklings (10-21 hours after hatching) made more responses and had shorter latencies to a call of their own species than to calls of other species.

Without doubt, gerbil infants that heard the low intensity social call responded toward the speaker segment more often than infants in any of the other groups. Although the subjects exposed to the white noise signal showed above chance initial approach on the more general measure (48.5% and 48.8% D+I approach responses for the low and high intensity white noise groups, respectively), their approach rate was not nearly as high as those subjects exposed to the low intensity social call (65.1% D+I). Further, only the subjects in the low intensity social group showed above chance approach on final D+I responses and on the more demanding direct only measures. Thus, subjects in the low intensity social group approached the signal more often and more accurately than subjects in other groups.

Generally, these results confirm Schneirla's biphasic (approach-withdrawal) hypothesis on orienting responses in young animals. Accordant with Schneirla's position, subjects approached the low intensity social signal, but not the high intensity version of this same call. To have been entirely consistent with a Schneirlan position, subjects would have had to approach all the low intensity signals and avoid all the high intensity signals. [Recall that Schneirla suggested that it was the quantitative component (i.e., intensity) of the stimulus and not the qualitative component (i.e., type of call) that determined approach or withdrawal behavior.] In fact, subjects approached certain of the low intensity sounds and not others. And, there was little evidence of avoidance behavior to the high intensity calls. With high intensity signals, the distribution of subjects' responses to the various maze segments was about what was expected by chance alone. However, it should be noted that the high intensity signals, which contained frequency components as high as 88 dB SPL (see Appendix 1), might not have been sufficiently intense to have led to avoidance.

VI. EXPERIMENT II

VI.1 Method

Subjects. Forty-eight Sprague Dawley rat pups (Rattus norvegicus), 13-20 days of age, were used in this experiment.

Eight rat litters, culled to six pups each, were obtained from the Department of Biology colony at Carleton University. Each litter was brought to the experimenter's laboratory when the pups were 1-2 days old. All litters were individually housed in breeding cages and provided food and water ad lib throughout the experiment.

Recording and Playback of Stimuli. Two sound signals were recorded for this study. The first was a distress call emitted by a rat pup (8 days of age) that had its tail pinched. The second stimulus was a "social vocalization" of rat pups (8 days of age) huddled in their cage. Sonograms of the two species calls are shown in Figures 5 and 6. While the particular portion of the rat social call depicted in Figure 5 indicates a descending frequency sweep, other parts of the call were characterized by ascending sweeps. Both types of sweeps were of similar duration and included many of the same frequencies. A major characteristic of the rat distress call (Figure 6) is the number of ascending and descending frequency sweeps within each portion. Interestingly, components of the distress call were about twice as

Figure 5. Sonogram of segment of rat social call.

Figure 6. Sonogram of segment of rat distress call.

long as components of the social call. A final stimulus consisted of noise in the sound system (see p. 37). Frequency analyses of these calls are included in Appendix 5.

The procedure and equipment used in recording and playing back the signals have already been described in detail (see pp. 36-37). In the present study, the social and distress calls were recorded on a Sony tape recorder (Model TC630) and made into a continuous loop (Sony recorder, Model TC377). In the test situation, the loop was played back repeatedly over a Sony Model TC630 tape recorder.

A white noise signal was not included in the present experiment because previous observations (Potash, unpublished data) had indicated that rat pups neither approached nor avoided this signal.

Apparatus. The same apparatus used in Experiment I was used in the present experiment.

Procedure. Eight animals were randomly assigned to one of six groups. Subjects in three of the groups received high intensity sounds and subjects in the other three, low intensity sounds. Subjects in one high and one low intensity group were exposed to either a distress call, social call or sound system noise.

Practice trials began when the animals were 9 days old and continued over the next three days. On each day, subjects were run for three trials. Because rats first show sensitivity to sound by about the 12th postnatal day (Wada, 1923), or perhaps

a few days earlier (Volokhov, 1968), it would have been futile to examine approach responses to sound prior to this time. However, pilot testing had shown that an acclimation period in the apparatus was essential, since rat pups often "freeze" during the first several days of testing. Thus, the subjects became accustomed to the test procedure (e.g., moving out of the start area) during the practice period (see Appendix 6).

Testing commenced on postnatal day 13 and continued through day 20. Subjects were given three trials/day. The intertrial interval was between 10-15 minutes.

The procedure for running the animals and scoring the responses was identical to that used in Experiment I, with one exception. In this study, subjects were given only 52 seconds to make a final response after the start gate had been raised. Pilot work had indicated that rat pups moved across the outer line much sooner than gerbil pups.

VI.2 Results

A 3 (Sound) X 2 (Intensity) multivariate analysis of variance, with number of initial and final responses, latencies to initial and final responses, percent D+I initial and final approaches and percent direct initial and final approaches as the dependent variables, revealed a significant Intensity effect ($F=3.32$, $df=8/35$, $p<.007$) and a significant Sound X Intensity interaction ($F=2.03$, $df=16/70$, $p<.022$), but the Sound effect failed to reach significance ($F=1.62$, $df=16/70$, $p>.05$). Wilkes Lambda values for the Intensity ($U=0.56$, $df=1/42$, $p<.05$) and

interaction ($U=0.46$, $df=2/42$, $p<.05$) effects were also significant.

The mean number of responses over the initial line and final line for all groups is shown in Table 5. There appears to be little difference between groups in the number of responses, either initial or final, and it is evident that subjects from all groups responded at a fairly high rate over the 24 trials. As anticipated, the 3 (Sound) X 2 (Intensity) analyses of variance indicated that there were no significant main effects nor any significant interaction effect for either the number of initial or final responses (see Table 6). Typically, an animal responded out of the start area within 3-4 seconds after the start gate was lifted (see latency data below), and moved quickly to the periphery without a change in direction.

The latency data for both initial and final responses are shown in Table 7. With mean latency to the initial response as the dependent measure, neither the main effects of Sound or Intensity nor the interaction term reached significance (see Table 6). With mean latency to the final response as the dependent measure, neither the Sound effect nor the Sound X Intensity interaction was significant, but the Intensity effect was statistically significant (see Table 6). The subjects in the high intensity groups crossed the outer line faster than subjects in the low intensity groups. The trend was in the same direction for the initial response data although, as noted, the latency difference between high and low intensity groups did not reach significance. Since subjects in the high intensity groups showed no better than a chance approach to sound (see p. 63), their rapidity in responding, especially over the outer line, may have resulted

TABLE 5

MEANS AND STANDARD DEVIATIONS FOR THE NUMBER OF INITIAL
AND FINAL RESPONSES (EXPERIMENT II)

Sound	Intensity	<u>Initial</u>		<u>Final</u>	
		M	SD	M	SD
Social	Low	23.88	0.35	23.25	1.75
Social	High	24.00	0.00	23.88	0.35
Distress	Low	23.62	1.06	23.38	1.77
Distress	High	23.88	0.35	23.75	0.71
Control	Low	23.75	0.71	23.25	1.74
Control	High	24.00	0.00	24.00	0.00

Note: Mean maximum number of responses was 24. (Subjects were run for 3 trials/day over 8 days.)

