

Development of Sound Production in Normal, Isolated, and Deafened Kittens during the First Postnatal Months

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The development of calls (quantified by a series of acoustic parameters) of (a) normal, (b) socially isolated, and (c) deafened kittens that were released in four different situations has been studied from birth to 170 days of age. All call parameters studied except noise components show developmental changes that can be related to the development of (a) the vocal tract (fundamental frequency, harmonic with maximum intensity, upper-frequency limit and frequency range, occurrence of frequency, and intensity modulations), (b) feedback control through the auditory system (sound-pressure level, harmonic with maximum intensity, call-variability), and (c) motivational valuation of the releasing situations (duration). Isolated and deafened kittens displayed quantitative differences in certain call parameters compared with normal animals. Calls of deafened animals are, on the average, louder, more tonal and uniform, and differentially pitched compared with those of normal, hearing animals.

Cats and kittens are frequently used in studies of auditory function, including physiological (see reviews by, e.g., Boudreau & Tsuchitani, 1973; Kiang, Watanabe, Thomas, & Clark, 1965; Romand, 1983) and behavioral (e.g., Ehret, 1983; Neff, 1975) measurements of sound-processing and auditory acuity and resolution. Thus, the cat has become the best investigated vertebrate with regard to many aspects of audition. On the other hand, vocal-, and sound-mediated behavior and acoustic communication in cats and kittens have been studied only occasionally (Brown, Buchwald, Johnson, & Mikolich, 1978; Härtel, 1975; Haskins, 1979; Moelk, 1944), so that many questions—such as those concerning the adaptation of the auditory system for processing and analyzing the intra-specific vocal repertoire, or about the possible influences of hearing on the development of call structures—have remained open. Quantitative data on the sound parameters of the calls and their development during the ontogeny of the cats are especially lacking.

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The present investigation on the development of sound production in kittens was designed to contribute information to the following questions: (a) What is the general time course and the amount of change of the main sound parameters in the calls of kittens during their development? (b) Are there temporal relationships between call development and maturation of auditory function? (c) Does the development of normal sound structures depend on hearing (auditory feedback) and on normal social interactions with adult cats (social feedback)? We will relate call production to defined releasing situations, to give a basis for comparisons of the parameters of the calls of normal, isolated, and deafened kittens. In this study, we do not intend to answer questions on whether the calls studied have significance in intraspecific communication. However, the present data may be used as a framework of perceptual conditions and behavioral contexts in which communication with these calls may become significant.

Materials and Methods

Subjects

We used two litters with six kittens each, which were delivered after 66–67 days of gestation by normal, healthy house cats (*Felis catus*) bred in the University of Konstanz. Three kittens of the first litter (two females, one male) stayed with their mother in a room (in a separate cage during the first 2 months) where other cats from the stock could move around freely. These kittens served as the *normal* group. The other three kittens (one female, two males) were isolated from the mother and the other cats on postnatal Day 7 and were kept together as a group for the rest of the experimental time. Two kittens of litter 2 (one of each sex) were isolated during the first 14 postnatal days. These five kittens formed the *isolated* group (data from the periods of isolation only are considered). Two kittens of litter 2 (one of each sex) were deafened on postnatal Day 3 by mechanical destruction of both cochleae under sodium pentobarbital (Nembutal) anesthesia and semisterile conditions. One of the deafened kittens was raised by his mother, while the other was hand-raised. These two kittens formed the *deafened* group.

During the lactation period, the kittens raised in isolation from their mothers were fed kittens milk (Gimpet) ad libitum in four or five feeding sessions per day and received dosages of vitamins and cattle serum (Boviserin) every second day. The kittens were housed in cages with heating pads and cotton and paper towels as nesting material. For at least 3 hr per day they could move freely in a room and play with a caretaking person. All kittens were subsequently weighed on the days when calls were recorded.

Recording of Calls

Calls of each kitten were recorded during the first 162 (first litter) or 170 (second litter) days of age under the following standard conditions: (1) *Alone*, i.e., a kitten was taken out of its home cage, carried to an unfamiliar laboratory, and placed on a table. Within a minute, the kittens either moved around slowly and emitted cries or crouched under the table and occasionally cried. (b) *Picked up by the skin of the neck*; after calls emitted during the *alone* situation were recorded, the kittens were gripped by the skin of their necks and held until they emitted sounds (it was intended to imitate the grip of the mother when carrying the kittens around). (c) *Tail-pressing*; after sounds in situation (b) were recorded, the kittens were held by their tails, which were pressed until they made efforts to escape or to attack. Under this condition, in which obviously agonistic ten-

dencies in the kittens were induced, many calls were usually emitted. (d) *Undisturbed social contact*; during the first 19 days, recordings of the first litter (normal group) were obtained when the kittens were undisturbed with the mother in the home cage playing, sniffing, feeding, or moving around and exploring.

The calls were recorded with a calibrated 6.35-mm condenser microphone (Bruel & Kjaer, 4135), were amplified (Hewlett-Packard, 466A), highpass filtered (Rockland, 856, with a lower cutoff at 100 Hz), and tape-recorded at a speed of 38 or 76 cm/sec on a high-frequency tape recorder (Philips Analog 7). The frequency response of the whole system was flat within ± 4 dB between 100 Hz and 100 kHz at a speed of 76 cm/sec and between 100 Hz and 50 kHz at a speed of 38 cm/sec. The input/output amplifiers of the recorder were calibrated so that the microphone output voltage could be calculated in dB sound-pressure level (SPL), re 20 μ Pa. The distance between the microphone and the mouth of the kittens varied around 10 cm in young kittens (up to about 1 month of age) and between 30 and 100 cm in older animals. Total ambient sound levels were always below 55 dB SPL.

Analysis of Calls

The calls were played back by the tape recorder simultaneously on a storage oscilloscope and a sonagraph (Kay, 7029A). From the oscilloscope picture, the peak-to-peak voltage was read and converted into dB SPL. Sonagrams were often taken with several playback speeds of the recorder in order to match the frequency range of the calls with the bandwidth of analysis of the sonagraph. Most of the time, five calls per condition per kitten per age, randomly selected from the calls recorded in one session, were evaluated. From the sonagrams the following information was obtained:

1. Duration.
2. Average fundamental frequency (usually taken in the middle of a harmonically structured call), or, if the call was very noisy, the lowest clearly visible frequency component.
3. The harmonic with the maximum intensity (only measurable in harmonically structured calls). The first overtone of the fundamental is called the first harmonic, etc.
4. The lowest-frequency component.
5. The highest-frequency component.
6. The total frequency range (highest minus lowest frequency).
7. Rapid frequency shifts and rapid frequency modulations (FM) in the beginning, the middle and the end part of a call.
8. Rapid intensity modulations (AM; detected if visible as sidebands or "noisy" components between the harmonics) in the beginning, middle, and end part of a call.
9. Noise (harmonics not visible) in the beginning, middle and end part of a call.

