Development of Hearing and Response Behavior to Sound Stimuli: Behavioral Studies

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I. Introduction

The onset of sensory function during the ontogeny is the basis of an animal's capacity to communicate with other individuals in its environment. Communication among animals always includes a sender, who emits a signal, and a receiver, who responds to the signal by changing his behavior. To know when an animal can begin to act as a receiver in the communication chain it is necessary to study the time course of the species' sensory development. For example, intraspecific acoustic communication between parents and offspring can only be understood if the roles of sender and receiver are clear; in other words, we have to know who is able to perceive, process, and recognize intraspecific acoustic signals.

In this chapter we shall be concerned with the development of the auditory system and of response behavior to sound stimuli in mammals, and from the data presented it will become evident when young mammals will be able to act as acoustic receivers and respond to calls of their parents. We shall find that there are great differences among species regarding when hearing begins. Those offspring that are born in a very altricial state, such as mouse pups, cannot hear for over 1 week after birth although they vocalize extensively with different calls during this time. In other species like the guinea pig, offspring are born in a precocial state and hearing onset occurs in the uterus before birth (see Ehret, 1980).

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We shall consider development not only from a behavioral point of view but also with respect to the physiology of auditory function. The measuring tool for studying the development of hearing in all investigations reviewed is a behavioral response, either unconditioned or conditioned. Behavioral auditory thresholds are determined in intact animals and thus measure the net output of the whole auditory sensory and motor pathway. The influence of maturation in different centers of the auditory pathway on behavioral thresholds can be determined by comparing sequences of anatomical and electrophysiological development in the brain with changes in behavioral sensitivity. Such comparisons will be made when we discuss the anatomical and physiological basis of hearing development and look for peripheral and central correlates of properties like sensitivity increase, broadening of frequency response range, and improvement of frequency selectivity and sound localization ability after the onset of hearing. Anatomical and electrophysiological studies on the developing acoustic system can show whether the structural basis for proper functioning is present and how far neural processing has matured to adult patterns of sensitivity, timing, and filtering. Only behavioral studies, however, can present the final evidence on the extent to which the intact animal is able to use and to respond to information processed by the developing auditory periphery and pathway.

In the following section I shall discuss methods of behavioral threshold measurement to set the stage for a critical review of the data and of the conclusions that will be drawn from them.

II. Methods of Behavioral Auditory Testing in Developing Mammals

One goal of psychoacoustical methods is to establish acoustical "stimulus control" of the animal's behavior. It is clear that, especially for developing animals, the only behavioral methods that will lead to reliable results—or to results at all—are those that consider the abilities (sensory and motor) and the normal behavioral repertoire of the animal under testing. For example, all attempts to condition shock avoidance or escape responses to tones in mouse pups younger than about 10 days of age will fail because (a) the mouse is not yet able to hear (Ehret, 1976), and (b) it cannot yet see and its motor coordination is still developing (Fox, 1965) so that an effective avoidance or escape from electric shock is not possible. In general, conditioning of newborn animals is difficult since their behavioral repertoire is limited and their responses are variable and change with maturation of the brain and motor system. A second problem arises with conditioning procedures in newborns. Since conditioning can be started only after the animals can hear and always takes a few days to reach a stable response criterion, the
onset of hearing and its development during the first days thereafter cannot be tested by conditioning techniques. In this case, unconditioned responses have to be used. After a few days one may switch to conditioned responses, usually with an accompanying increase in measurement sensitivity.

A. Unconditioned Responses

In auditory threshold measurements employing unconditioned responses, a naturally occurring response to sound is observed and used as an indicator of auditory sensitivity. One may also habituate a response to a sound stimulus and then change sound parameters in order to dishabituate and elicit the response again. The following unconditioned responses have been used to test the development of auditory thresholds in mammals and man.

1. STARTLE RESPONSE

A startle response is not usually described as a specific reaction to sound, but it includes pinna, head, and body movements, movements of limbs and facial muscles, or any behavioral change. Thus, a startle response can be any reaction of any part of the body to sound stimulation so that in any particular study what is considered to be a startle response is totally dependent on criteria set by the investigators.

A startle response has been used to study the development of hearing in the opossum (Larsell and McCrady, 1935; Larsell et al., 1935, 1944; McCrady et al., 1937), in various strains of house mice (SH-1: Hack, 1968; CBA-J: Powers et al., 1966; C57BL/6J: Shnerson and Willott, 1980), in the rat (Paris and Ison, 1979; Wada, 1923), and in the rabbit, dog, mink (Foss and Flottorp, 1974) and cat (Foss and Flottorp, 1974; Olmstead and Villalba, 1980).

2. PREYER REFLEX

The term Preyer reflex also has not been consistently applied to a well-defined behavior, although one component, a twitching of the pinna, has always been mentioned. In some studies, Preyer reflex is used as a synonym for startle response, whereas in others it is explicitly stated that only pinna movements are considered. Preyer (1908) originally described a twitching of the pinna of guinea pigs to soft sounds and pinna and body movements to louder tones. Thus, the Preyer reflex is a kind of startle response the most sensitive form of which, however, may involve only pinna movements. To avoid further confusion in terminology in the literature, it is proposed that the term startle response be used when body and limb movements are observed, the term Preyer reflex being reserved for movements of the pinna and/or facial muscles only. The Preyer reflex, as defined here, was used to
test the development of hearing in house mice, strain CBA-J (Alford and Ruben, 1963; Mikaelian and Ruben, 1965) and in cats (Ehret and Romand, 1981).

