



Postnatal Development of Absolute Auditory Thresholds in Kittens

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Postnatal development of absolute auditory thresholds in the kitten was behaviorally measured from birth up to 1 mo of age. Unconditioned reactions to pure tones were observed for kittens up to Day 12, and conditioned responses were used for animals from Day 10 onward. At 1 day after birth, the first noticeable responses were obtained in 4 of 11 kittens at frequencies of .5–2 kHz. At 2 days of age, 12 of 16 kittens responded. Thresholds remained high (above 100 dB SPL) up to the sixth day, but the range of behaviorally effective frequencies extended from .2 to 6 kHz. All conditioned response thresholds at Day 10 and most at Day 12 were significantly lower than those measured by unconditioned reactions. From 10 days onward, all threshold curves showed a characteristic sensitivity optimum at 4 kHz. For frequencies below 1 kHz, maximum sensitivity was reached at Day 15; for frequencies up to 20 kHz, at Day 20; and for even higher frequencies, at Day 30. At 1 mo of age, the frequency range is adultlike. The present behavioral results on developing acoustic function in the kitten closely followed structural maturation of the acoustic pathway and demonstrated limitations of the ability for acoustical communication during the first week of life.

Studies of the time course of postnatal development of auditory sensitivity generally try to answer two important questions: First, what is the sequence of development and the pattern of maturation of the acoustic periphery versus higher brain centers; second, when does the ability to communicate acoustically appear (this obviously depends on sufficient auditory sensitivity and resolution)? Anatomical and electrophysiological work on the developing acoustic pathway can show whether the structural basis for a proper functioning is present and how far neural coding has matured to adult patterns of sensitivity, timing, and filtering. However, only behavioral studies can present the final evidence, namely, to what

extent the intact animal is able to use and to respond to information processed by the developing acoustic periphery and acoustic pathway.

Investigations of the development of the acoustic system have been carried out in a number of mammals (for references see Ehret, 1980). Unfortunately, however, data for most of these mammals relate only to periphery or to behavior or to single stations of the auditory system, so that a complete picture of the interdependence of events and of the significance of progress in one center for the whole system cannot really be established. The cat (Aitkin & Moore, 1975; Brugge, Javel, & Kitzes, 1978; Carlier, Lenoir, & Pujol, 1979; Carlier & Pujol, 1976; König, Pujol, & Marty, 1972; Marty, 1962; Moore & Irvine, 1979; Pujol, 1972; Pujol, Carlier, & Devigne, 1978; Pujol & Marty, 1970; Romand, 1971, 1979; Romand, Granier, & Marty, 1973; Romand & Marty, 1975; Romand, Sans, Romand, & Marty, 1976) has been studied in most detail and can provide a good basis for comparison with other species. At present, the line of data for the cat from periphery to behavior ends with the behavioral absolute thresholds measured by

This study was supported by grants from the Deutsche Forschungsgemeinschaft to G. Ehret (Eh 53/1,3,5) and from Centre National de la Recherche Scientifique (ERA, No. 187) and Délégation Générale de la Recherche Scientifique et Technique (No. 79-7-1073) to R. Romand. We thank Franz Gruber and Karen Mirsch for animal supply and care.

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Foss and Flottorp (1974). Since their technique—detection by the experimenter holding the kitten in his hand of unconditioned movement in response to sound—is rather unsatisfactory and since their results disagree with electrophysiological determination of the onset of hearing (Pujol, 1972; Romand, 1971; Romand & Marty, 1975), we decided to carry out measurements in kittens with improved behavioral methods similar to those applied by Ehret (1976, 1977) in mice. The tests were devised to examine whether kittens can behaviorally respond to sound from birth, as electrophysiology suggests, and when their behavioral sensitivity and auditory bandwidth are adequate for them to hear calls of siblings and their mother.