The characteristics of each call (amplitude and sonagram parameters), together with the code of each kitten, its age, weight, treatment, recording situation, and tape codes, were stored on floppy disks of a microcomputer (Apple II) for further data handling and statistical analysis. The parameter-free *U*-test was used to compare mean values and the χ^2 -test was applied for comparison of occurrence rates.

Hearing Tests

After all recordings were finished, the deafened kittens were tested for potential residual hearing. Tone-evoked compound action potentials were recorded from both audi-

tory nerves at the round window under Nembutal anesthesia. Compound action potentials were summed over 500 or 1000 tone bursts and were plotted on a x-y plotter. The lowest threshold of activity measured in this way in the frequency range between .1 and 15 kHz was 99 dB SPL at 8 kHz. This shows that the kittens were profoundly deaf and certainly unable to hear and analyze calls of their own or of other sources.

Results

As is obvious from Figure 1, the kittens of all three experimental groups showed the same kind of average weight development throughout the observation period. This similarity of weight increase suggests normal physical development of isolated and deafened kittens.

General Comment

The results of the call analysis are based on a total of 2,304 sonograms of kitten calls. As can be seen from the sonogram examples in Figure 2, kittens can already produce structurally very different calls on their first postnatal day. The calls can have a simple harmonic structure, often with some rapid frequency increase at the beginning and decrease at the end (Fig. 2A); they can include rapid frequency (Fig. 2B,F) and/or intensity (Fig. 2C,G) modulations and noise (Fig. 2C,H), or can consist only of noise (spitting noise, Fig. 2D). They can be restricted to low frequencies (Fig. 2A,F) or extend into the high ultrasonic range (Fig. 2D,K). We found that among the call characteristics investigated, there was none that could unambiguously be related to a certain releasing situation. Calls with the features mentioned above were obtained in all situations. One exception to this rule was spitting, which was not recorded in the "alone" situation.

In all three experimental groups of kittens, calls from tail-pressing could be released throughout our study. Calls from the "alone" kittens could always be obtained until 32 days, then only in one-half to one-third of the tests thereafter, up to Day 103, and rarely from that day onwards, especially from normal and isolated kittens. Calls from the "picked up" kittens were rarely released after Day 103 in normal and isolated kittens, and after day 46 in deafened ones.

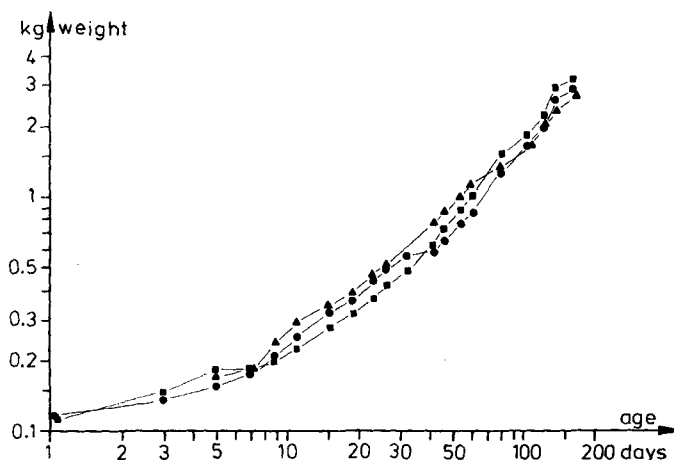


Fig. 1. Average weight development for normal (●), isolated (■), and deafened (▲) kittens.

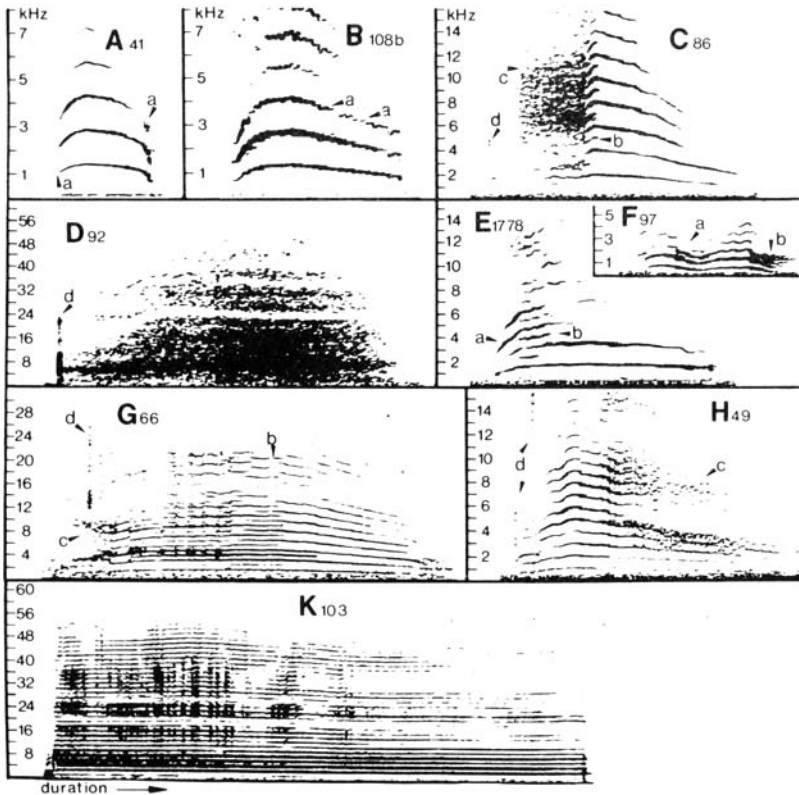


Fig. 2. Sonograms of examples of calls of 1-day-old kittens from different releasing situations ("alone:" sonograms C, G, H; "picked up:" sonograms E, K; "tail-pressing:" sonograms A, B, D, F). a = frequency shifts and modulations; b = rapid intensity modulations causing sidebands to harmonics; c = noise components; d = clicks caused by opening of the mouth at the beginning of a call.