The reliability of the startle response and the Preyer reflex as measures of auditory sensitivity has been discussed by Anderson and Wedenberg (1965), Denes and Kocher (1961), Francis (1975, 1979), Knecht (1958), and Markl and Ehret (1973). All agree that neither are particularly suitable for quantitative measurements of auditory sensitivity. The thresholds for the startle response or the Preyer reflex in adult animals are not only much higher than the thresholds of sensation determined by other methods (Ehret, 1983; Francis, 1975, 1979; Markl and Ehret, 1973) but also depend very much on how the animal is restrained during the test, how it is observed, whether or not it pays attention, and whether or not the stimulus is familiar. The only unambiguous statement that can be made is that when both responses can be elicited repeatedly, the animal hears. The converse, that the absence of both responses indicates deafness, need not be true; more sensitive methods may indicate quite normal hearing. Despite the fact that observations of startle responses and Preyer reflex are the most commonly used methods for measuring the development of auditory thresholds in mammals, they give only qualitative information about thresholds. Preyer reflex audiograms do not necessarily parallel conditioned response audiograms (Markl and Ehret, 1973) and seem to reflect equal loudness contours rather than absolute sensitivity (Francis, 1979).

3. ORIENTATION RESPONSE

An orientation response to sound consisting of pinna movements to low-intensity sound often accompanied by head movements toward the sound source and sniffing around has been described for mouse pups (Ehret, 1976). This response seems to be one of “attention” to an unfamiliar, low-intensity sound. To stop crawling as a result of sound stimulation may be one of the same class of responses (Ehret, 1976). Mouse pups stopped crawling and often started sniffing around when they heard rather low-intensity sound pulses.

When an orientation response is used as a measure of auditory sensitivity the environment has to be quiet (sound-proof room), the animals have to be alert, and habituation to the sound signal must be avoided (e.g., by handling the animals between tests). Orientation response thresholds are lower than those for the startle response, and the audiograms come closer to, but still do not coincide with, conditioned response sensitivity (Ehret, 1976).

4. HEART RATE RESPONSE

Heart rate acceleration or deceleration from a baseline in response to a sound stimulus has been used as an indicator of hearing in developing rats
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(Haroutunian and Campbell, 1981). Acceleration was noticed during the first days after onset of hearing whereas deceleration was found later in development. Auditory threshold curves have not been presented, thus a comparison of the sensitivity of this method with that of other methods for measuring absolute auditory thresholds in developing mammals is not possible.

5. GALVANIC SKIN RESPONSE

As a method for estimating auditory sensitivity, the galvanic skin response has so far been used only in adult mammals (see Ehret, 1982); however, it may also be applied in developmental studies. A change in the skin resistance in response to sound stimulation is measured. Since skin resistance changes and heart rate changes can be absolutely quantified, they have the advantage of being objective measurements.

6. DIRECTIONAL MOVEMENTS

Movement toward a sound source has been used to determine ability to localize sound. Measurements of such a response require that motor coordination in the animals under testing be sufficiently well developed to allow them to maintain their direction of movement over a given distance. To test directional auditory sensitivity also requires the animal to have some sensitivity at least to a small frequency range.

Directional hearing tests in infant mammals have been carried out in guinea pigs (Clements and Kelly, 1978a), rats (Potash and Kelly, 1980), and cats (Clements and Kelly, 1978b; Olmstead and Villablanca, 1980).

7. UNCONDITIONED RESPONSES OF HUMAN INFANTS

A variety of methods have been reported in the literature (reviews by Eisenberg, 1969; Morse, 1979) for estimating absolute auditory sensitivity, frequency and intensity discrimination, sound localization, and speech perception in infants. A comprehensive review can be found in Eisenberg, Chapter 9, this volume.

B. Conditioned Responses

In procedures measuring conditioned responses, animals are trained to respond to an auditory stimulus that previously elicited no response. This is done by combining the sound with a reinforcing stimulus (to which animals react naturally) to form a sound–reinforcer pair and training the animals with this combined stimulus until a conditioned response to the sound can be observed in the absence of the reinforcing stimulus. For conditioned response techniques to produce meaningful results, it is necessary that the responses be stable with time and have a low spontaneous occurrence rate.
So far only one method, a conditioned blink response, has been successfully used to measure auditory thresholds in developing house mice (Ehret, 1976) and kittens (Ehret and Romand, 1981). Both mice and cats show an eyelid blink in response to an electric shock. Eyelid conditioning can start after the eyes are open, and eyelid blinks are best observed through an operation microscope. After about 3–4 days of conditioning with tone–shock pairs (about 20 pairs per 10-min session, one or two sessions per day) the animals exhibit a stable eyelid response to sound stimulation without being followed by a shock. The animals require frequent reconditioning in order to stabilize the response during the time of testing.