Method

Subjects

Altogether, 22 kittens from four litters (with 7, 6, 5, and 4 kittens, respectively) were involved in the tests. The kittens were delivered by normal healthy house cats (*Felis catus*) bred in the University of Konstanz. Gestation times were 65 (two litters) or 66 days (one litter); that for the last litter was not known. The mothers with their litters were housed in separate cages in rooms where other cats from the stock were freely moving around. All kittens used in the test were healthy and behaving normally. Kittens were tested on the following postnatal days (numbers in the brackets indicate the numbers of kittens used): 1 (11), 2 (16), 4 (16), 6 (20), 10 (18), 12 (13), 15 (12), 22 (12), and 30 (8). Table 1 presents the testing schedule for each individual kitten. The weight of each kitten was determined each day on which it was tested.

Apparatus

The tests were conducted in an industrial sound-isolated and anechoic room (390 × 300 × 250 cm). Background noise levels could not be measured for frequencies above 500 Hz (Brüel & Kjaer .5-in. microphone Model 4133 with measuring amplifier Model 2606). For lower frequencies, the background noise level was at least 10 dB lower than the lowest measured mean thresholds (Figure 1). Rock-wool wedges on all walls prevented standing waves over the whole frequency range of the tests (.2–60 kHz).

Pure tones of known frequency and defined amplitude were generated in a frequency synthesizer (Rockland Model 5100, with a programming unit), amplified (Hewlett-Packard, 466A), attenuated (Hewlett-Packard, 350D), and passed either directly or through a filter (Krohn-Hite, 3500) to a power amplifier (Exact, 170). From there the tone signal passed to one of the two speakers. For frequencies ≤10 kHz, we used a com-

Table 1
Testing Schedule for All Kittens

Kitten no.	Postnatal day									
	1	2	4	6	10	12	15	22	30	
1.1	—	—	—	+	+u	—	—	—	+	
1.2	—	—	—	+	+u	—	+	—	—	
1.3	—	—	—	+	+u	—	+	—	—	
1.4	—	—	—	+	+u	—	+	+	—	
1.5	—	—	—	—	—	—	+	+	+	
1.6	—	—	—	—	—	—	+	+	—	
2.1	+	+	+	+	+c	+c	—	+	—	
2.2	+	+	+	+	+c	+c	—	+	—	
2.3	+	+	+	+	+c	+c	—	—	—	
2.4	+	+	+	+	+c	—	+	—	—	
2.5	+	+	+	+	+c	—	+	+	—	
2.6	+	+	+	+	+c	+c	+	—	—	
2.7	+	+	+	+	—	—	+	—	—	
3.1	—	+	+	+	+u	+u	—	—	—	
3.2	—	+	+	+	+u	+u	—	+	+	
3.3	—	+	+	+	+u	+u	—	—	—	
3.4	—	+	+	+	+u	+u	—	+	+	
3.5	—	+	+	+	+u	+u	—	—	—	
4.1	+	+	+	+	+c	+c	+	+	+	
4.2	+	+	+	+	+c	+c	+	+	+	
4.3	+	+	+	+	+c	+c	—	+	+	
4.4	+	+	+	+	—	+c	+	+	+	

Note. Each kitten has two identification numbers: The first indicates the litter; the second, the individual of this litter. u: tested by unconditioned reactions; c: tested by conditioned responses (indicated at Days 10 and 12 when both methods were applied).

pression chamber speaker (Philips LBC 3404 + LBN 9001/00) and for frequencies ≥12.5 kHz a condenser speaker after Machmerth, Theiss, and Schnitzler (1975). The frequency synthesizer was programmed to produce a tone burst of 1,000-msec duration, with additional rise and fall times of 8 msec. The tone burst gated the time base of an oscilloscope which triggered a stimulator (Grass, S 88 with isolation unit, SIU 5) to produce an electric shock. The shock consisted of a 50-Hz square-wave signal, had a duration of 500 msec, and started 100 msec before the tone burst ended. The shock amplitude was adjusted to between 10 and 30 V, depending on the response of the kittens. All equipment except the speakers was placed outside the anechoic room.

The sound-producing system was calibrated after every test session by measuring the average sound pressure level (SPL) at each test frequency (at a known attenuation) in the area in which a kitten could move its pinnae. The measurement was done with a calibrated .5-in. or .25-in. condenser microphone (Brüel & Kjaer, 4133 or 4135) and a measuring amplifier (Brüel & Kjaer, 2606). The highest SPLs that could be produced without distortion are shown in Figure 1. All SPLs in decibels are relative to μ Pa.