TABLE 6

SUMMARY TABLE OF ANALYSES OF VARIANCE FOR INITIAL AND FINAL RESPONSES (EXPERIMENT II)

Dependent Variable	Source of Variance	Initial				Final			
		df	MS	F	SIG	df	MS	F	SIG
Number of responses	Sound	2	0.14	0.47	ns	2	0.02	0.01	ns
	Intensity	1	0.52	1.67	ns	1	4.08	2.48	ns
	Interaction	2	0.02	0.07	ns	2	0.14	0.09	ns
	Within Cell	42	0.31			42	1.64		
Latency	Sound	2	0.26	0.13	ns	2	1.12	0.25	ns
	Intensity	1	2.38	1.12	ns	1	26.10	5.81	P<.02
	Interaction	2	0.71	0.33	ns	2	2.99	0.67	ns
	Within Cell	42	2.12			42	4.49		
Percent D+I	Sound	2	567.58	8.67	P<.001	2	367.77	4.11	P<.05
	Intensity	1	768.00	11.73	P<.001	1	760.02	8.48	P<.01
	Interaction	2	1033.00	15.78	P<.001	2	629.65	7.03	P<.01
	Within Cell	42	65.44			42	89.57		
Percent direct	Sound	2	85.89	1.62	ns	2	31.93	0.91	ns
	Intensity	1	10.08	0.19	ns	1	420.08	11.95	P<.001
	Interaction	2	364.77	6.90	P<.01	2	123.52	3.51	P<.05
	Within Cell	42	52.86			42	35.14		

TABLE 7

MEANS AND STANDARD DEVIATIONS FOR LATENCY TO INITIAL
AND FINAL RESPONSES (EXPERIMENT II)

Sound	Intensity	Initial Latency (in secs.)		Final Latency (in secs.)	
		M	SD	M	SD
Social	Low	3.62	1.28	7.52	1.46
Social	High	3.05	1.37	5.38	1.50
Distress	Low	3.84	1.77	7.74	3.07
Distress	High	3.05	1.39	5.96	1.98
Control	Low	3.18	1.73	7.20	2.44
Control	High	3.20	1.08	6.70	1.80

from the aversiveness of the high intensity sound, which they learned could be terminated by crossing the outer line.

The mean percent D+I approach for initial and final responses are shown in Figures 7 and 8, respectively. Analyses of mean initial and final D+I approach responses indicated that the main effects of Sound and Intensity as well as the Sound X Intensity interaction were all significant (see Table 6). The high level of directional responding by subjects in the low intensity social group largely contributed to these statistically significant results. Newman-Keuls' comparisons ($p < .05$) of both initial and final responses indicated that there was a significant difference between the low intensity social group and the other five groups and that the latter groups did not differ.

For mean percent direct initial approach, the analysis of variance indicated a significant interaction effect, but neither main effect was significant. For mean percent direct final approach, both the interaction effect and Intensity effect were statistically significant, but the Sound effect was not (see Table 6). As in the previous D+I case, the significant effects can largely be accounted for by the preponderance of approach responses by subjects in the low intensity social group.

Single-sample t tests were used to determine if groups showed above chance approach behavior toward the sound on initial or final responses. The results of these analyses are relatively clearcut (see Table 8). For the D+I and direct approach measures, only subjects in the low intensity social group approached the speaker

FIGURE 7. Mean percentage of initial D+I approach responses made by each of the six groups (Experiment II). Note: 37.5% represents chance level of approach responding.

FIGURE 8. Mean percentage of final D+I approach responses made by each of the six groups (Experiment II). Note: 37.5% represents chance level of approach responding.

TABLE 8

VALUES FOR SINGLE SAMPLE t TESTS USED TO DETERMINE ABOVE
/CHANCE D+I AND DIRECT APPROACH BEHAVIOR (EXPERIMENT II)

t values for D+I approach		
Group	Initial	Final
Social Low	10.78*	6.38*
Social High	0.33	0.24
Distress Low	1.01	1.48
Distress High	1.20	0.29
Control Low	1.20	1.49
Control High	2.35	1.64
t values for direct approach		
Group	Initial	Final
Social Low	3.38**	4.83*
Social High	0.40	0.60
Distress Low	0.39	0.83
Distress High	0.92	0.63
Control Low	0.28	2.79**
Control High	2.12	0.14

* $p < .01$

** $p < .05$

segment at an above chance level for both initial and final responses. In addition, the low intensity control group subjects performed at an above chance basis for final responses on the percent direct measure only. However, even on this measure, the approach performance of the low intensity control group (17.75%) was not nearly as strong as that of the low intensity social group (23.12%).

VI.3 Discussion

Rat infants showed an extremely high rate of responsiveness, irrespective of the intensity or type of sound. Unlike gerbil infants that showed a greater tendency to respond out of the start area and over the final line to a species call, rat infants in all groups crossed over the initial and final lines at close to a 100 percent rate to all of the auditory signals. Perhaps there are signals that might have led to a diminution in the response rate; the identification of these sounds, however, was outside the scope of the present study.

The analyses for latency indicated that the high intensity groups (none of which showed approach behavior) had shorter latencies in crossing over the outer line than the groups exposed to the low intensity signals. Perhaps, the infants found the high intensity signal to be aversive and learned to escape from the sound by more quickly crossing over the final line. (Crossing over any part of the final circle - either in approach, avoidance or neutral territory - would have led to a termination of the sound.) Consistent with this explanation is

the fact that the low intensity control and distress groups, which also did not show above chance behavior, nonetheless, showed the longer latencies characteristic of the low intensity social group, which did show approach behavior. Thus, it is not likely that subjects took longer to make an approach response to the sound source; rather, the shorter latencies probably reflect the aversive qualities of the high intensity signals.

The analyses for the approach measures (percent D+I, percent direct and the single-sample t tests) consistently indicate that subjects approached the low intensity social call more frequently than any of the other calls. For both initial and final responses and on both D+I and direct approaches, rat pups exposed to the low intensity social call approached the sound segment at levels well above chance. Only one other group, the low intensity control group, showed above chance performance on any of the measures, and this was for final responses on the direct approach measure. However, the significance of this finding is limited if we consider that subjects in the low intensity control group did not show initial direct approach nor any approaches (either initial or final) on the more general percent D+I measure. Thus, the one clear, definitive finding concerning directional responding emerging from this study is that rat infants have a fairly strong tendency to approach a low intensity species social call.

Support for Schneirla's approach-withdrawal hypothesis comes from two findings: 1) The high intensity social call did not facilitate approach responding, whereas the low intensity

social call did. 2) The fact that subjects in the high intensity groups showed the shortest latencies can be interpreted as an indication of the subjects' attempt to avoid these signals. On the other hand, infants did not approach any of the low intensity signals besides the social call. According to Schneirla's argument, any low intensity signal should have elicited an approach reaction. Considering the results of the previous experiment and other work reported for avian species (Gottlieb, 1965; Beer, 1970) and Homo sapiens (Eisenberg, 1976), it seems that a modification of Schneirla's hypothesis that, in addition to the emphasis he already places on the quantitative aspects of the stimulus, incorporated the importance of the type of stimulus, would have greater validity and generalizability.

VII. EXPERIMENT III

In Experiments III and IV, the effects of blocking one ear and two ears on approach behavior in gerbil and rat infants were examined. Specifically, these studies were designed to investigate the importance of binaural cues in the localization behavior of infants. On the basis of previous results (Clements and Kelly, 1978; Payne and Drury, 1958) that have indicated impairments in approach performance following monaural blocking but not binaural blocking, it was anticipated that subjects with one ear blocked, but not with two ears blocked, would show a decline in directional approach responses. This finding would clearly suggest that young altricial mammals are capable of processing binaural cues.

VI.1 Method

Subjects. Twenty-four gerbil pups, 16-23 days of age, served as subjects. The subjects were the offspring of five pregnant gerbils that were purchased from High Oak Ranch. Conditions for housing the animals in the laboratory have been described previously (see p. 34).