III. Development of Hearing and Response Behavior to Sound in Various Mammals and in Man

Many of the studies mentioned in Section II present data on the onset of hearing in the corresponding mammals; not all of them, however, specify the acoustic stimuli in terms of frequency, intensity, and duration, and only a few show threshold curves that quantitatively indicate the development of auditory sensitivity with age. With the exception of one study on the development of frequency resolution in mice (Ehret, 1977), there have been no behavioral studies in which basic psychoacoustical measures like frequency and intensity discrimination, frequency selectivity, and temporal resolution were investigated during ontogeny of a mammal.

In this section, data will be presented separately for species from the orders Marsupialia, Chiroptera, Carnivora, Rodentia, and Primates. In order to give a more complete picture and to include more species, results from electrophysiological studies on the developing acoustic system will be included where appropriate.

A. Marsupialia

The two species of opossum (Didelphis virginiana and D. marsupialis) are the only marsupials studied so far. The investigations of Larsell and McCrady (1935) and Larsell et al. (1935, 1944) on D. virginiana and of McCrady et al. (1937) on D. marsupialis indicate that onset of hearing occurs (startle response to a shrill whistle) after the fiftieth (virginiana) and before the fifty-ninth (marsupialis) postnatal day. First responses to tones between 1 and 1.6 kHz occur at day 51 (virginiana). By day 52 the frequency response range in D. virginiana had extended to 0.25–2 kHz and probably reached the adult range at day 77, when the inner ear appears to be fully developed. In D. marsupialis, hearing starts before day 59 (the earliest test-
ed), at which the frequency range is between 1 and 4.5 kHz. The range extended to 0.8–6 kHz by day 60 and probably reached the adult range by day 80 when responses to frequencies between 0.1 and 19 kHz (lowest and highest ones tested) were observed. Measurements of cochlear microphonic (CM) potentials in *D. virginiana* (Larsell et al., 1944) indicate a development similar to that of the behavioral response. First electrical responses were obtained at day 48 between 1 and 7 kHz, and adult sensitivity may be reached by about day 77.

In conclusion, hearing in the opossum starts very late in the postnatal development, and the animals first respond to a narrow-frequency band right in the middle of the adult auditory range (expressed in octaves).

**B. Chiroptera**

There are no behavioral studies on the development of hearing in bats. However, there is evidence from mother–infant communication and from behavioral development that some bats, like *Macrotus californicus, Phyllostomus hastatus, Desmodus rotundus* and *Myotis lucifugus*, can hear from birth (Gould, 1971, 1975). *Eptesicus fuscus* can hear 1 day after birth since at this time the young change their rate of emission of isolation sounds when their mothers respond with ultrasounds (Gould, 1971). On the other hand, no behavioral reactions to sound could be elicited from newborn *Antrozous pallidus*, and evoked potentials from the inferior colliculus (IC) could not be recorded until the sixth postnatal day (Brown, Grinnell, and Harrison, 1978). Konstantinov (1973) measured evoked potentials in the IC of *Myotis oxynathus* and *Rhinolophus ferrumequinum* and found onset of responses at postnatal days 10 and 7, respectively. In these two bats and in *Antrozous*, the best-frequency response ranges were first very narrow and were situated in the middle of the adult hearing range (expressed in octaves). During development, frequency response ranges widened toward lower (more rapidly) and higher (more slowly) frequencies until at about 1 month of age adult hearing was achieved.

**C. Carnivora**

1. MINK (*MUSTELLA VISON*)

Foss and Flottorp (1974) studied hearing development by means of the startle response. They first found responses to frequencies between 0.5 and 0.75 kHz at postnatal day 20, which is very late. This apparent delayed onset of hearing, however, may be due to the rather insensitive method of measurement used, since Sugiura and Hilding (1970) could measure whole eighth nerve action potentials at day 21. Hearing range increased to both lower and higher frequencies with age.
2. DOG (*CANNIS FAMILIARIS*)

The first startle responses to sound were observed in puppies at day 14 after birth with a 0.75 kHz tone stimulus. By day 20, the hearing range had broadened to 0.25–8 kHz (Foss and Flottorp, 1974). Again, electrophysiological measurements indicate an earlier onset of function of the auditory system. The first CM potentials occurred at day 7 (Pujol and Hilding, 1973), and the first evoked potentials from the auditory cortex to sound stimulation were found at postnatal day 6 (Chaloupka et al., 1968). Fox (1968) could not measure cortex evoked responses to clicks earlier than day 12. This, however, may be due to the stimulus used and to the intensity of the clicks, which was not specified.

3. CAT (*FELIS CATU*)

a. *Development of Absolute Auditory Thresholds to Tones.* Foss and Flottorp (1974) first observed startle responses to tones at day 5 after birth. Olmstead and Villablanca (1980) tested a 2 kHz tone at 75 dB SPL and found that the time of the first observable behavioral response differed among individual kittens; it ranged from postnatal day 1 to 8, the average being at day 5. Similar results were obtained by Ehret and Romand (1981), who observed preyer reflexes in 4 of 11 kittens on the first postnatal day, in 12 of 16 on day 2, in 14 of 16 on day 4, and in all 20 kittens tested on day 6. Clearly, there are individual differences in the degree of maturation of the auditory system and/or the motor system at birth and during the first week thereafter.