Tests

Two methods were employed. An unconditioned

response to tone bursts was used to determine auditory thresholds of kittens up to 12 days of age. A conditioned response was used for kittens of 10 days and older. Thus 10- and 12-day-old kittens were divided into two groups and tested by one or the other method in order to distinguish true development of auditory thresholds from effects of changing methods at these days.

1. Unconditioned movements of the pinnae and/or facial muscles in response to tone bursts were observed through an operation microscope (Zeiss, OPMI 1) at a magnification of five times. The kittens were restrained in a Styrofoam box so that only the head was free. The box was placed on a small platform suspended right in front of the speaker. The head of the kitten was, on average, 80 cm from the dynamic speaker and 30 cm from the ultrasonic speaker. Speakers and kittens were supported independently, so that a mechanical coupling (by way of vibration) was excluded.

A kitten of a given age was tested in one test session at all frequencies in question. Tests were performed only when kittens were nearly motionless and not crying. A threshold test at a given frequency and SPL ran as follows: A tone burst was presented every minute for 4 min, and the responses were noted. Thirty seconds after each trial with a tone burst, a sham trial was run with the tone attenuated by 85 dB. From the responses to the four tone bursts and to the four sham trials, the probability of a positive response to the tone signal was calculated with an equation used in signal detection theory (Swets, 1964):

$$p = \frac{p_S - p_{FA}}{1 - p_{FA}}, \quad (1)$$

where p_S is the probability of a response to a presented tone burst, i.e., the number of positive responses recorded to the tone bursts divided by the total number of tone bursts presented, and p_{FA} is the probability of a false alarm (a response in the absence of a tone), i.e., the number of recorded false alarms in the sham trials divided by the sum of false alarms and positive responses recorded to the tone bursts. All tests with probabilities $\geq 50\%$ were taken to indicate that the animal heard the tone bursts (positive response). From this, the auditory threshold at a given frequency was defined as the mean of the lowest SPL at which the animal responded positively to the tone bursts and the highest SPL at which no positive response (defined above) occurred. Tests started with SPLs close to the estimated threshold, and then the SPL was either decreased or increased in 5-dB steps until the threshold was reached.

2. Conditioned movements of eyelids and pinnae were observed after the animals were trained with tone-shock pairs. Kittens were restrained in a cage ($20 \times 7 \times 7$ cm) made of metal bars (diameter, .3 mm). Through the bottom grid with alternatingly poled bars, an electric shock could be given. Before conditioning and test sessions started, the paws of the kittens were coated with an electrode cream to decrease their skin resistance to the electric shock. Conditioning started at the 8th postnatal day (when the eyes had just opened) for two litters and at the 12th postnatal day for the other two litters. Two 10-min conditioning sessions were held per day in each of which about 30 tone-shock pairs (tone frequency, 2 kHz) were presented at random times.

The shock intensity was adjusted such that the animals were obviously shocked but did not cry vigorously. After five conditioning sessions the response, blinking of the eyelids and/or twitching of the pinnae, stabilized and could be observed on superthreshold tone bursts without being followed by shock. Not all kittens, however, reached or maintained a stable response level because they got excited or apathetic in the cage. Those kittens were excluded from the tests.

A kitten of a given age was tested in one test session at all frequencies in question. Tests were performed only while kittens were nearly motionless and not crying. Tests had to be complete in a minimum of time because after about 20 min the kittens tended to make vigorous efforts to escape from the cage. Therefore the following rapid method for threshold determination was employed: The reactions of a kitten to three tone presentations of a given frequency and SPL were observed and counted as a positive response if at least two reactions were positive and if not more than one false alarm occurred during the time interval in which the three tone bursts were presented. This criterion corresponds to a 50% value when calculated by Equation 1. Again, the auditory threshold for a given frequency was defined as the mean of the lowest SPL at which a positive response occurred and the highest SPL at which the response was negative. The SPLs were varied in 5-dB steps near threshold.