Ear Blocking. The method of ear blocking used in the present study has been described in Clements (1973). Briefly, wax plugs were inserted into the external meatus(es) and held in place by elastoplast bandages. The subjects were under ether

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anesthesia while the ears were being blocked. The plugs were checked daily to ensure that they were firmly in place. Following the final day of testing, the ear plugs were removed and the ears were examined with an otoscope for middle ear infection. No signs of abnormality or infection were found in any of the subjects.

Procedure. Subjects were randomly assigned to one of three groups: 1) no ears blocked (control); 2) one ear blocked (left ear for half the subjects, right ear for the other half); and 3) both ears blocked.

Animals in the experimental groups had their ear(s) plugged on the 11th postnatal day. Subjects in the control group were put under ether anesthesia and received an equivalent amount of handling at that time.

The low intensity social signal, which proved most effective in eliciting approach behavior in Experiment 1, was used as the sound stimulus in the present experiment.

Subjects in all groups were given three practice trials/day in the test apparatus from the 12th to the 15th postnatal days. Testing began on postnatal day 16 and continued through day 23. Details of the test procedure and apparatus have been described previously (pp. 38-42).

VII.2 Results

With the number of initial and final responses, latencies to initial and final responses, percent initial and final D+I responses and percent initial and final direct

responses as the dependent measures, the multivariate analysis of variance was statistically significant ($F=4.55$, $df=16/28$, $p<.001$). The Wilkes Lambda value was also significant ($U=0.08$, $df=2/21$, $p<.05$). In fact, the blocking manipulation accounted for approximately 90 percent of the variability ($R=0.951$).

The means and standard deviations for the number of initial and final responses are presented in Table 9. Subjects in the monaurally blocked, binaurally blocked and control groups did not differ on either of these measures (see Table 10).

The means and standard deviations for latencies to initial and final responses are presented in Table 11. One-way analyses of variance indicated a statistically significant difference between groups on initial latency but not on final latency (see Table 10). However, because of the fairly small mean differences between groups and the relatively low power of the Newman-Keuls test, none of the pairwise comparisons for initial latency reached significance (Newman-Keuls, $p<.05$).

The mean percent D+I initial and final responses are shown in Figures 9 and 10; respectively. The analyses of variance indicated significant differences in percent D+I approach for both initial and final responses (see Table 10). Subsequent Newman-Keuls' tests ($p<.05$) indicated that for initial responses, the control group made a greater percentage of D+I responses than either of the blocked groups and the 2-ears blocked group made a greater percentage of D+I approaches than the 1-ear blocked group. For final responses,

TABLE 9

MEANS AND STANDARD DEVIATIONS FOR THE NUMBER OF INITIAL
AND FINAL RESPONSES (EXPERIMENT III)

Group	<u>Initial</u>		<u>Final</u>	
	M	SD	M	SD
Normal	23.62	0.52	21.12	2.10
Binaurally Blocked	24.00	0.00	21.50	2.14
Monaurally Blocked	23.75	0.46	20.62	1.99

Note: Mean maximum number of responses was 24. (Subjects were run for 3 trials/day over 8 days.)

TABLE 10

SUMMARY TABLE OF ANALYSES OF VARIANCE FOR INITIAL AND FINAL RESPONSES (EXPERIMENT III)

Dependent Variable	Source of Variance	Initial				Final			
		df	MS	F	SIG	df	MS	F	SIG
Number of responses	Blocking	2	0.29	1.81	ns	2	1.54	0.36	ns
	Within Cell	21	0.16			21	4.32		
Latency	Blocking	2	51.65	3.71	p<.05	2	28.45	1.04	ns
	Within Cell	21	13.92			21	27.43		
Percent D+I	Blocking	2	1787.50	40.42	p<.001	2	1903.60	23.80	p<.001
	Within Cell	21	44.22			21	79.97		
Percent direct	Blocking	2	471.29	10.20	p<.001	2	334.04	4.44	p<.05
	Within Cell	21	46.20			21	75.20		

TABLE 11

MEANS AND STANDARD DEVIATIONS FOR LATENCY TO INITIAL
AND FINAL RESPONSES (EXPERIMENT III)

Group	Initial Latency (in secs.)		Final Latency (in secs.)	
	M	SD	M	SD
Normal	10.84	4.05	24.56	6.98
Binaurally Blocked	11.24	3.72	23.04	4.52
Monaurally Blocked	15.42	3.40	26.79	3.63

FIGURE 9. Mean percentage of initial D+I approach responses made by each of the three groups (Experiment III). Note: 37.5% represents chance level of approach responding.

FIGURE 10. Mean percentage of final D+I approach responses made by each of the three groups (Experiment III). Note: 37.5% represents chance level of approach responding.

the control and binaurally blocked groups had significantly more D+I approaches than the monaurally blocked group and the former two groups did not differ. Results of the single-sample t tests indicated that for initial and final D+I responses the control and binaurally blocked groups approached the sound at above chance levels but that the monaurally blocked group did not (see Table 12).

Analyses of mean initial and final direct responses indicated a significant difference between groups (see Table 10). Newman-Keuls' comparisons ($p < .05$) showed that animals in the normal and binaurally blocked groups, which did not differ, directly approached the sound source a greater percentage of the time than did animals in the monaurally blocked group for both initial and final responses. Further, only the 2-ears blocked and normal groups showed above chance direct approach behavior for both initial and final responses (see Table 12).

An "away-toward" score was computed for each subject in the monaural condition to determine whether these subjects showed a preference to respond to the sound source on the side toward or away from the blocked ear. The away-toward score represents the number of responses made away from the side of the plug minus the number of responses made toward the side of the plug for all indirect and neutral responses (i.e., the two segments on each side of the speaker segment). For both initial and final responses, away-toward scores

TABLE 12

VALUES FOR SINGLE SAMPLE t TESTS USED TO DETERMINE ABOVE
CHANCE D+I AND DIRECT APPROACH BEHAVIOR (EXPERIMENT III)

t values for D+I approach		
Group	Initial	Final
No Blocks	11.26*	9.06*
2-ears Blocked	22.74*	11.67*
1-ear Blocked	1.56	0.65

t values for direct approach		
Group	Initial	Final
No Blocks	3.39**	2.44**
2-ears Blocked	4.40*	4.04*
1-ear Blocked	1.40	0.48

* $p < .01$

** $p < .05$

were computed for all subjects in the monaural group and the means and standard deviations of these scores were analyzed using single-sample t tests.¹² Results of this test for initial responses indicated that there was a significant preference to respond to the sound on the side away from the block ($t=3.56$, $df=7$, $p<.01$). Although the trend was in the same direction for crossings over the outer line, the analysis for final responses did not reach statistical significance ($t=1.77$, $df=7$, $p>.05$).

VII.3 Discussion

As in Experiment I, subjects in all groups responded at a fairly high rate to the low intensity social call. Thus, blocking either one ear or two ears had little effect on subjects' responsiveness.

In terms of directional responding, subjects in the control group and 2-ears blocked group approached the sound segment at above chance levels and this was the case for both the general (percent D+I) and the more accurate (percent direct) measures. With the exception of initial D+I responses, there were no differences between the normals and binaurally blocked subjects in their tendency to approach the sound stimulus. On initial D+I responses, the normals approached somewhat more often than the binaurally blocked subjects, but as noted above, both groups approached at well above the 37.5% level expected by chance. In contrast, on both initial and final responses and for both the percent D+I and percent direct measures, subjects in the monaural condition did not approach the sound segment at above chance levels. The

results of the present experiment are in close agreement with the findings reported by Clements and Kelly (1978). In their study, guinea pig infants with 2-ears blocked and neither ear blocked approached the sound source, whereas infants with 1-ear blocked did not.