Figure 1 shows the average auditory threshold curves at different times after birth (from Ehret and Romand, 1981). Data points were plotted when at least four of the animals tested showed a response. Threshold determinations are based on observations of the Preyer reflex up to day 10 and on conditioned eyelash responses from day 10 onwards. Threshold curves from both methods are plotted for day 10, and it is evident that the conditioned response yielded lower thresholds at all test frequencies than the unconditioned reflex. The frequency response range widened from 0.5 to 2 kHz, first toward lower frequencies where the lowest thresholds to elicit an eyelash were reached earlier than in the high-frequency range, where frequency range extention and sensitivity increase continued until at least day 30. The lowest thresholds from day 10 onward are always measured at 4 kHz. Although thresholds measured by eyelash showed no further decrease after day 22 (for frequencies lower than 25 kHz, Figure 1), adult thresholds measured by a conditioned shock avoidance procedure (Neff and Hind, 1955) are lower, most probably because this a more sensitive method.

Figure 2 is a plot of threshold sound pressure level at four representa-
Figure 1. Development of absolute auditory thresholds in the kitten, measured by unconditioned Prep反射 reflex up to day 10 (filled symbols) and by conditioned eyelink responses from day 10 onward (open symbols). Filled triangle, day 2; filled circle, day 4; filled square, day 6; filled upside-down triangle, day 10; open upside-down triangle, day 10; open square, day 12; open circle, day 15; open diamond, day 22; open triangle, day 30. For purposes of comparison, the lower, dotted line shows the absolute auditory thresholds of the adult cat (Neff and Hind, 1955). The upper, dashed line represents the maximum sound pressure level produced by the equipment without distortion. (Adapted from Ehret and Romand, 1981.)

tive frequencies versus age and demonstrates clearly three phases of threshold development: (a) high but constant thresholds up to day 6; (b) rapid threshold decrease by more than 50 dB between days 6 and 10; (c) a slow decrease of thresholds mainly at high frequencies from day 10 to day 30. The anatomical and physiological correlates of this development will be discussed later.

b. Development of Responses to Various Natural and Artificial Sounds. Olmstead and Villablanca (1980) studied the development of startle responses to some cat vocalizations and to artificial sounds. Figure 3 shows that at the first postnatal day few kittens respond to the stimuli presented at 70–80 dB SPL. By day 5 about 50% of the animals responded to most of the stimuli, and by day 12 all kittens responded to all the sounds except the hand clap, which seemed not to be an efficient stimulus at all. The greatest increase in response probability occurred between the third and the tenth postnatal day. This coincides with auditory threshold development, es-
especially at the relatively low frequencies (Figures 1 and 2) of which the sound stimuli in Figure 3 are composed. Therefore, the increase in response probability to the sound stimuli in Figure 3 is most probably due to the sensitivity increase found by Ehret and Romand (1981, Figure 1 and 2).

c. Development of Directional Responses. The orientation of kittens toward attractive stimuli (mother and kitten sounds) or away from unattractive sounds (threat, growl, air blast) has been studied by Olmstead and Villalba (1980). They found directional responses toward a sound source to occur earlier than those away from the stimulus (Figure 4). However, more than 50% of the animals showed no directional responses at all until the fifteenth postnatal day, that is, well after the onset of hearing (Figure 1). By about day 25, animals responded consistently and their ability to discriminate and localize sounds became stable.

Very similar results were obtained by Clements and Kelly (1978b), who measured approaches directed toward a speaker playing kitten cries. Directional approach responses were first clearly observed between days 15 and 25, and the response probability increased thereafter.
FIGURE 3. Cumulative percentage of kittens (N = 37) responding with a startle response to various natural and artificial sounds during the first 15 postnatal days. Sounds in diagram (a) were tape recorded and played back in the response tests, those in diagram (b) were presented directly. Less than 50% of the kittens respond to the sounds until day 4. At day 12 all the kittens respond to all sounds except the handclap. (Adapted from Olstead and Villalba, 1980.)
FIGURE 4. Development of orienting responses in kittens (turning toward or away from a sound source). The stimuli presented were mother and kitten sounds (usually eliciting approach) and threat or growls, and air blasts (usually eliciting withdrawal). The number of animals tested on different days varied between 10 and 32. (From Obinstand and Villablanca, 1980.)

D. Rodentia

1. RABBIT (Oryctolagus cuniculus)

Startle responses to a 0.75-kHz tone were first obtained at day 7 after birth (Foss and Flottorp, 1974). By day 10, the animals responded to tones between 0.125 and 8 kHz.