Results

Behavioral response to tones was observed in 1-day-old kittens. However, only 4 of 11 kittens responded, and they did so to a very restricted frequency range (.5–2 kHz). Two kittens responded at 1 kHz, one at .5 kHz and another at 2 kHz. Thresholds ranged between 112 and 124 dB. By the second day of age (Figure 1), 12 kittens reacted to pure tone stimulation, while 4 showed no response. The frequency range to which the animals responded widened toward lower (300 Hz) and higher frequencies (6 kHz); however, only two animals showed a response at 300 Hz and 4 kHz and only one animal at 6 kHz. All thresholds were higher than 100 dB (Figure 1). By the fourth postnatal day, only 2 of 14 kittens did not respond to sound. Threshold sensitivity and frequency range did not increase compared with that of 2-day-old animals. By the sixth day, all kittens reacted to sound. With regard to body weight, most kittens start responding when they reach 120–140 g. No sex differences could be measured.

Mean threshold values for 2–6-day-old kittens did not show significant variations with frequency at one age or among ages ($p > .05$, rank test after Wilcoxon, here and in

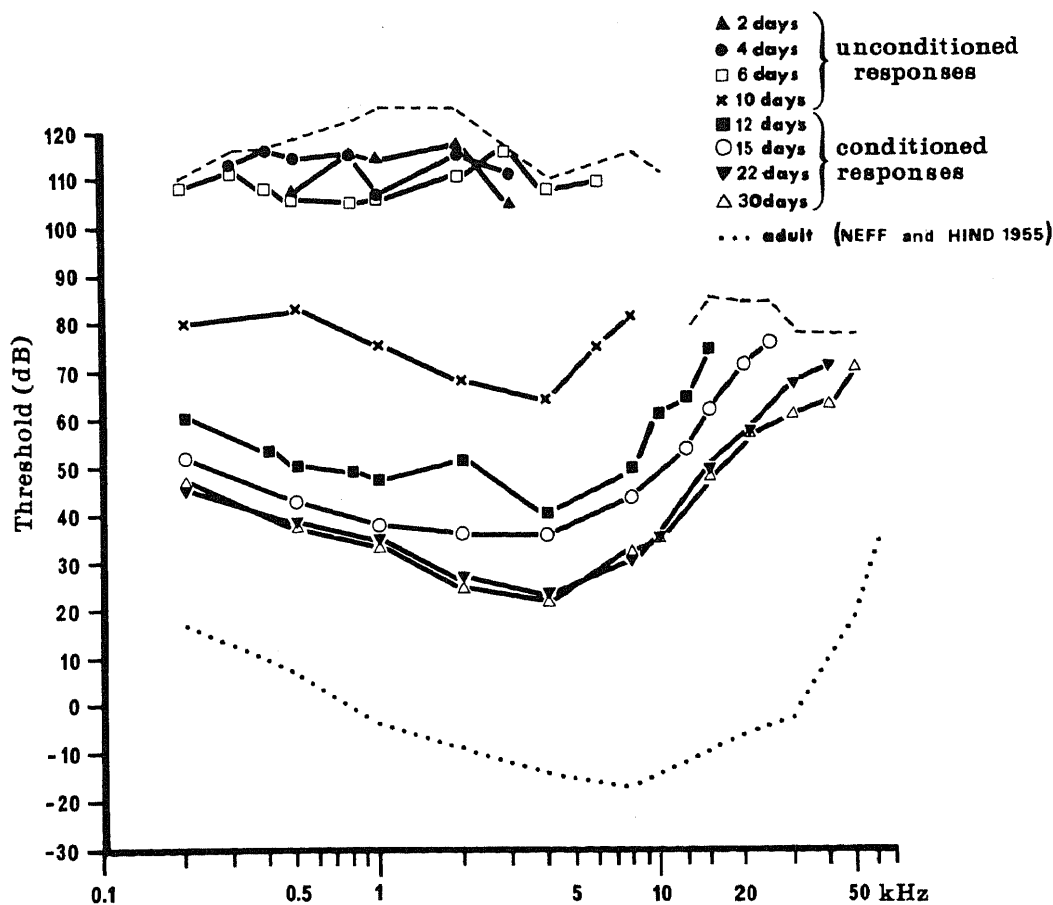


Figure 1. Postnatal development of absolute auditory thresholds in the kitten. (Thresholds were obtained by unconditioned reactions for kittens 2–10 days old and by conditioned responses at the older ages. For comparison, the lower dotted line shows the absolute auditory thresholds of the adult cat. The upper dashed line represents the maximum sound pressure level produced by the equipment without distortion. Sound pressure levels are always relative to 20 μ Pa.)