Normal Call Development

The development of call characteristics is shown in Figures 3 to 7 separately for all situations. Most values include at least 15 calls. Only values for some of the kittens older than 53 days in the "alone" and "picked up" conditions are based on smaller samples (minimally 5 calls). In the following, only the main developmental trends will be mentioned.

Duration (Fig. 3A). There were different trends in the development of durations of calls from different situations. Up to Day 11, calls from being picked up were significantly longer ($p < .01$) than calls from all the other conditions. At around Day 19, the duration of the calls from all situations were similar, and at a minimum for the calls from tail-pressing. After Day 19, calls from being alone remained significantly shorter than calls from being picked up and from tail-pressing ($p < .01$). The length of the calls from tail-pressing increased dramatically after Day 19, reaching a maximum at Day 82. The longest call obtained in the whole sample was 5.0 sec (picked up, 3 days old); the shortest (except for spitting) was 0.11 sec (alone, 60 days old and picked up, 19 days old).

Sound-pressure level (Fig. 3B). The SPLs of calls from all situations varied mostly between 65 and 75 dB. A pronounced dip of the SPL of all calls occurred on Day 19. Mean SPLs of calls from tail-pressing remained, with little variation, on a high level from Day 53 onwards. In general, SPLs with 10 dB and more difference were significantly different ($p < .05$). The loudest call was at 96 dB SPL (tail-pressing, 135 days) and the softest one was only 54 db (alone, 7 days; picked up, 19 days; tail-pressing, 19 and 60 days).

Fundamental frequency (Fig. 3C). Except for calls from the undisturbed group, the average fundamental frequency increased significantly ($p < .01$) from Day 1 to Day 11 and then varied on a lower level until a significant ($p < .01$) decrease followed for all calls between Days 32 and 46. From then onward, the fundamental frequency remained rather constant but was significantly lower for calls after tail-pressing compared with that for calls from all the other situations ($p < .05$).

Harmonic with intensity maximum (Fig. 4A). At 1 day of age, the intensity peak in the spectrum of all calls was, on the average, at the first or second harmonic. The intensity peak shifted significantly upwards ($p < .01$) close to the fourth harmonic for calls from undisturbed kittens at Day 5, close to the third harmonic for calls from the alone and tail-pressing conditions at Day 7 and for calls from being picked up at Days 9-11. This marked increase was followed by a sharp decrease ($p < .01$) to a minimum at Day 19, when it was at the fundamental or first harmonic. Then the intensity maximum shifted again to higher frequencies ($p < .01$) and remained near the second harmonic until

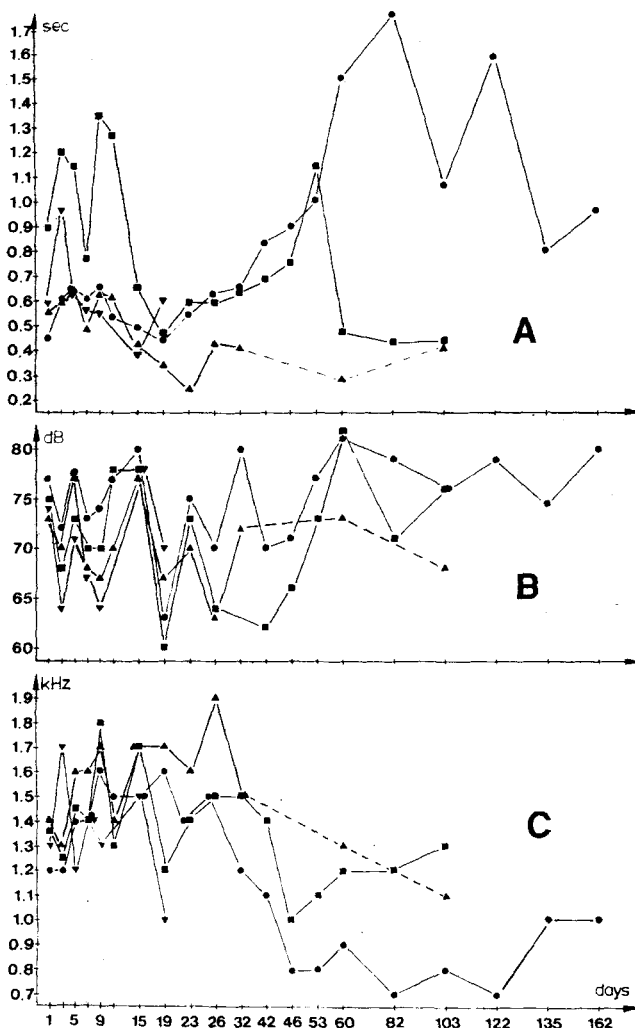


Fig. 3. Development of call duration (A), sound pressure level (B), and fundamental frequency (C) for normal kittens. The means of calls from being alone (▲), from being picked up (■), from tail-pressing (●), undisturbed (▼).

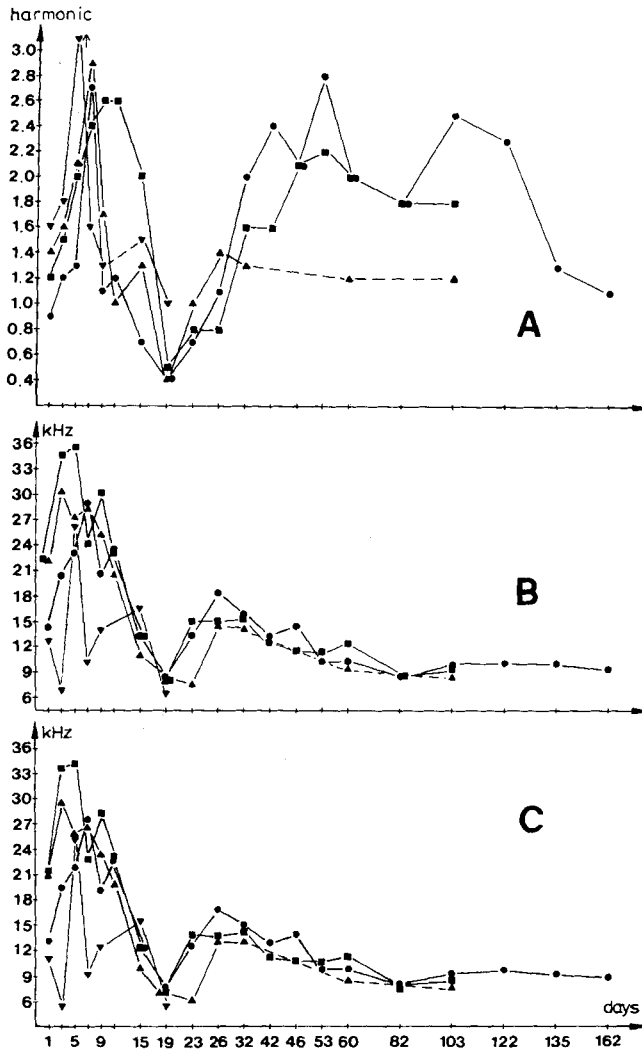


Fig. 4. Development of the means for the harmonic with maximum intensity (A), upper frequency limit (B), and frequency range (C) of the calls of normal kittens. Same symbols as in Fig. 3.