2. GUINEA PIG (Cavia porcellus)

The guinea pig is a precocial animal that is born with eyes and ears open, with good motor control, and with the ability to control its body temperature. Behavioral responses indicate that hearing begins 5–6 hours before birth (Wada, 1923). That CM potentials could be measured 15 days before
birth (Pujol and Hilding, 1973; Romand, 1971), whole-nerve action potentials 12 days before birth (Romand, 1971), and EEG responses to sound 2 days before birth (Scibetta and Rosen, 1969) indicates that guinea pigs certainly can hear in the uterus. Directional approaches toward guinea pig vocalizations were already observed in 1–4 day old animals (Clements and Kelly, 1978a).

3. RAT (RATTUS NORVEGICUS)

First startle responses in rats were recorded on day 10 after birth (Wada, 1923). Between days 16 and 20, the startle-response amplitude to a 10-kHz tone increased to the adult level (Parisi and Ison, 1979).

Cochlear microphonic potentials were first recorded on days 8 or 9 (Crowley and Hepp-Reymond, 1966; Uziel et al., 1981), whole-nerve action potentials on days 11 or 12 (Uziel et al., 1981), and brainstem evoked potentials on days 12 or 13 (Jewett and Romano, 1972; Osako et al., 1979). Sensitivity increases and frequency range widens up to day 20, by which time adult levels seem to have been reached (Crowley and Hepp-Reymond, 1966; Osako et al., 1979) Directional responses to rat calls were observed from day 13 onward (Potash and Kelly, 1980).

4. HOUSE MOUSE (MUS MUSCULUS)

a. Absolute Thresholds to Tones. Onset of hearing was found to occur between days 9 and 14 in CBA-J mice (Alford and Ruben, 1963; Mikaelian and Ruben, 1965; Powers et al., 1966), at day 13 in the sh-1 strain (Hack, 1968), and at day 10 in NMRl mice (Ehret, 1976, 1977). Figures 5 and 6 show that the development of auditory sensitivity starts in the middle of the frequency range and then extends rapidly to lower frequencies and more slowly to higher frequencies. Until day 13, the frequency range responded to is rather narrow, and no sensitivity maximum is obvious. From day 14 onward, a sensitivity optimum at 15 kHz occurs. After day 15, there is no further systematic sensitivity increase at 10 kHz and below and, at day 18, adult threshold levels (as determined by unconditioned responses) can be measured throughout the frequency range (Figure 6). This is also true for CBA-J and sh-1 mice, where adult and maximum sensitivity, respectively, were found between days 16 and 20 (Hack, 1968; Powers et al., 1966).

Although threshold development appears to end around day 18 (Figures 5, 6), thresholds in adult mice (2–3 months old) are very much lower (Figure 5). Most of the difference can be explained by the different sensitivity of the methods of threshold determination, since unconditioned responses were used for the young mice and conditioned responses for the adults. The conditioned eyeblink response was also used to estimate thresholds in 17–19-day-old mice, and higher sensitivity was found there than in 18-day-old mice for which unconditioned responses were used (Figure 5).
There still remains a qualitative difference between conditioned response thresholds in 17–19-day-old mice and those in young adults, which is that the relative sensitivity maximum at 50 kHz occurs only in adult mice. Apparently this sensitivity maximum in the high ultrasonic range is established late in the development.

b. Masked Thresholds and Critical Ratio Bands. The perception of tone-bursts in a continuous white noise background depends on the frequency resolution of the auditory system. If the filters in the system are very broadly tuned (i.e., the resolution is poor), then a broadband noise can influence the perception and processing of a tone in the center of the filter (i.e., relatively low noise levels can effectively mask the tone). If, on the other hand, filters are narrow (i.e., the resolution is high) then only a small band of noise can influence tone perception and the noise levels required to mask the tone are higher. Masked thresholds are thus a measure of the

![Figure 5](https://example.com/f5.png)

**FIGURE 5.** Postnatal development of auditory thresholds at different frequencies in house mice, strain NMRI, as measured by an orienting response. Filled square-day 14; filled triangle-day 15; filled upside down triangle-day 16; filled diamond-day 16; open circle-day 24; open square-day 30; open triangle-days 17 to 19, conditioned eyelid response; open upside down triangle-second to third months conditioned responses. (From Ehret, 1976.)
frequency-resolution power of the auditory system. In order to calculate filter bandwidths from masked thresholds it is generally assumed (a) that the filtering is linear and (b) that the intensities of the tone and the total noise within the filter bandwidths are equal at the masked threshold (Fletcher, 1940; Scharf, 1970). Under these assumptions the filter bandwidth is equal to the ratio of tone and noise intensities (expressed as spectral intensity)

\[ \text{CR-band} = \frac{I_{\text{tone}}}{I_{\text{noise}}/\text{Hz}} \]  

(1)
or equal to the difference of tone and noise levels (expressed as spectrum level of noise)

\[ \text{CR-band} = L_{\text{tone}} - l_{\text{noise}} \]  

(2)
and is called critical ratio band (CR-band).