all further tests). The only important change was the widening of the average frequency range from .5–3 kHz at Day 2 to .2–6 kHz at Day 6 (Figure 1). Between Day 6 and Day 10, a significant ($p < .01$) decrease in absolute thresholds (unconditioned response) was observed over the whole frequency range. This decrease of threshold was most pronounced at 4 kHz, at which it had a value of more than 40 dB. In addition, a sensitivity maximum at 4 kHz became obvious at Day 10. The mean threshold at 4 kHz was significantly lower than those at 1 and 6 kHz ($p < .02$) and .5 and 8 kHz ($p < .01$).

At Day 10, first conditioned response thresholds could be measured (Figure 2). These were significantly lower ($p < .01$) than the values for the unconditioned responses

at all frequencies tested. The conditioned response is about 10–20 dB more sensitive than the unconditioned response. Similar results were obtained by comparing unconditioned and conditioned auditory thresholds at Day 12. The latter values at .4, .5, 1, and 4 kHz were significantly lower ($p < .01$) than the corresponding former ones. At the 12th day, the frequency response range had widened to 15 kHz, and in two animals it had widened to 20 kHz. The frequency range increased steadily and reached 25 kHz at Day 15, 40 kHz at Day 22, and 50 kHz at Day 30. Three animals responded also to 60 kHz at the highest available SPLs (80 dB).

Between Day 12 and Day 15, sensitivity generally increased for all frequencies tested. For frequencies between .2 and 1 kHz,

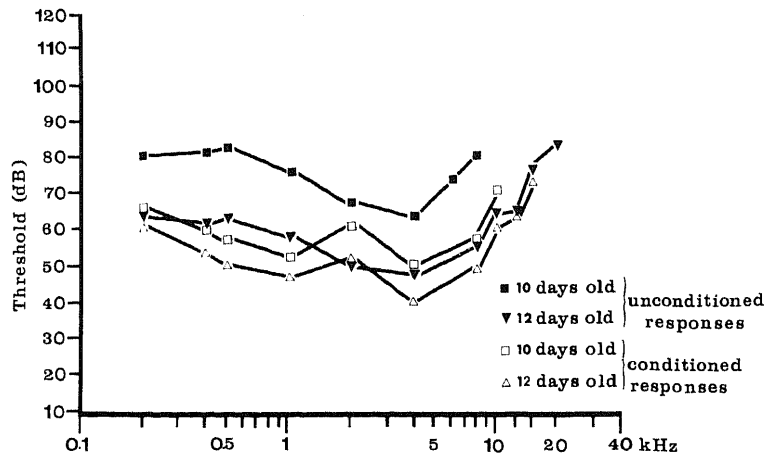


Figure 2. Comparison of threshold values measured with unconditioned and conditioned responses in 10- and 12-day-old kittens. (Conditioned response thresholds are mostly lower at both ages. The shapes of the threshold curves, however, are similar, which suggests that the results from both methods are comparable and are consistently indicating the same relative sensitivity.)

maximum sensitivity was reached by Day 15 since thresholds on this day were not significantly different from those at Days 22 and 30 ($p > .05$). For higher frequencies, threshold significantly decreased ($p < .01$) until at Day 22 the lowest values were reached. Only thresholds at 30 kHz and higher showed further significant ($p < .02$) decreases up to Day 30, the final day of our testing. The lowest threshold from Day 10 onward was always measured at 4 kHz

(Figure 1). Figure 3 shows the postnatal development of absolute thresholds for three representative frequencies. The standard deviations of the means were similar to those shown (Figure 3) for all threshold values measured. The rapid decrease in threshold between Day 6 and Days 10–12 is most obvious; for instance, the threshold at 2 kHz decreased by 66 dB between Day 2 and Day 12 but only by another 24 dB between Day 12 and Day 22.