The failure of the monaurally blocked subjects to approach a stimulus that obviously elicits this response in normal and binaurally blocked animals probably resulted from a disruption of binaural cues. Because of the high frequency content of the stimulus used in this study and the known importance of the Δf_i binaural cue to animals with high frequency hearing (such as gerbils and rats), the lack of approach in monaural subjects is probably specifically related to a disruption of the Δf_i cue, although other binaural cues (e.g., pinnae) may also have been altered.

Whereas Clements and Kelly (1978) observed that subjects with one ear blocked showed no tendency to approach the speaker segment on one side or the other, the monaural subjects in this study showed a preference to respond on the side away from the block. This finding lends further support to the previous interpretation. The Δf_i cue represents a frequency-intensity spectra difference at the two ears (see p. 3). Blocking both ears does not change the relative balance of the frequency-intensity spectra at the two ears whereas blocking one ear does. Blocking only one ear should result in 1) greater binaural spectral differences and 2) the subject perceiving the locus of the sound source as being further to the side away from the

plug than it actually is. Thus, for example, if a subject's left ear is blocked, the signal should sound louder to the right ear and the subject should estimate the sound source too far toward that side.

VIII. EXPERIMENT IV

VIII.1 Method

Subjects. Twenty-four rat pups, 13-20 days of age, served as subjects. Four litters, culled to six animals each, were purchased from the Biology Department at Carleton University.

Ear Blocking. The same blocking procedure used in Experiment III was used in the present study. After testing, the ears were checked for middle ear infection. The tympanic membrane appeared normal in all subjects and no signs of infection were observed.

Effectiveness of the Ear Blocks. In order to assess the effectiveness of the blocks in attenuating sound, evoked potentials (EPs) were recorded from the auditory cortex of animals that had one ear and both ears blocked.

Three rats, approximately 16 days of age, were used in this investigation. Each animal was anesthetized with metofane and the right external meatus was plugged with wax and then covered with an elastoplast bandage. The skull was opened over the right hemisphere and a silver ball electrode was placed over the exposed region. A loudspeaker was positioned approximately 2 inches from the subject's left ear.

Repetitive clicks (50 μ sec in duration) at a rate of 1/sec were generated by a Grass Instruments Stimulator (Model

S105). Starting at an intensity well above threshold - 83 dB SPL re 0.0002 dyne/sq. cm. - the intensity was decreased in 5 or 10 dB steps until no evoked responses were seen on the oscilloscope screen (Advance Instruments, Model No. OS100A), where the EPs were being visually monitored. Data were also recorded on tape [using an A.R. Vetter Model 3 recording adapter (data bandwidth: DC-300 Hz) and a Sony Model TC366 tape recorder], for later computer analysis (Digital Equipment Corporation, PDP 8/F). The computer analysis time was 148 msec with the sweep starting 24 msec before each click. Approximately 50 clicks were used at each intensity to obtain an averaged evoked response. This procedure was repeated with both ears blocked and then one final time with the block again only in the right ear.

Results for two subjects are shown in Figures 11 and 12.¹³ Obviously, the ear blocks did not eliminate sound but attenuated the sound on the order of 7-10 dB. This attenuation factor is in close agreement with that reported by Clements and Kelly (1978⁹); they found that wax ear plugs inserted into the external meatus of guinea pigs resulted in an attenuation of approximately 10 dB. Comparisons of evoked responses with the left ear blocked and not blocked (the right ear was always blocked) are shown in Figures 13 and 14. Again, it is clear from the figures that plugging the external meatus did not wholly eliminate sound but merely reduced the intensity of the sound signal.

2 2

OF/DE

4 CORNER MARKS
FROM POINT OF NO. 1000 BUMP

FIGURE 11. N_1P_2 amplitudes of averaged evoked responses to click stimuli (50 μ sec in duration, 1/sec) of various intensities recorded from the auditory cortex, Rat 1. B: both ears were blocked. N: only the right ear was blocked. On all trials, the sound stimulus was presented to the left ear and EPs were recorded from the contralateral (right) hemisphere. Note that the effect of blocking was to attenuate sound approximately 7-10 dB.

FIGURE 12. N_1P_2 amplitudes of averaged evoked responses to click stimuli (50 μ sec in duration, 1/sec) of various intensities recorded from the auditory cortex, Rat 3. B: both ears were blocked. N: only the right ear was blocked. On all trials, the sound stimulus was presented to the left ear and EPs were recorded from the contralateral (right) hemisphere. Note that the effect of blocking was to attenuate sound approximately 7-10 dB.

Figure 13: Comparison of averaged evoked responses with only the right ear blocked vs. both ears blocked. EPs were to clicking stimulation, 63 dB SPL, and were recorded from the right auditory cortex. (Rat 1).

Figure 14. Comparison of averaged evoked responses with only the right ear blocked vs. both ears blocked. EPs were to click stimulation, 78 dB SPL, and were recorded from the right auditory cortex. (Rat 3).

Procedure. Subjects were randomly assigned to one of three groups: 1) no ears blocked (control); 2) one ear blocked (left ear for half the subjects, right ear for the other half); and 3) both ears blocked.

Animals in the experimental groups had their ear(s) plugged on the 8th postnatal day. Subjects in the control group received an equivalent amount of handling at that time.

The low intensity social signal, which proved most effective in eliciting approach behavior in Experiment II, was used in the present study.

Subjects in all groups were given three practice trials/day from the 9th to the 12th postnatal days. Testing commenced on postnatal day 13 and continued through day 20.

VIII.2 Results

The multivariate analysis included the following dependent measures: number of initial responses, number of final responses, latency to initial response, latency to final response, percent D+I initial response, percent D+I final response, percent direct initial response and percent direct final response. The analysis indicated a statistically significant Blocking effect ($F=3.77$, $df=16/28$, $p<.001$). The corresponding Wilkes Lambda value ($U=0.10$, $df=2/21$, $p<.05$) was also significant. Indeed, the blocking manipulation accounted for some 86 percent of the variability ($R=0.928$).

Table 13 lists the mean number of initial and final responses made by subjects in each of the three groups. One-

TABLE 13

MEANS AND STANDARD DEVIATIONS FOR THE NUMBER OF INITIAL
AND FINAL RESPONSES (EXPERIMENT IV)

Group	<u>Initial</u>		<u>Final</u>	
	M	SD	M	SD
Normal	24.00	0.00	23.75	0.71
Binaurally Blocked	24.00	0.00	24.00	0.00
Monaurally Blocked	23.87	0.35	23.75	0.46

Note: Mean maximum number of responses was 24. (Subjects were run
for 3 trials/day over 8 days.)

way analyses of the number of initial and final responses indicated that there were no differences between groups (see Table 14). Similarly, no differences were found for either the initial or final latency measures (see Tables 14 and 15). Thus, subjects in all groups crossed over the initial and final lines at about the same rate and with approximately the same rapidity.

On most trials, the subjects would quickly leave the start area and move directly toward one of the peripheral segments. In comparison, the somewhat longer latencies observed for subjects in the previous experiment (see p. 72), might reflect a tendency of gerbil pups to explore the apparatus before responding to the sound.