Day 22 (except for calls from "alone"), when it shifted downward to close to the first harmonic.

Upper frequency limit and total frequency range (Figs. 4B,C). Both sets of curves in Figure 4B and C are very similar, which shows that the lower frequency limit of the calls did not vary much between the different situations. On Day 1, the upper frequency limit is higher and the frequency range wider in calls from the "alone" and "picked up" conditions, compared with those from situations (c) and (d) ($p < .05$). Both measures increased significantly ($p < .05$) to a maximum at Days 3, 5, or 7 for the different situations and then decreased significantly ($p < .01$) to a minimum at Day 19, when the average frequency range for all calls was only about 7 kHz. A small increase, significant only for calls from tail-pressing ($p < .05$), followed for up to Days 26–32. Finally, the upper frequency limit and the total frequency range showed a shallow decrease until a plateau near 9 kHz was reached at Day 82. From Day 23 onward, the frequency contents of all calls was always below 30 kHz. Between Days 1 and 23, calls from "alone" and "picked

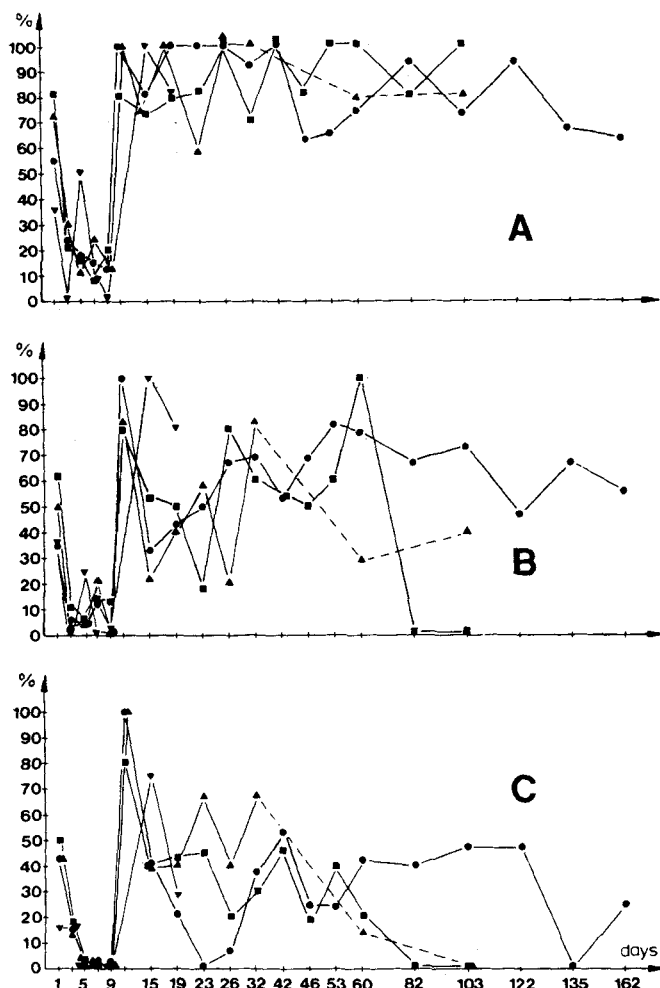


Fig. 5. Development of the relative occurrence rates of rapid frequency shifts and modulations (FM) in the beginning (A), middle (B), and end (C) parts of the calls of normal kittens. Same symbols as in Fig. 3.

up" had significantly more often frequency components above 30 kHz as compared with those from the other conditions ($p < .01$).

Relative occurrence rates of rapid frequency shifts and modulations (Fig. 5A-C). The relative occurrence rates of FM are plotted separately in Figure 5 for the beginning, middle, and end parts of the calls. In general, FM was found most frequently at the beginning of the calls. This was due to the frequent rapid frequency increase at the beginning of a call (compare Fig. 2A,B). On Day 1, FM occurrence was at a medium level. It then rapidly decreased to a minimum level on postnatal Days 3-9. A dramatic increase followed, reaching a maximum at Day 11. Throughout the rest of the observation time, the occurrence of FM in the beginning part of the calls stayed at that high level, while decreasing until Day 19 to a medium level in the middle part and to a low level at the end. Systematic differences between calls from the different conditions were not present, except for FM at the end of the calls between Days 19 and 23 (between "alone" and "tail-pressing") and for FM in the middle and end of the calls from Day 60 onward (between "alone," "picked up," and "tail-pressing").

Relative occurrence rates of rapid intensity modulations (Fig. 6A-C). The occurrence of AM is shown separately in Figure 6 for the beginning, middle and end of the calls. The curves from the different conditions are similar in shape, with systematic differences only for AM at the end of the calls from Day 32 onward (AM rate is lower in the "alone" and "picked up" conditions than for "tail-pressing"). As for FM occurrence, there was some decrease of AM rate from Day 1 to 3, with a minimum between Days 3 and 9, and a sharp increase to a maximum at Day 11. In the beginning and the middle parts of the calls, AM occurrence stayed on a medium-high level throughout the rest of the time, while at the end it decreased, until from Day 19 onward a low level was reached.

Relative occurrence rate of noise (Fig. 7A and B). After inspection of the data, it seemed unnecessary to plot noise of the beginnings, middles, and ends of the calls separately because of very similar occurrence rates and development. Thus Figure 7A shows any occurrence of noise in the calls (purely noisy spitting sounds are not included). On the average, about 10-15% of all calls contained noise components (compare Fig. 2C, G,H). Noise in calls from tail-pressing is less frequent between Days 23 and 32 and more frequent from Day 42 onward compared especially with that from being picked up. (Fig.