Ehret (1977) measured masked thresholds in developing NMRI mice (Figure 7); from these curves, development of frequency resolution and filtering may be deduced. Also included in Figure 7 are plots of absolute thresholds, and comparing them shows that absolute thresholds exhibit the characteristic sensitivity optimum at 15 kHz from day 14 onward, whereas masked thresholds do not. Masked threshold curves always have the same shape: they are relatively flat below 15 kHz and then increase. From day 11 to 13, masked thresholds at zero-decibel spectrum level and absolute thresholds are the same because mice do not yet hear the masking noise used.
Although absolute thresholds decrease continuously until about day 18 (Figure 6), the decrease in masked thresholds is interrupted by an increase between days 12 and 14 (Figure 8). Decreasing masked thresholds mean that, for a constant spectrum level of noise, the influence of noise on tone perception decreases (i.e., masking becomes less efficient). There are two possible reasons for a threshold decrease: (a) the “internal noise” of the functionally incomplete nervous system is reduced when the system becomes mature (this internal noise may add to the stimulus noise from the speaker) and (b) the CR-band filters narrow during maturation so that less and less noise becomes effective in masking a tone in the center of the CR-band. If this is the reason, it would indicate an improvement in frequency resolution during development between days 10 and 18.

The increase in masked thresholds between days 12 and 14 is more difficult to explain. A loss of frequency resolution due to a broadening of CR-band filters seems rather unlikely and would conflict with the development of tuning observed in the cochlear nucleus of the mouse (Saunders et al., 1980). Instead, the reason may be the rapid improvement of sound transfer through the middle and inner ear between days 11 and 14 (Boshier and Warren, 1971; Kraus and Aulbach-Kraus, 1981; Mikaelian and
Ruben, 1965). An improvement of sound transfer over a frequency band has the effect of increasing masked thresholds because the increase of total noise energy within the bandwidth is larger than the increase of energy at the tone frequency. Thus, Figure 8 seems to reflect two processes with opposing effects on masking in the auditory development of the mouse; one process reduces effective noise energy by taking away "internal noise" and/or narrowing the filter bandwidths, and the other increases the efficiency of sound transfer in the ear and thereby the efficiency of masking. The first process is effective from days 10 to 18, the second is most prominent between days 12 and 14.

E. Primates

There are no reports on the development of the auditory system in nonhuman primates. Since development of hearing in man is discussed in a later chapter, I will only mention some major steps. The 26- to 28-week fetus can hear (Berkson et al., 1974; Fleischer, 1955; Goodlin and Schmidt, 1972; Grimwade et al., 1971; Tanaka and Arayama, 1969) and, immediately after birth, neonates can orient toward a sound source (e.g., Wertheimer, 1961) and can discriminate the pitch of the sound (Leventhal and

![Graph showing development of masked thresholds versus age for five representative frequencies in the house mouse. Standard deviations of the means are also shown. Thresholds decrease until day 12, then show a slight increase until day 14, and then decrease again until the adult values are reached at day 16 to 18. (Modified from Ehrin, 1977.)](image-url)
Lipsitt, 1964; Muir and Field, 1979). One-month-old babies show categorical perception of speech signals based on voice onset times (Eimas et al., 1971); at about 6 months after birth, cortical evoked potentials to sound show adult waveforms (Salamy and McKeen, 1976). Infants about 1 year old show adult temporal resolution as reflected by the latency of evoked potentials (Barnet et al., 1975). Auditory threshold curves demonstrating the development of sensitivity are apparently not available.

IV. Anatomical and Physiological Correlates of the Development of Hearing in Mammals

The following discussion is based on the quantitative behavioral data available for the cat and the mouse. My aim is to find correlates of the sensitivity increase and of the expansion of frequency response range (Figures 1, 2, 5, and 6) as well as for the improvement of frequency resolution (Figure 7 and 8) and of directional hearing (Figure 4) that occur during development.

A. Cat

An animal cannot show a behavioral response to sound before the onset of function of at least a part of the inner ear and the cochlear nerve. In kittens, CM potentials as well as action potentials in the eighth nerve and in the cochlear nucleus can be recorded immediately after birth (Mair et al., 1978; Romand, 1971; Romand and Marty, 1975). However, sound pressures required to evoke these responses are high (about 100 dB SPL), and the frequency response range is very narrow (0.8–4 kHz). Auditory-nerve potential thresholds remain high, and the responses are very broadly tuned until the sixth postnatal day (Carlier et al., 1979). These results are in very good agreement with those obtained by the behavioral measurements up to day 5 after birth (Figure 1), when thresholds were also around 100 dB and no tuning, that is, no best frequency, was apparent.

These threshold curve characteristics are a result of the immature state of the cochlea and of the eighth nerve of the kitten at that age. In addition, membranes in the ear canal attenuate sound transfer to the tympanic membrane (TM) and thus contribute to the high thresholds (Olmstead and Villablanca, 1980). By about the fourteenth postnatal day, cochlear structures resemble, by qualitative observation, those of adults (Carlier et al., 1979; Pujol and Hilding, 1973; Pujol and Marty, 1970; Pujol et al., 1978); however, such processes as myelination of spiral ganglion cells and nerve fibers continue for more than 1 month after birth (Romand et al., 1976, 1980).