Figures 15 and 16 show the mean percent D+I initial and final approach responses for each group. Clearly, subjects without ear blocks and subjects with both ears blocked approached the sound source to a much greater extent than subjects with one ear blocked. This was confirmed by analyses of the percent initial and final D+I responses (see Table 14). Newman-Keuls' comparisons ($p < .05$) for both initial and final approaches indicated that subjects in the binaurally blocked and normal groups did not differ from each other, but both approached the sound signal a significantly greater percentage of the time than subjects in the monaural group. Single-sample t tests were computed for each group to examine whether D+I approach behavior was above what could have been expected on a chance basis. Only the control and binaurally blocked groups

TABLE 14

SUMMARY TABLE OF ANALYSES OF VARIANCE FOR INITIAL AND FINAL RESPONSES (EXPERIMENT IV)

Dependent Variable	Source of Variance	df	Initial			Final		
			MS	F	SIG	MS	F	SIG
Number of responses	Blocking	2	0.04	1.00	ns	0.16	0.70	ns
	Within Cell	21	0.04			0.23		
Latency	Blocking	2	0.98	1.67	ns	2.37	1.28	ns
	Within Cell	21	0.58			1.84		
Percent D+I	Blocking	2	1738.20	26.28	p<.001	1683.50	25.41	p<.001
	Within Cell	21	66.14			66.26		
Percent direct	Blocking	2	565.17	10.95	p<.001	906.50	24.75	p<.001
	Within Cell	21	51.59			36.61		

TABLE 15

MEANS AND STANDARD DEVIATIONS FOR LATENCY TO INITIAL
AND FINAL RESPONSES (EXPERIMENT IV)

Group	Initial Latency (in secs.)		Final Latency (in secs.)	
	M	SD	M	SD
Normal	1.70	0.43	4.70	1.08
Binaurally Blocked	2.32	0.97	5.77	1.54
Monaurally Blocked	2.29	0.80	5.39	1.41

FIGURE 15. Mean percentage of initial D+I approach responses made by each of the three groups (Experiment IV). Note: 37.5% represents chance level of approach responding.

FIGURE 16. Mean percentage of final D+I approach responses made by each of the three groups (Experiment IV). Note: 37.5% represents chance level of approach responding.

TABLE 16

VALUES FOR SINGLE SAMPLE t TESTS USED TO DETERMINE ABOVE
CHANCE D+I AND DIRECT APPROACH BEHAVIOR (EXPERIMENT IV)

t values for D+I approach		
Group	Initial	Final
No Blocks	13.61*	10.04*
2-ears Blocked	8.39*	11.02*
1-ear Blocked	0.33	0.52

t values for direct approach		
Group	Initial	Final
No Blocks	7.37*	8.01*
2-ears Blocked	3.19**	4.15*
1-ear Blocked	1.31	3.80*

* $p < .01$

** $p < .05$

approached the sound source at above chance levels for initial and final responses, (see Table 16).

A similar pattern emerged when the mean percent direct approach responses were analyzed: subjects with two ears blocked approached the sound source as often and as accurately as subjects without ear blocks (Newman-Keuls, $p < .05$) and subjects in both these groups made significantly more initial and final direct approaches than subjects in the monaural group (see Table 14). Further, only the initial and final direct approach responses of subjects in the control and binaurally blocked groups were significantly above what could have been expected by chance (see Table 16). The significant t value for the monaural group on final responses (see Table 16), indicates that these subjects directly approached the speaker segment fewer times than expected by chance. This was almost entirely the result of subjects approaching the indirect and neutral segments on the side away from the block (see below).

An away-toward score was computed for indirect and neutral responses for each subject in the monaural condition. These tests indicated that subjects showed a marked preference for responding toward the sound on the side away from the ear plug for both initial ($t=7.96$, $df=7$, $p < .001$) and final ($t=6.25$, $df=7$, $p < .001$) responses.

VIII.3 Discussion

As in Experiment II, subjects that heard the low intensity social signal showed a large number of crossings

over the initial and final lines. Further, subjects in all groups had similar latencies to initial and final crossings. Thus, blocking one ear or both ears had little effect on either the responsiveness or the speed of response in rat infants.

Results of the approach measures for the rat pups are similar to those found in the previous study: while binaural and control subjects showed above chance approach, the monaural subjects did not. Once again, the most reasonable explanation for these findings is that binaural cues were disrupted in subjects with one ear blocked. And again, this interpretation is supported by the fact that monaural subjects showed a marked preference to respond to the sound segment on the side away from the block.

IX. GENERAL DISCUSSION

The ability to localize a sound source is "one of the most important features of hearing" (Masterton, 1974, p. 1904) and at present, is assumed to exist in all adult vertebrates (Erulkar, 1972). Until recently, few investigators have focused on the developmental course of this behavior, and of these, most have chosen to work with avian species (Gottlieb, 1965; Beer, 1970, 1969; Evans, 1970). Generally, the results of these studies have indicated that young birds approach species calls.

Previous research on localization behavior in young mammals has been limited to three species. Human infants have been shown to discriminate sounds to the right and left of midline and to orient to the side where a sound was produced (Leventhal and Lipsitt, 1964; Wertheimer, 1961; Turkewitz et al., 1966). Clements and Kelly (1978, 1978, in press), who have worked with infrahuman mammals, have found that kittens and guinea pig infants execute directional approaches to sound but have only demonstrated the importance of binaural cues in the maintenance of this behavior for the guinea pig.

Results of the present experiments have confirmed and extended these findings: binaural cues are used by gerbil and rat pups to localize sounds (i.e., to execute spatially directed auditory responses). Thus, the ability to approach a sound source

is present early in ontogeny in a number of altricial and precocial species and has been demonstrated in infants of every species tested to date. At this point, it appears that localization behavior is as prevalent in infants as it is in adults, although the possibility that future testing might reveal exceptions to this generalization cannot be ruled out.

Relationship to Onset of Hearing

The temporal relationship between the onset of auditory function and the onset of localization behavior is not clearly defined. Obviously, an animal cannot localize a sound it cannot hear. But whether the ability to hear and the ability to directionally respond to sound come in simultaneously during development remains a moot point. This question has arisen, in part, because of difficulties in determining the precise time of hearing onset. For example, the use of different acoustical stimuli across laboratories has led to conflicting reports on time of onset. Several investigators have noted that not all auditory signals are equally effective in evoking early responses (e.g., see Eisenberg, 1976). Further the initial responses from auditory structures in most young animals are elicited only to extremely intense stimuli and only to a limited range of frequencies. As the auditory system matures, it becomes responsive to a wider range of frequencies and shows increasing sensitivity. Because of the rapid changes that occur over the short span between onset of auditory function and final functional maturation, much

uncertainty exists about what the young animal is capable of hearing (Potash, 1976).

The fact that each of several measures that has been used to assess the growth of the auditory system reveals a slightly different maturational timetable has led to additional problems in establishing an exact onset date for hearing. For example, electrophysiological responses (e.g., cochlear microphonics, eighth nerve action potentials, cortical evoked potentials) are usually observed prior to behavioral responses (e.g., Preyer reflex).

Any attempt to compare onset times of auditory sensitivity and localization ability is further complicated by the use of different behavioral responses as criteria. The typical behavioral measure of auditory sensitivity is a reflexive response (Preyer), whereas many behavioral measures of localization require the subject to approach the sound, a task which has greater locomotor and motivational demands. Further, extremely intense sounds are used to elicit the Preyer reflex, whereas low intensity signals are the most effective in demonstrating approach behavior (Schneirla, 1965). Thus, one could reasonably expect a slight difference between onset dates for sensitivity and localization based on differences in the intensity of stimuli that are used to elicit the response and the effectiveness of methods used to motivate the subjects.