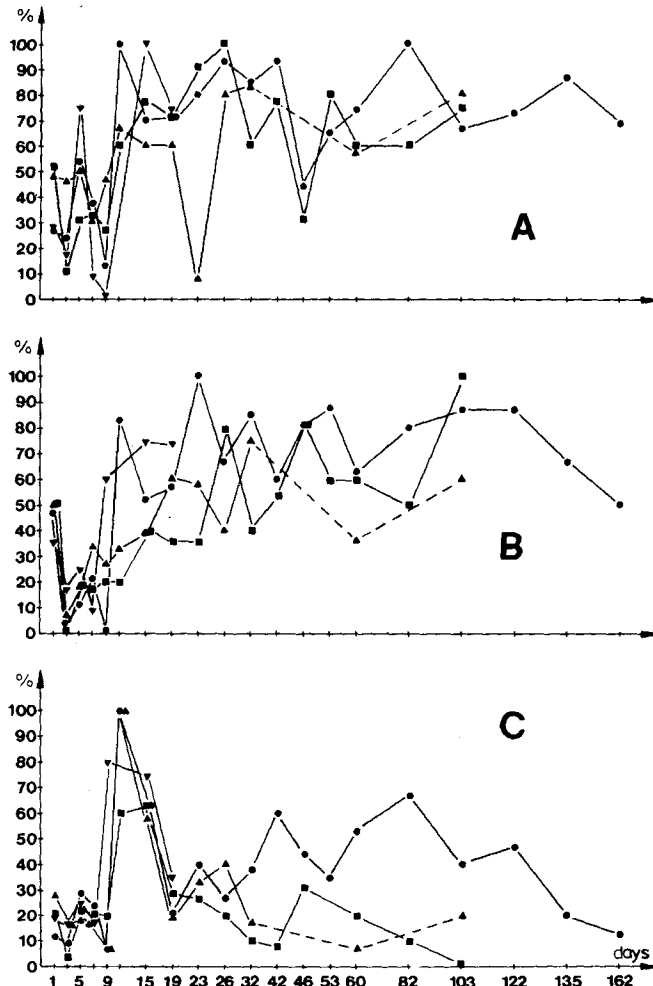


Fig. 6. Development of the relative occurrence rates of rapid intensity modulations (AM) in the beginning (A), middle (B), and end (C) parts of the calls of normal kittens. Same symbols as in Fig. 3.

7B). The differences are significant only if occurrence rates are summed over days ($p < .01$).

According to these results, the major differences among the calls from the different situations occur in the development of call duration, fundamental frequency, harmonic with maximum intensity, upper frequency limit, frequency range, and FM and AM at the end of the calls.

The development described for the mean values of the call parameters is paralleled in the development of the standard deviations (SDs). In general, SD development follows the development of the means, i.e., the larger the means, the larger the SDs. This means that, if we look at Figures 3 and 5, not only the means but also the variabilities are high during the first 9–15 days, then decreasing and maybe increasing again, as is obvious for call duration (Fig. 3A, tail-pressing).

Development of Calls from Isolated and Deafened Kittens Compared with that of Normal Animals

In the following, we shall use the calls from the “alone” condition as an example of some differences and similarities between calls from the three groups of kittens in one condition, and we shall also work out major and consistent differences among the three groups from plots of the means (or sums) of calls from all conditions.

Duration (Figs. 8A, 9A). In the “alone” condition (Fig. 8A), calls from normal kittens were significantly shorter ($p < .01$) than those of isolated and deafened ones on Days 23, 60, and 103. Calls of deafened kittens increased significantly in duration between Days 42 and 135 ($p < .01$), while those of isolated ones increased ($p < .01$) from Day 15 to Day 60 (last day data obtained).

The average duration of all calls from the three experimental groups (Fig. 9A) varied around .6 sec from birth to Day 42. Then the duration generally increased, mainly through the lengthening of the calls from “tail-pressing” (compare Fig. 3A), and showed strong variations among days, averaging around 1.3 sec from Day 60 onward. A tendency for calls from normal kittens to be shorter than calls from isolated (Day 53 onward) and

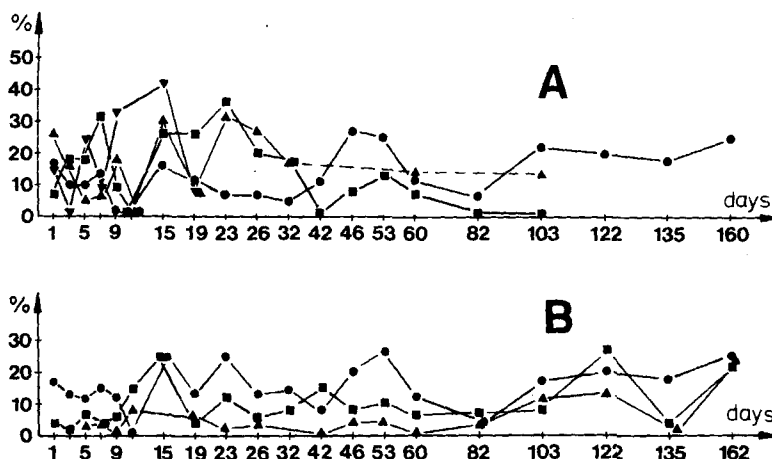


Fig. 7. A, Development of relative occurrence rates of noise components in the calls of normal kittens. Same symbols as in Fig. 3. B, Same as in A for all calls of normal (●), isolated (■), and deafened (▲) kittens.