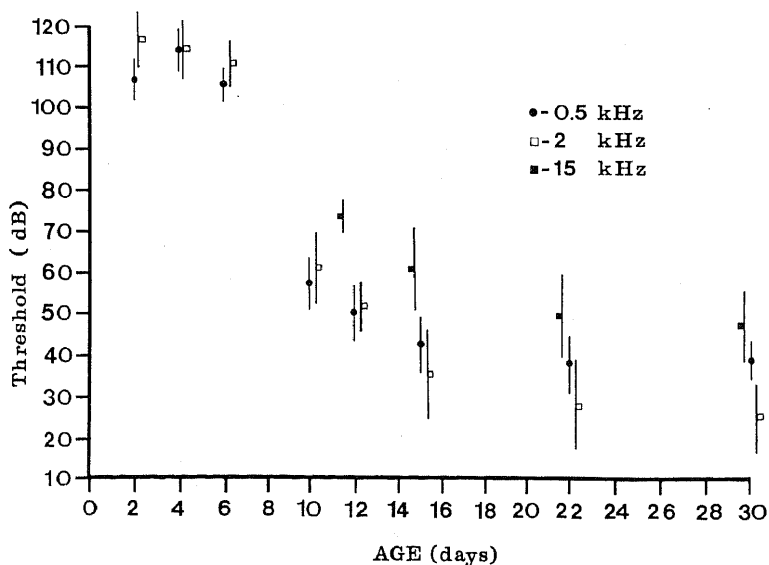


Figure 3. Threshold development versus age for three representative frequencies. (The sharp drop of thresholds between the 6th and the 10th days is obvious. Standard deviations [vertical lines] shown here are typical; they are of the same magnitude at all other frequencies tested.)

Discussion

We have shown that kittens are able to respond to sound on the second or even sometimes on the first day of postnatal life. This result is different from that of Foss and Flottorp (1974), who found the onset of hearing in the kitten to occur at Day 6 on the average. Although the criteria for threshold were not very different in the two studies, the experimental procedure differed, and this may explain the different findings. In our tests, kittens were restrained in a box and observed under an operation microscope. Foss and Flottorp held the kittens in their hands, which probably made it difficult to observe small movements like a local twitching of the pinnae.

Our results clearly indicate that conditioned responses are more sensitive than unconditioned ones. We started conditioning as early as possible (at Day 8), when we could be sure that (a) all kittens were able to perceive the test stimulus and (b) the mechanism for the conditioned response used—a blinking of the eyelids—was operative, since eyes had opened. Compared with that of mice (Ehret, 1976), the eye-blink response to electric shock was less pronounced and less stable in kittens. The first conditioned responses in the kittens could not be obtained before Day 10. Conditioning was limited to two sessions per day; otherwise, the stress to the experimental animals was too great as indicated by increased excitement, irritability, or apathy. The absolute behavioral thresholds we measured are the lowest yet reported for developing kittens; however, because of the restrictions mentioned, these thresholds probably do reach the true "absolute" sensitivity. Nevertheless, they indicate a relative development which is consistent in itself.

Our behavioral results are in excellent agreement with data on the onset of cochlear function which starts at birth and which was measured by cochlear microphonics and whole nerve action potentials (Romand, 1971). Whole nerve action potentials have the same high thresholds (above 100 dB) at Day 6 as our behavioral values; they are very broadly tuned (Carlier et al., 1979) and reflect the present finding that no best

frequency of hearing can be found up to Day 6.

Single-unit responses in the cochlear nucleus are abnormal in their characteristics up to the 9th or 10th postnatal day (Romand & Marty, 1975). They then change to adult patterns, although with lower average discharge rates at Day 10 (40 spikes/sec) than the 232 spikes/sec measured in the adults (Romand & Marty, 1975). Our present behavioral results seem to reflect this single-unit characteristic inasmuch as at Day 10 a clear sensitivity maximum at 4 kHz and a dramatic sensitivity increase occur (Figures 1 and 3). Further sensitivity increases seen later may be due to increases in average single-fiber activity. If at behavioral threshold a certain minimum output of a number of single fibers in the auditory nerve or cochlear nucleus is required, then an increase in fiber activity should mean a decrease in threshold which, in fact, has been measured. Since it has been shown that full maturation of the cat's cochlear nerve (Romand, 1979; Romand et al., 1976), cochlear nucleus (Brugge et al., 1978; Romand & Marty, 1975), and higher brain centers (Jewett & Romano, 1972; Mair, Elverland, & Lauki, 1978) has not been reached by the 30th postnatal day, our behavioral threshold curve at that age cannot be expected to indicate adult sensitivity. In fact, measurements of adult thresholds revealed much lower values (Neff & Hind, 1955; Sokolowski, 1974; cf. Figure 1). However, the large differences between our 30-day threshold curve and the lowest adult sensitivity measured may partly be due to the different methods of measurement and may not totally reflect properties of the developing acoustic system.