With the above considerations in mind, we shall briefly review the evidence on the development of hearing and of directional

responses to sound in gerbils and rats. In the only published report on the maturation of the auditory system in gerbils, Finck et al. (1972) first observed cochlear microphonics at 12 days of age, action potentials recorded from the eighth nerve at 14 days, and the Preyer reflex on the 17th day. The onset of hearing occurs somewhat sooner in rats than in gerbils. Using a variety of stimuli (e.g., hand clap, whistle), Wada (1923) found that rats first exhibited a Preyer reflex between 10-12 days, but only to the most intense sounds (no SPL cited). Volokhov (1968) reported that rats showed a "primitive orienting response" to a sound stimulus between days 5-8. Unfortunately, no data were provided on the parameters of the acoustical stimulus or the specific dependent measures which were recorded. Ashida (1972) has observed a deceleration in mean evoked heart rate in rats in response to a 2500 Hz tone (80 dB SPL) after the fourth day. This response, though, was most likely to tactile rather than auditory stimulation, since others (e.g., Crowley and Hepp-Reymond, 1966), using signals twice as intense, have been unable to pick up even cochlear microphonic responses at this early age.

The results of the present series of experiments indicate that gerbil and rat infants are capable of making directional responses to sounds at around the same time that basic sensitivity to sound first appears. Gerbil pups start to approach an auditory signal by the beginning of the third week of life and rat pups by the end of the second week.

It is also interesting to note that these early behavioral and physiological responses to sound occur at a time when auditory structures are not fully mature (Wada, 1923; Crowley and Hepp-Reymond, 1966). For example, in the rat, the development of most cochlear structures (e.g., tectorial and basilar membranes, inner and outer hair cells) occurs rapidly during the first nine days and then more gradually to the third week, at which time the general features of the cochlea have an adult appearance (Wada, 1923). Crowley and Hepp-Reymond (1966) reported that cochlear microphonic potentials first appear in rat pups between 8-9 days and reach adult sensitivity between 16-20 days. Cortical evoked potentials to sound do not approximate adult values (in terms of latency and amplitude) until at least the end of the first month (Chaloupka and Titman, 1973). Clearly, rat pups are capable of hearing prior to the time that peripheral or central nervous structures have fully matured. It would be reasonable to expect that nervous system structures underlying approach behavior might not be fully mature when approach responses first appear, but as in the case of hearing, might mature over an extended period of time.

To summarize: the ability to respond directionally to sound appears at the same time or shortly after the onset of auditory function. In the rat, basic sensitivity to sound appears towards the end of the first week (or beginning of the second), and

a few days later (days 13-20), rat pups are able to approach a sound source. Similarly, for gerbils, basic sensitivity to sound comes in sometime during the middle of the second week and the results of Experiment II indicate that gerbils are capable of approaching a sound source by at least the third week. Further, in species such as the guinea pig, where auditory function occurs early (on the first day of life), the ability to localize sound also occurs early (during the first four days of life), and in species such as the cat, where the capacity to hear appears later (during the second week of life), the ability to localize sound also occurs later (towards the end of the second or beginning of the third week) (Clements and Kelly, 1978, in press). Without debating the issue of whether or by how many hours the capacity for hearing precedes the ability to make directional responses during development, it is apparent that there is a close temporal correspondence between the maturation of auditory sensitivity and of directional responding to sound and that both these functions are present very early in ontogeny.

Rate of Directional Responding

Neither young avian nor young mammalian subjects have been found to approach sound signals at exceptionally high levels. For example, Gottlieb (1969) reported that only 85% of the ducklings and 73% of the chicks responded to a species call. Clements and Kelly (1978) found an approach rate of approximately 55% for guinea

pig infants (compared to a 37.5% level expected by chance). Although 55% represents above chance performance, it also means that subjects failed to approach the sound on almost half of all trials. In the present study, the approach rate (to the low intensity social call) for gerbil and rat pups was between 60-65% for both initial and final responses. Since 100% approach was possible, these rates represent less than maximum performance.

A number of factors might account for this suboptimal level of approach responding. First, there often is no obvious reward to approach the sound in the test situation other than that provided by the approach itself. Perhaps if reinforcement was given following the response, there would be an increase in the approach response rate. However, Clements and Kelly (1978) found that a food reward did not noticeably affect performance in guinea pigs. Second, after subjects have responded to the species call, they never encounter a species member. If subjects were able to come in contact with or see their mother or littermates, or were exposed to other non-auditory cues (olfactory) commonly associated with a species call, approach responses might occur more frequently (also see Allin and Banks, 1972). Finally, the species call played back to the subjects are usually recorded from a litter other than the subjects' own. Possibly, playing a call of the subject's litter (see Beer, 1970), or a different quality stimulus, would result in improved approach responding. Further testing is needed to determine whether changes in the sound signal or changes in test conditions, or perhaps some combination of these, might push the approach rate closer to the maximum level.

Schneirla's Hypothesis

Schneirla (1966, 1965, 1959) has proposed one of the few theories that directly pertains to the behavior of infant organisms. According to his biphasic hypothesis (see p. 15), infant subjects display a tendency to approach low intensity stimuli and to avoid high intensity stimuli. Consistent with Schneirla's position, rat and gerbil subjects in Experiments I and II approached a low intensity species call but not the high intensity version of this same call.

While some of the present data can most simply be accounted for by Schneirla's approach-withdrawal hypothesis, other results are not entirely consistent with this hypothesis. For example, since Schneirla made no distinction between qualitatively different stimuli, one would anticipate that all low intensity signals should facilitate approach reactions. Considering only the low intensity signals in the initial experiments (I and II), it is obvious that certain sounds (e.g., species social calls) evoked more approach reactions than others (e.g., white noise or distress calls). Indeed, Gottlieb (1965), as well as others (Eisenberg, 1976), have reported that infants orient to and approach some auditory signals and not others. Further, since Schneirla asserted that his hypothesis is valid across phyletic levels, one would expect that high intensity signals should elicit avoidance reactions in the young of all species. While rat pups did show shorter latencies to the higher intensity calls (which probably reflects the aversiveness of these signals), gerbil infants exhibited similar latencies to the low and high intensity signals and displayed no preference to move toward the avoidance segments of the test apparatus during the playback of the high intensity signals. Thus, a modification of Schneirla's position, that recognized the importance of qualitative stimulus differences, as well as possible species differences, might have greater predictive validity.

Binaural Processing in Infants

Because rat and gerbil pups showed a tendency to approach the low intensity social call in the initial experiments (I and II), this signal was selected for the blocking studies. Yet, subjects with one ear blocked failed to approach the sound segment. The lack of approach responses did not result from the blocking procedure per se, since animals with both ears blocked approached the sound. The crucial difference between blocking both ears and blocking one ear is that in the former case the binaural cues remained intact whereas in the latter case these cues were disrupted. Thus, the failure of monaural subjects to accurately approach a sound source can likely be attributed to a disruption of binaural cues. This interpretation assumes that auditory structures important in localization behavior are functional early in development and that binaurally responsive units are present at this time. The limited evidence available supports these assumptions and no evidence to date contradicts them.

Aitkin and Reynolds (1975) have found that the majority of cells in the inferior colliculus of cats are influenced by binaural stimulation by as early as the first week of life (i.e., both EE and EI responses are recognizable at this age). They concluded that "developmental alterations will take the form of a refinement of binaural processing rather than in the molding of binaural connections" (p. 318). Similarly, Clopton and Silverman (1977) have found binaural interaction in inferior colliculus cells of infant rats (14-17 days after birth) and have concluded that the

"essential connections for binaural interaction are genetically predetermined and present at the onset of hearing" (p. 1275).

They suggested that further growth of binaural projections would consist of a "fine tuning" of the binaural system, which, they observed, is most likely to occur during the first 60 postnatal days (see p. 32).