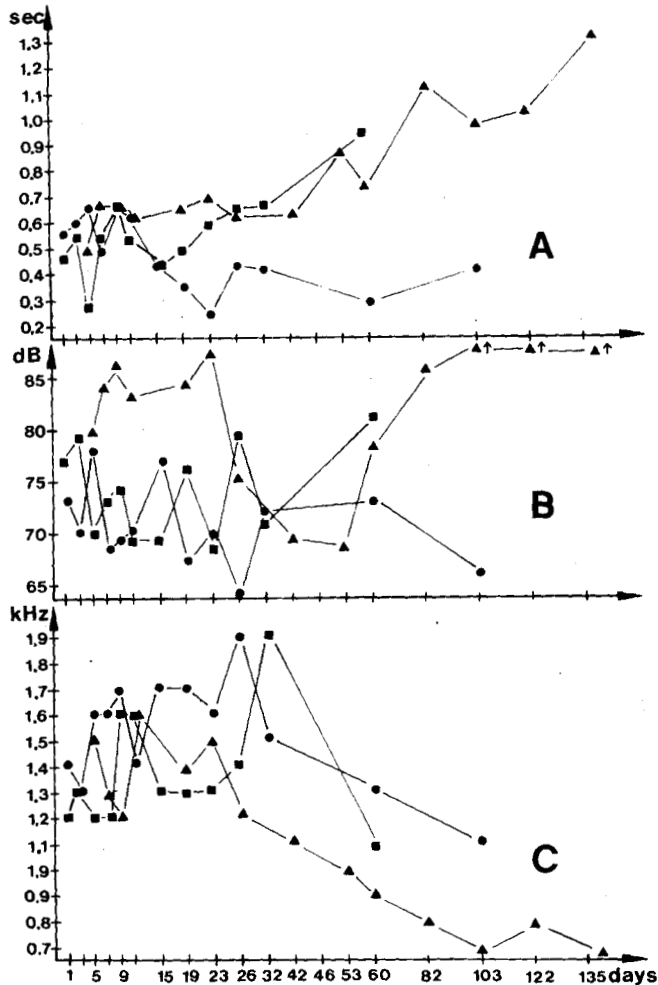


Fig. 8. Development of the means of calls from the "alone" condition for normal (●), isolated (■), and deafened (▲) kittens. A, duration; B, sound pressure level; C, fundamental frequency.

deafened (Day 135 onward) kittens is also evident. Statistically significant differences occurred on Days 53, 82, 135, and 162 ($p < .05$).

Sound-pressure level (Figs. 8B, 9B). Both calls from the loneliness situation (Fig. 8B) and the means from all situations (Fig. 9A) showed a similar course in normal and isolated kittens. During development, the SPL stayed rather constant (mostly between 70 and 75 dB). Calls from deafened kittens, however, developed consistently differently in that they were significantly louder ($p < .05$) than calls from the two other groups between Days 9 and 23 and between Days 82 and 135.

Fundamental frequency (Figs. 8C, 9C). If we consider only the calls from being alone (Fig. 8C), normal kittens have significantly higher fundamentals ($p < .05$) than isolated ones between Days 15 and 26 and compared with deafened ones from Day 26 onward. Looking at calls from all conditions together (Fig. 9C), significant differences among the groups did not occur except on Day 135, when deafened kittens had a lower fundamental than the other animals ($p < .05$). After an increase between Days 1 and 9 (statistically significant in normal kittens only; $p < .01$), the fundamental frequency decreased, first

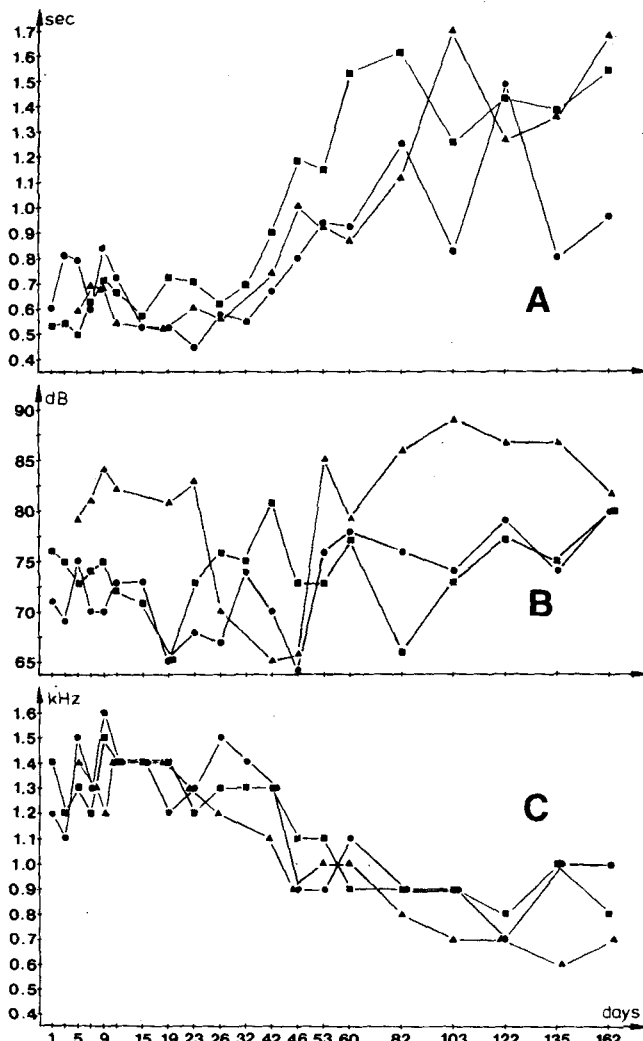


Fig. 9. Development of the means of call duration (A), sound pressure level (B), and fundamental frequency (C) from all calls of normal, isolated and deafened kittens. Same symbols as in Fig. 8.

slowly then more rapidly, until Days 46-60. A further significant decrease ($p < .05$) was found only in deafened kittens (until Day 135).

Harmonic with intensity maximum (Figs. 10A, 11A). The development of the harmonic with maximum intensity is similar in both Figures 10 and 11. Here significant differences occur among the three groups of kittens. At Days 5 and 7, the intensity peak is at a higher frequency in normals compared with isolated and deafened kittens ($p < .05$). From Day 15 (or 11) to Day 42, deafened kittens stay on a lower level than isolated animals ($p < .05$). On Days 135 and 162 (also on Day 103 for calls from being alone), deafened kittens have an intensity peak at a significantly higher frequency ($p < .01$) than normal kittens. The minimum at Day 19 (and 23) in normal kittens is not present in isolated ones. All this shows that the development of the intensity peak in the call spectrum is very different in the three experimental groups.

Upper frequency limit and total frequency range (Figs. 10B, 11B). The only significant differences among groups occurred on Day 23 (Fig. 10B) and Days 19 and 23 (Fig.

11B), when the upper frequency limit and the frequency range of deafened kittens was higher (larger) than in normals ($p < .05$). The shapes of the curves in Figures 10B and 11B are very similar, with an increase from Day 1 to Day 5 or 7, a rapid decrease to Day 19, and an increase to Day 23 or 26, with a shallow decrease until, at Day 82, a plateau is reached. From Day 23 onward, frequency components above 30 kHz have not been observed in any calls of the three groups.