There is a general trend in mammals and birds for hearing to start in the lower and middle frequency range of the adult auditory field. During development hearing extends to lower frequencies first then to higher frequencies (e.g., human: Berkson, Wasserman, & Behrman, 1974; cat: present study; Pujol, Granier, & Marty, 1966; mouse: Mikaelian & Ruben, 1965; Ehret, 1976; rat: Crowley & Hepp-Reymond, 1966; guinea pig: Romand, 1971; Mongolian gerbil: Finck, Schneck, & Hartman, 1972; bat (*Antrozous pallidus*): P. Brown, Grinnell, & Harrison,

1978). This general pattern of development may be related to structural maturation within the middle ear and the cochlea. It has been shown anatomically that the maturation of the organ of Corti in humans (Bast & Anson, 1949), rat (Wada, 1923), mouse (Mikaelian & Ruben, 1965), and cat (Pujol & Marty, 1970) proceeds from the basal turn up to the apex. This seems to contradict the behavioral finding in these mammals, namely, that hearing starts in the lower and mid-frequency range. This discrepancy, however, can be resolved by looking at the middle ear and the basilar membrane. Finck et al. (1972) demonstrated in the Mongolian gerbil that ossification of the middle ear ossicles continues to Day 16 after birth. Cartilaginous middle ear ossicles with incompletely formed connections between them can be assumed to produce high attenuation for high frequencies. Similarly, the basilar membrane in developing cochleae appears to be not as stiff as in adults. It has fewer filaments, is more cellular, and is less compact (Kikuchi & Hilding, 1965; Mikaelian & Ruben, 1965). Therefore it is not likely to show a good response at high frequencies. Taking all this evidence together, it seems that mammals start hearing in the rather low frequency range but use the basal part of their cochlea which is stimulated in adults at low frequencies only by high-intensity sound. This may be another reason why thresholds are so high during the first days after onset of hearing.

Kittens up to the age of 6 days may be able to get some sensation of the presence of a sound signal; however, it seems unlikely that they can clearly recognize, for example, conspecific calls and discriminate them from other sound. Isolation calls, which are produced from birth, have a fundamental frequency of about 1 kHz with harmonics reaching up to 100 kHz (K. Brown, Buchwald, Johnson, & Mikolich, 1978; Härtel, 1975). Sound pressure levels of the isolation calls are not reported in the literature but can be assumed not to exceed approximately 100 dB which is close to the maximum SPL of the human voice near the mouth (Lullies, 1972). Therefore, according to the present threshold measurements (Figure 1), these sounds should not be perceived by siblings and can be directed only toward the mother

(and father). At the same time, calls of adult cats should also be rather inaudible for the kittens up to the age of 6 days, which means that acoustical communication up to this age may be possible only with kittens as senders and adults as receivers. It is interesting to note that the call repertoire of kittens increases to six distinct call types between Day 15 and Day 30 (cf. Ehret, 1980), which is just the time during which absolute (present work) and differential sensitivity measured by tuning curve shapes (Aitkin & Moore, 1975; Brugge et al., 1978; Carlier et al., 1979; Romand, 1979) become well established. At that age (18–24 days) kittens also start showing directional responses to sound (Clements & Kelly, 1978), which is possible only if sound is clearly perceived. One can conclude that different call types develop when kittens can act not only in the role of senders but also in the role of receivers. It seems worthwhile to test the hypothesis that normal differentiation of the call repertoire in cats needs sufficient auditory sensitivity as is well known for speech development in humans.

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Received July 7, 1980 ■