Results of current electrophysiological work on how space is represented in the auditory system indicate that differences in the localization ability of monaurally blocked and normal subjects are related to differences in neural activity. In a recent report, Knudsen and Konishi (1978) demonstrated that individual neurons in the owls' auditory system¹⁴ are sensitive to restricted portions of auditory space (i.e., each neuron fires only when a sound is located within its receptive field). According to Knudsen and Konishi, binaurally sensitive units respond to particular interaural intensity or time differences. Further, they noted that plugging one ear severely alters the receptive field of these units. If these findings in the owl can be related to the behavior of subjects in Experiments III and IV, then it is likely that 1-ear blocked subjects were responding on the basis of different binaural cues than subjects in either the control or 2-ears blocked groups; and further, it is likely that this disparity in cue (and resulting difference in neural activity), might have led to divergent perceptions of the location of the sound stimulus.

Previous reports on humans (Bauer, Matuzsa, Blackner and

Glucksberg, 1966; Butler and Naunton, 1967), owls (Konishi, 1973) and treefrogs (Feng et al., 1976) have all indicated that blocking one ear of a normal subject results in the subject perceiving the sound as being further toward the side of the unoccluded ear than it actually is. The behavior of monaural subjects in the present studies is consistent with these findings: rat and gerbil pups with the right ear plugged showed a left side bias in localization and conversely, subjects with the left ear plugged showed a right side bias in localization. Although the explanation for the bias in 1-ear blocked subjects has typically been based on an alteration of the binaural intensity cue (e.g., see Butler and Naunton, 1967; Feng et al., 1976), the possibility that other binaural cues are being disrupted cannot be discounted.

It is also interesting to note that monaural deprivation during the first several months modifies subsequent electrophysiological responses in the central nervous system. Silverman and Clopton (1977) found that the inferior colliculus cells of infant rats that had undergone sound deprivation in only one ear displayed marked changes in binaural interaction (e.g., absence of normal ipsilateral inhibition of ~~that~~ activity), but that IC cells of those subjects that had ~~both~~ ears deprived showed normal binaural interaction.

In conclusion, the results of Experiments I and II provided evidence that the young of two altricial mammalian species - mongolian

gerbils and albino rats - approach a low intensity species vocalization. The results of Experiments III and IV pointed out the importance of binaural cues in the localization behavior of rat and gerbil infants. These behavioral findings strongly suggest that central nervous system structures involved in sound localization are present early in ontogeny.

RESEARCH NOTES

1. To detect the source of a sound, information is needed as to distance, elevation and azimuth. That is, a subject needs to know how far away the sound is and where it is along the vertical and horizontal planes. Information on how distance and elevation cues are processed by the nervous system is meager (Masterton, 1974). However, a considerable amount of evidence--amassed from anatomical, electrophysiological and behavior-ablation experiments--has confirmed the relevance of two cues for localizing sounds in the azimuthal plane. These cues are the binaural time disparity (Δt) and binaural frequency-intensity spectra disparity (Δfi) at the two ears.
2. A special case of this temporal discrimination when pure tones are used is referred to as the binaural difference in phase ($\Delta \phi$). The difference in time of arrival of a specified phase of the sound waves at the two ears (i.e., the peaks of the sound waves arrive at different times) provides a potential cue for the localization of tones.
3. A special case of the frequency-intensity spectra discrimination, applicable when pure tones are used, is an intensity discrimination (Δi). (Obviously, when both ears are stimulated by the same frequency, a cue based on differences in frequency content becomes irrelevant.) For the localization of pure tones, discriminations are based on differences in intensity at the two ears. As in the previous Δfi case, the effectiveness of the head as an acoustic shadow increases directly with the frequency of the stimulating tone (since high frequencies are more attenuated than low frequencies). Thus, the higher the frequency of the stimulus, the greater the intensity difference at the two ears.
4. MSO neurons in the cat have two primary dendrites, one pointing medially and the other laterally; many LSO cells are also arranged with two long dendrites, one reaching rostrally and one caudally (Stotler, 1953). In the MSO, fibers from the cochlear nucleus of the ipsilateral side terminate mostly on the lateral dendrite and fibers from the contralateral side terminate predominantly on the medial side (Stotler, 1953). A similar pattern of innervation is found in the dog (Goldberg and Brown, 1968). Thus, information from both peripheral receptors arrives in an orderly spatial pattern at the MSO; this, in turn, could facilitate subsequent binaural analysis.

5. Most LSO units show an excitatory-inhibitory interaction, with the ipsilateral side being excitatory and contralateral side inhibitory (Goldberg and Brown, 1968). These cells are sensitive to interaural intensity differences (i.e., a greater increase in intensity at one ear relative to the other ear) and are important in localizing high frequency stimuli.
6. Altman (1968) used a click-train stimulus with gradually changing time differences. According to Altman (1968), "this signal presented to human subjects was heard...as a fused sound image moving from the leading ear to the midline and backwards" (p. 15).
7. Monaural subjects can learn, after extensive training, to localize sounds, although never with the same accuracy as binaural subjects (Neff and Casseday, 1977). A number of researchers have emphasized the importance of the pinnae in localizing sound (Batteau, 1968; Butler, 1975; Fisher and Freedman, 1968; Gardner and Gardner, 1973). Batteau (1968) has pointed out that a distortion of the pinna produces distortions in judgments of the location of a sound source. Butler (1975) has reported the case of a unilaterally deafened subject who could proficiently localize sounds, even with restricted head movements, but who failed to localize when the pinna of his good ear was distorted. Gardner and Gardner (1973) have reported that localization ability decreases directly as a function of the amount of pinna area that is occluded.
8. Hubel and Wiesel (1962) have shown that visual cortex neurons are sensitive to a particular orientation and that every orientation throughout 360° is represented by different cells.
9. A cat's eyes are not aligned accurately in their orbits until about the fourth postnatal week. Blakemore and Van Sluyters (1974) have pointed out that the critical period does not begin until 1) both eyelids are open (~~they~~ do not open simultaneously) and 2) the visual axes are properly aligned. Thus, at the onset of the critical period, the binocular input to a cell is normal (Blakemore and Van Sluyters, 1974).
10. The frequency at which a cell is most sensitive is referred to as its best frequency.
11. Mean percent D+I and mean percent direct approach measures were based only on responses that were executed. In calculating the mean percentage of initial D+I approach responses, the number of D+I approach responses out of the start area was divided by the total number of responses (including approach, avoidance and neutral responses) out of the start area. In calculating the mean percentage of final D+I approaches, the number of D+I approach responses over the outer circle was divided by the total number of responses over the outer circle. Similarly, in calculating the mean percent initial (or final) direct

approach responses, the number of direct approaches out of the start area (or over the outer circle) was divided by the total number of responses out of the start area (or over the outer circle).

12. If subjects, on average, had shown an equal tendency to approach the speaker segment on the right and left sides, their score would not have differed from zero, the value that represents chance performance.
13. As a result of equipment failure, data for the third subject were not recorded on tape. However, visual inspection of the EPs on the oscilloscope screen indicated that the attenuation of sound due to the block was equivalent to that observed for the other two subjects.
14. Units were recorded from the nucleus mesencephalicus lateralis dorsalis (MLD), which is the avian homolog of the inferior colliculus.

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Appendix 7 Common and scientific names

Figure 1. Frequency analyses of low intensity (L) and high intensity (H) species social call and of background noise (N) using Bruel and Kjaer sound level meter (Type 2204) and octave band filters (Type 1613). All measurements were taken from the center of the circular apparatus with the microphone (Bruel and Kjaer, Type 4133) directed toward the loud speaker segment.