The opening of the ear canal and the rapid development of the cochlea
and of the auditory nerve and cochlear nucleus between days 6 and 14, especially as indicated by the sensitivity increase and the sharpening of tuning, is reflected in corresponding changes in the behavioral threshold curves that show an increase in sensitivity and frequency response range. A sensitivity optimum at 4 kHz also becomes apparent during this time (Figures 1 and 2). Behavioral threshold development seems to stop at about day 30. Since it has been found that the cat's auditory nerve (Romand, 1979; Romand et al., 1976), cochlear nucleus (Romand and Marty, 1975), and higher brain centers (König et al., 1972; Moore and Irvine, 1979) may not be fully mature 30 days after birth, the behavioral threshold curve at day 30 may not indicate adult sensitivity. The large differences, however, between the day 30 and the adult threshold curve (Figure 1) are probably due to differences in sensitivity of the methods of measurement, as was discussed earlier.

A comparison of average behavioral threshold development with corresponding threshold decreases in the cochlear nucleus and the IC (Figure 9) reveals striking similarities in the time course of threshold decreases. This

![Figure 9](image-url)

**FIGURE 9.** Comparison of the development of behavioral absolute auditory thresholds in the kitten (values averaged from frequencies between 0.2 and 15 kHz; Elsor and Romand, 1981) with average single-unit threshold development in the cochlear nucleus (Brugge et al., 1978) and in the IC (Ashlin and Moore, 1973; Moore and Irvine, 1979; units with best frequencies lower than 3 kHz, units with best frequencies equal to or higher than 3 kHz). The development of behavioral and physiological thresholds have essentially the same time course and both follow Eq. 3.
can be more quantitatively described by power functions approximating the curves in Figure 9, which have the general form
\[ L_t = L_a + A e^{-tB} \]  
where \( L_t \) is the threshold on any particular postnatal day, \( L_a \) is the adult threshold, \( t \) is a postnatal day, and \( A \) and \( B \) are constants. The values for \( A \) and \( B \) are: behavior, \( A = 200, B = 4.55 \) (correlation coefficient \( r = 0.974 \)); cochlear nucleus, \( A = 240, B = 4.13 \) \((r = 0.956)\); IC (Aitkin and Moore, 1975), \( A = 446, B = 4.35 \) \((r = 0.837)\); IC (Moore and Irvine, 1979, both values at any given day included in the calculation), \( A = 196, B = 8.0 \) \((r = 0.759)\). Equation 3 was developed by Eggermont (1981), who discusses in detail the general significance of this power function in relation to development of auditory function in brain centers of mammals. The apparent similarity of developmental processes described by the curves in Figure 9 is reinforced by the fact that the constants \((A \text{ and } B)\) for the functions have similar values. We may therefore conclude that the development of auditory sensitivity as measured behaviorally in the kitten is clearly correlated with the development of brainstem and midbrain responses. Since pinna movements, which were observed as behavioral responses, seem to be controlled at the midbrain level (Henkel and Edwards, 1978) these correlations may be especially meaningful.

Aitkin and Reynolds (1975) and Moore and Irvine (1980, 1981) studied the sensitivity of cells in the IC to interaural cues that may be used for sound localization. By the end of the first postnatal week, cells with binaural response properties similar to those of cells in adult animals were found, although the variability of the responses during the first 1 or 2 months seemed to be larger than in adults. Thus, the lack of directional responses during the first 15 days of life that was found behaviorally (Figure 4) may be due to the high thresholds of the neurons (Figure 9) rather than to a general inability to process binaural information. One could therefore predict that repetition of the behavioral sound localization experiment with higher-intensity sounds would show earlier onset of directional responses than found in the studies by Clements and Kelly (1978b) and Olmstead and Villablanca (1980).

**B. Mouse**

All aspects of the preceding discussion for the cat are also valid for the house mouse (as far as they have been investigated). By the time the inner ear has become functional, at postnatal day 10 (Kikuchi and Hilding, 1965; Mikaelian and Ruben, 1965), eighth-nerve action potentials (Alford and Ruben, 1963; Mikaelian and Ruben, 1965) and behavioral responses (Figures 7 and 8) can be observed. Thresholds are initially high, the frequency response range is small, and tuning, in form of a sensitivity optimum, is
absent up to day 14. From day 15, thresholds of units in the cochlear nerve, cochlear nucleus, and IC rapidly decrease, and frequency tuning becomes much sharper (Saunders et al., 1980; Shnerson and Pujol, 1982; Shnerson and Willott, 1979; Willott and Shnerson, 1978). This correlates with an increase in behavioral sensitivity and the appearance of the sensitivity optimum at 15 kHz (Figures 5, 7). The maturation of tuning and response properties of neurons is largely completed by day 18, which coincides with the maturation of absolute behavioral thresholds (Figures 5 and 6) and masked thresholds (i.e., frequency resolution expressed in the bandwidth of CR-band filters, Figures 7 and 8).