Relative occurrence rate of rapid frequency shifts and modulations (Fig. 12A-C). In Figure 12, only percentages from calls of all situations are shown. Values from each of the four situations are rather similar. If one takes Days 3-9 together, the rate of FM is lower in normal kittens than in isolated and deafened ones ($p < .01$). On Day 11, we find more FM in normal kittens than in the others ($p < .01$). From Day 15 onward, the curves of the three groups do not show systematic differences except that, up to Day 42, FM rate at the beginning of the calls of deafened kittens is lower than that of normal ones.

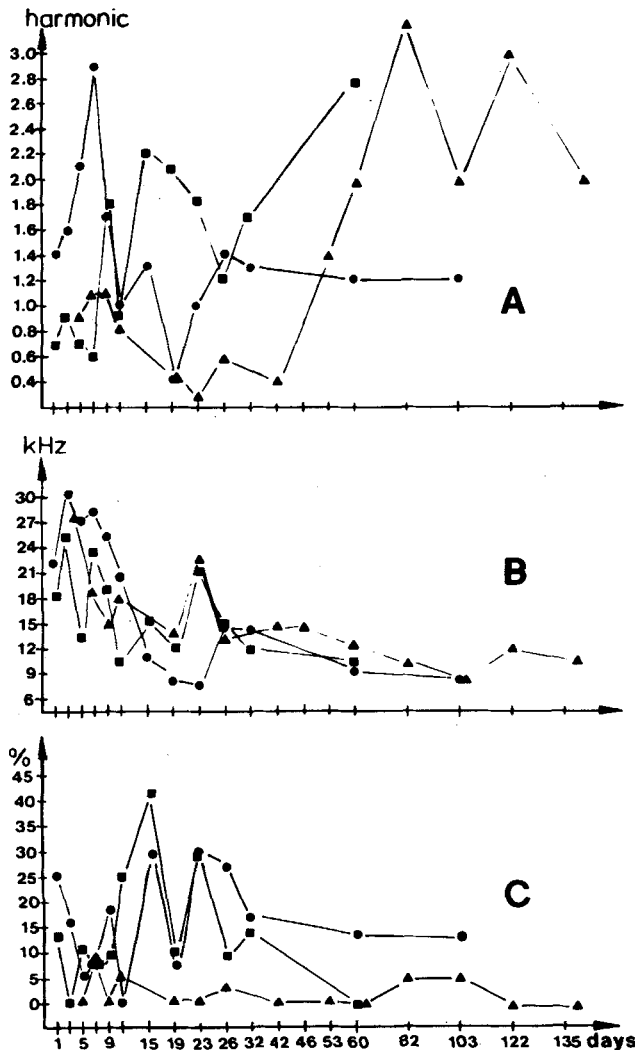


Fig. 10. Development of the means of calls from the "alone" condition for normal, isolated, and deafened kittens. A, harmonic with maximum intensity; B, frequency range; C, occurrence rate for noise components. Same symbols as in Fig. 8.

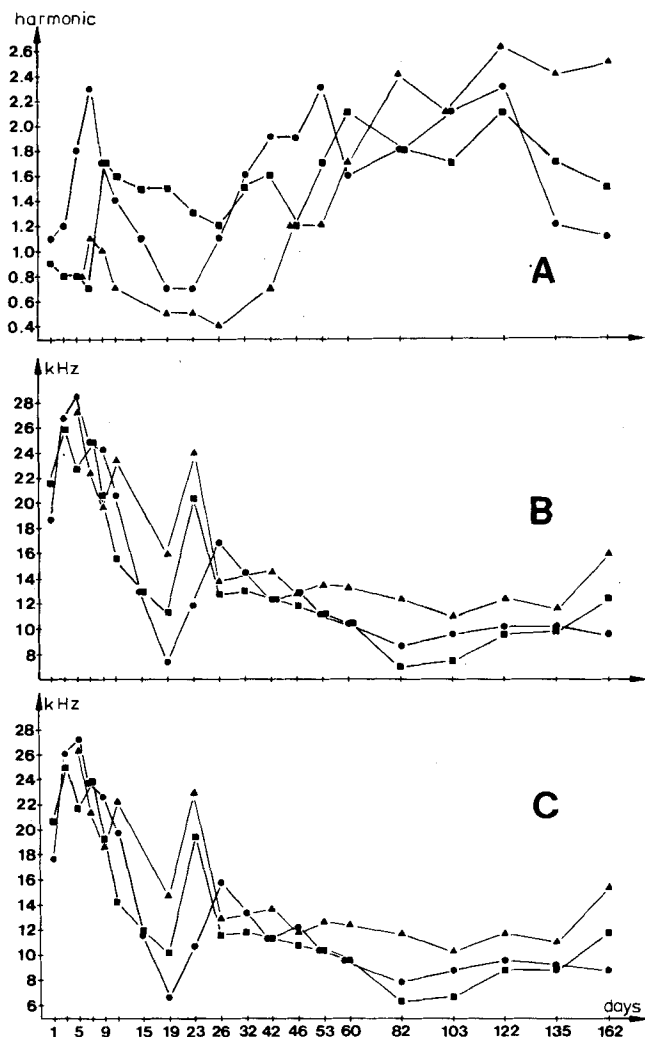


Fig. 11. Development of the means of harmonics with maximum intensity (A), upper frequency limit (B), and frequency range (C) from calls of normal, isolated, and deafened kittens. Same symbols as in Fig. 8.

Thus, up to Day 42, the rate of occurrence of FM in normal kittens shows a course that approximately mirrors that of deafened kittens.

Relative occurrence rate of rapid-intensity modulations (Fig. 13A-C). Again, in Figure 13, only values for all calls together are shown. Here we have to distinguish between AM in the first, second and third part of the calls. For the first part of the calls, the development of AM is rather similar in the three experimental groups if we consider only the main trends. A closer look shows, however, that the curves for isolated and deafened kittens are mostly mirror those of the normal ones. AM in the middle part occurred less frequently (a) in normal kittens compared with the others from Day 1 to Day 7 and (b) in deafened kittens compared with the others between Days 23 and 42. In the end part of the calls, the deafened kittens did not show a peak at Day 11 or at Days 15-23, as the others did, which is a significant difference ($p < .01$). From Day 42 onward the shapes of

all curves are similar and AM remains about constant at a medium level at the beginning and middle of the calls, and at a lower level at the end.