Figure 2. Frequency analyses of low intensity (L) and high intensity (H) white noise signal and of background noise (N) using Bruel and Kjaer sound level meter (Type 2204) and octave band filters (Type 1613). All measurements were taken from the center of the circular apparatus with the microphone (Bruel and Kjaer, Type 4133) directed toward the loud speaker segment.

Figure 3. Frequency analyses of low intensity (L) and high intensity (H) control noise signal and of background noise (N) using Bruel and Kjaer sound level meter (Type 2204) and octave band filters (Type 1613). All measurements were taken from the center of the circular apparatus with the microphone (Bruel and Kjaer, Type 4133) directed toward the loud speaker segment.

APPENDIX 2

APPROACH RESPONSES TO SOUND IN GERBIL PUPS
(PILOT DATA)

Six gerbil pups were tested for their ability to respond to a species vocalization. The test apparatus and procedure have been described previously (see pp. 34-42). Testing began when the pups were 12 days of age and continued over the next 16 days. Table I shows the percentage of initial and final D+I approach responses over each block of four days. For each value in Table I, a single-sample t test was computed, comparing the observed approach behavior against what would be expected by chance alone. For days 16-19 and 20-23, the values for both initial and final approach responses were significant at the 0.05 level. None of the other values were significant.

Table I
Mean Percentage of Initial and Final Approach Responses
Over Each Block of Four Days

<u>Days</u>	<u>Initial</u>	<u>Final</u>
12-15	42.3%	41.8%
16-19	62.3	63.6
20-23	73.7	61.0
24-27	49.3	47.7

Note: 37.5% represents chance level of approach responding.

APPENDIX 3

TABLE 1

TOTAL NUMBER OF INITIAL RESPONSES MADE BY EACH OF THE
SIX GROUPS OVER EACH OF THE FOUR PRACTICE AND EIGHT TEST DAYS
(EXPERIMENT I)

Sound	Intensity	Practice Days								Test Days							
		1	2	3	4	1	2	3	4	5	6	7	8				
Social	Low	9	9	20	22	24	23	22	24	24	24	24	24				
Social	High	20	22	22	24	24	24	23	24	24	24	24	24				
White Noise	Low	16	22	21	22	20	20	23	22	24	24	24	24				
White Noise	High	16	20	18	24	23	22	22	22	24	23	24	24				
Control	Low	16	22	22	24	23	24	23	19	22	24	23	24				
Control	High	16	20	23	20	21	20	22	20	23	23	24	24				

Note: The maximum possible number of responses/day was 24 (i.e., 3 trials/day for each subject, 8 subjects/group).

APPENDIX 3

TABLE 2

TOTAL NUMBER OF FINAL RESPONSES MADE BY EACH OF THE
SIX GROUPS OVER EACH OF THE FOUR PRACTICE AND EIGHT TEST DAYS
(EXPERIMENT I)

	Intensity	Practice Days				Test Days							
		1	2	3	4	1	2	3	4	5	6	7	8
Sound													
Social	Low	1	3	4	16	18	21	18	24	23	24	22	23
Social	High	6	10	9	12	18	16	18	17	22	23	23	24
White Noise	Low	1	7	9	13	8	13	17	13	20	23	23	23
White Noise	High	4	3	8	10	10	8	16	15	20	20	22	21
Control	Low	2	12	15	15	16	21	19	17	18	20	22	24
Control	High	7	8	6	7	10	12	11	17	18	22	24	24

Note: The maximum possible number of responses/day was 24 (i.e., 3 trials/day for each subject, 8 subjects/group).

Data Sheet

SUBJECT _____
 LETTER _____
 AGE (in years) _____
 COLOR _____
 SEX _____
 AGE EYES _____
 HRS. _____

Date Time

DAY 1	_____
DAY 2	_____
DAY 3	_____
DAY 4	_____
DAY 5	_____
DAY 6	_____
DAY 7	_____
DAY 8	_____
DAY 9	_____

0 - LATENCY

0 - LATENCY

0 - LATENCY

0 - LATENCY

0 - LATENCY

0 - LATENCY

0 - LATENCY

0 - LATENCY

0 - LATENCY

0 - LATENCY

0 - LATENCY

0 - LATENCY

RAT SOCIAL CALL

132

Figure 1. Frequency analyses of low intensity (L) and high intensity (H) species social call and of background noise (N) using Bruel and Kjaer sound level meter (Type 2204) and octave band filters (Type 1613). All measurements were taken from the center of the circular apparatus with the microphone (Bruel and Kjaer, Type 4133) directed toward the loud speaker segment.

Figure 2. Frequency analyses of low intensity (L) and high intensity (H) species distress call and of background noise (N) using Bruel and Kjaer sound level meter (Type 2204) and octave band filters (Type 1613). All measurements were taken from the center of the circular apparatus with the microphone (Bruel and Kjaer, Type 4133) directed toward the loud speaker segment.

Figure 3. Frequency analysis of low intensity (L) and high intensity (H) control noise signal and of background noise (N) using Bruel and Kjaer sound level meter (Type 2204) and octave band filters (Type 1613). All measurements were taken from the center of the circular apparatus with the microphone (Bruel and Kjaer, Type 4133) directed toward the loud speaker segment.

APPENDIX 6

TABLE 1

TOTAL NUMBER OF INITIAL RESPONSES MADE BY EACH OF THE
SIX GROUPS OVER EACH OF THE FOUR PRACTICE AND EIGHT TEST DAYS
(EXPERIMENT II)

		Practice Days				Test Days							
		1	2	3	4	1	2	3	4	5	6	7	8
Sound	Intensity												
Social	Low	4	3	21	18	23	24	24	24	24	24	24	24
	High	6	8	15	19	24	24	24	24	24	24	24	24
Distress	Low	2	5	12	22	23	23	24	24	24	24	24	23
	High	3	3	13	16	23	24	24	24	24	24	24	24
Control	Low	3	6	21	22	23	23	24	24	24	24	24	24
	High	3	7	13	21	24	24	24	24	24	24	24	24

Note: The maximum possible number of responses/day was 24 (i.e., 3 trials/day for each subject, 8 subjects/group).

APPENDIX 6

TABLE 2

TOTAL NUMBER OF FINAL RESPONSES MADE BY EACH OF THE SIX GROUPS OVER EACH OF THE FOUR PRACTICE AND EIGHT TEST DAYS (EXPERIMENT II)

Sound	Intensity	Practice Days								Test Days							
		1	2	3	4	1	2	3	4	5	6	7	8	1	2	3	4
Social	Low	0	3	18	17	21	21	24	24	24	24	24	24	24	24	24	24
Social	High	1	1	11	18	23	24	24	24	24	24	24	24	24	24	24	24
Distress	Low	0	5	9	20	21	23	24	24	24	24	24	24	24	24	24	23
Distress	High	0	2	10	15	22	24	24	24	24	24	24	24	24	24	24	24
Control	Low	0	5	18	21	21	23	24	24	24	24	24	24	24	24	24	22
Control	High	0	4	12	21	24	24	24	24	24	24	24	24	24	24	24	24

Note: The maximum possible number of responses/day was 24 (i.e., 3 trials/day for each subject, 8 subjects/group).

APPENDIX 7

Table 1

Common and Scientific Names

Common Name	Scientific Name
bat	<u>Myotis lucifugus</u>
bushbaby	<u>Galago senegalensis</u>
cat	<u>Felis domesticus</u>
gerbil	<u>Meriones unguiculatus</u>
guinea pig	<u>Cavia porcellus</u>
hedgehog	<u>Paraechinus hypomelas</u>
monkey	<u>Macaca mulatta</u>
rat	<u>Rattus norvegicus</u>
tree shrew	<u>Tupaia glis</u>

END

2000 79

FIN