As in the cat, the average development measured behaviorally or by neural response thresholds is very similar (Figure 10) and can be described by the same power function used for the cat (Eq. 3). For the mouse, the constants (A and B) have the following values: behavior, $A = 1360, B = 2.9$ (correlation coefficient $r = 0.956$); CM, $A = 1.56 \times 10^6, B = 1.0$ ($r = 0.949$); cochlear nucleus, $A = 5.23 \times 10^4, B = 1.75$ ($r = 0.986$). Data from the IC cannot be evaluated in this way. As compared to the cat, the development of auditory function in the mouse proceeds more quickly (smaller

**FIGURE 10.** Comparison of the development of behavioral absolute auditory thresholds in the house mouse (values averaged from frequencies between 5 and 30 kHz, Ehret, 1976) with average threshold development of the CM potential (Mikhazian and Ruben, 1965), of evoked responses from the cochlear nucleus (Saunders et al., 1980), and of single units in the IC (Shnerson and Willott, 1979). As was demonstrated for the cat (Figure 9) the development of behavioral and physiological thresholds is very similar and both can be described by Eq. 3.
time constants, $B$, in Eq. 3). In the mouse, the adult state is reached about 2 weeks after the onset of hearing, whereas in the cat, it takes more than 1 month. In a mammal with slower general development, like man, development of auditory capacity continues for even longer periods of time.

V. General Discussion

There is a general trend among mammals for hearing to start in the lower and middle frequency parts of the adult auditory range. During development, hearing extends to lower frequencies first and then to higher frequencies (e.g., cat: Ehret and Romand, 1981; Romand, 1971; mouse: Ehret, 1976, 1977; Mikaelian and Ruben, 1965; rat: Crowley and Hepp-Reymond, 1966; guinea pig: Romand, 1971; Mongolian gerbil: Finck et al., 1972; bat (Antrozous pallidus): Brown, Grinnell, and Harrison, 1978). In contrast, it has been shown that, anatomically, the inner ear in man (Bast and Anson, 1949), the cat (Pujol and Marty, 1970; Romand et al., 1980), the mouse (Mikaelian and Ruben, 1965), and the rat (Wada, 1923) matures from the basal turn (where high frequencies are represented) to the apex (low frequencies). This seeming discrepancy between cochlear maturation pattern and developing frequency range of hearing can be resolved if one also considers the development of the middle ear and of the basilar membrane. Finck et al. (1972) showed that ossification of the middle-ear bones in the Mongolian gerbil continues until day 16 after birth. Cartilagenous middle-ear ossicles incompletely connected to each other can be assumed to severely attenuate high frequencies. Similarly, the basilar membrane in developing cochleae seems not to be as stiff as it is in adults. It has fewer filaments and is more cellular and less compact (Kikuchi and Hilding, 1965; Kraus and Aulbach-Kraus, 1981; Mikaelian and Ruben, 1965). Therefore, it, too, is unlikely to have a good high-frequency response. Thus, it appears that although mammals first hear in a rather low-frequency range, they use the more basal part of their cochlea, which, in adulthood, is stimulated at low frequencies only by high intensity sound. This may be another reason for the high thresholds seen during the first days after the onset of hearing.

It seems trivial to state that the development of response behavior to sound depends on the development of hearing; however, hearing alone appears to be insufficient for eliciting behaviors other than diffuse reflex responses like startle or Freyer responses. Differentiated behavior to sound stimulation such as directional responses (Figure 4) is possible only after marked sensitivity increase and improvement in frequency selectivity and resolution in the auditory system. Thus, we cannot expect acoustic communication with infants as receivers to begin immediately after the onset of hearing, although infants may produce a variety of sounds from birth (see
Ehret, 1980). A change from sender to sender–receiver status in the young of bats (Brown, 1976; Gould, 1971) and cats (Brown, Buchwald, Johnson, and Mikolich, 1978) takes place not after the onset of hearing, but only after sufficient sensitivity and resolution has developed.

VI. Conclusions

The development of hearing in mammals has been discussed on the basis of behavioral measurements of auditory function. First responses to high-intensity sound are reported for a variety of animals (opossum, some bats, the mink, dog, cat, rabbit, guinea pig, rat, house mouse, and man). The following are general characteristics of auditory development after the onset of hearing:

1. The response range broadens toward lower and higher frequencies until the adult auditory range is reached.
2. Auditory thresholds decrease (increase of sensitivity) according to an exponential function.
3. Frequency selectivity (frequency resolution) improves, as indicated by the appearance of sensitivity optima in absolute threshold curves; this improvement can be measured quantitatively in masking experiments (CR-bands) and frequency-tuning curves.
4. Differentiated responses to sound such as directional movements do not occur with the onset of hearing but only after sufficient sensitivity of the auditory system has been achieved.

Anatomical and physiological correlates of behavioral auditory development are discussed in detail for the cat and mouse, which are the species most thoroughly investigated so far. Onset of hearing takes place when the ear canal is still closed, the middle ear is not well ossified, the inner ear structures are only partly (near the base of the cochlea) developed, and development of higher nervous centers is still in progress. The rapid early improvement of sound transfer through the outer, middle, and inner ear is the reason for the rapid increase of sensitivity and frequency response range and for the improvement of frequency selectivity. The late stages of behavioral sensitivity increase may be due to more central maturation processes and it may be predicted that complex sound analysis and recognition, although present since shortly after onset of hearing, will reach the adult capability with central maturation.

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References