Relative occurrence rate of noise (Figs. 7B, 10C). Average rates of occurrence of noise in calls from all kittens were generally low. During the time of our tests, the occurrence of noise in the calls of deafened kittens was rare and significantly lower ($p < .01$) than that of normal animals. This is evident both from calls in the "alone" situation (Fig. 10C) and from all situations (Fig. 7B). Noise components in calls of isolated kittens have occurrence rates similar to those of normal kittens if the "alone" situation only is considered. If we sum up noise rates from all situations over all days, isolated animals have significantly less noise in their calls compared with normal kittens ($p < .01$).

Taking these comparative data together, significant differences among the three experiment groups of kittens occur in the development of most of the parameters

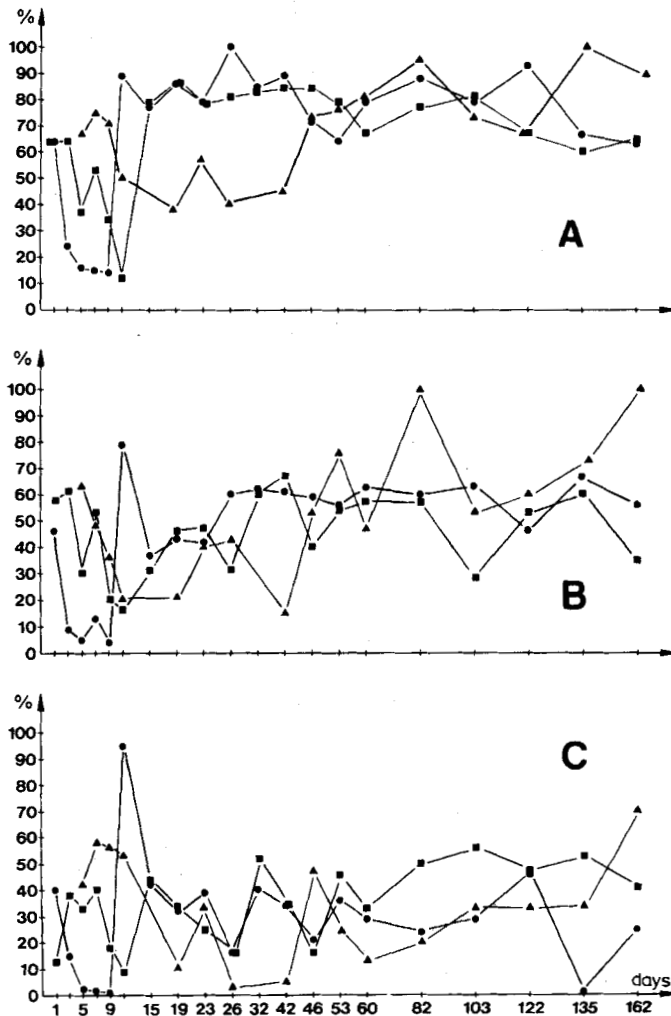


Fig. 12. Development of relative occurrence rates of frequency shifts and modulations (FM) in the beginning (A), middle (B), and end (C) parts of all calls of normal, isolated, and deafened kittens. Same symbols as in Fig. 8.

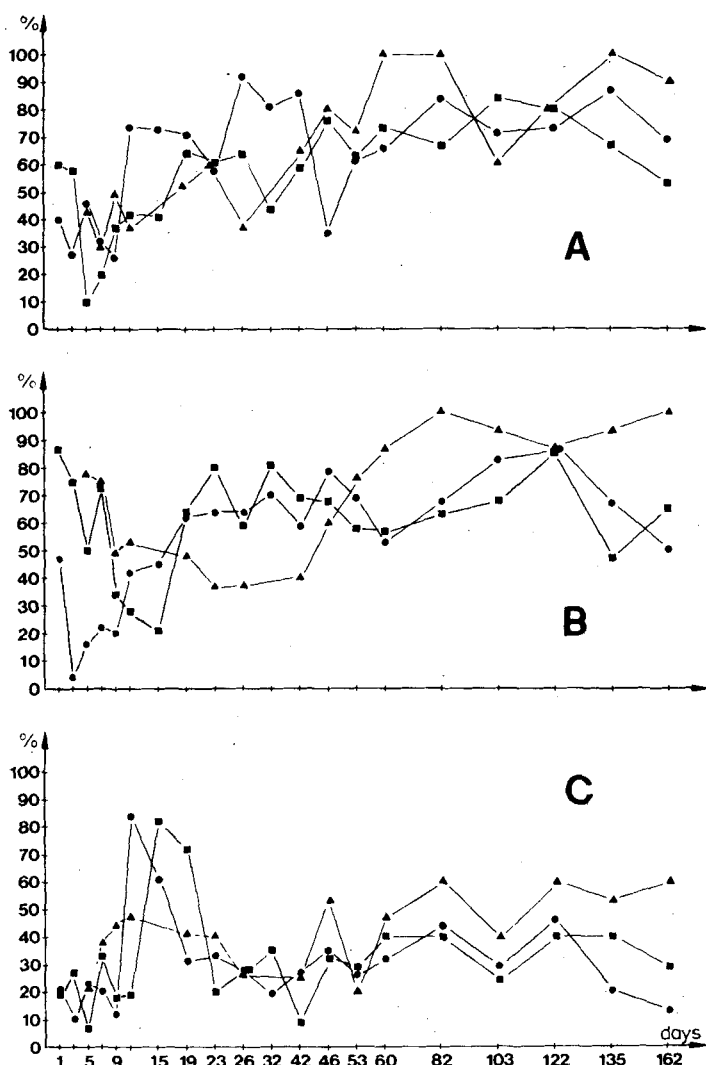


Fig. 13. Development of relative occurrence rates of rapid intensity modulations (AM) in the beginning (A), middle (B), and end (C) parts of the calls of normal, isolated, and deafened kittens. Same symbols as in Fig. 8.

studied. The fewest differences are found in the upper frequency limit and the total frequency range.

Again, we can also compare the standard deviations of the means. For normal and isolated kittens, the development of the SDs is comparable to that of the means shown in Figs. 8–11. SDs of deafened kittens, however, are different in that they are more independent of the means, in other words, a high (low) mean must not cause a high (low) SD, as is generally the case in the two other groups. In addition, SDs of calls of deafened kittens are, if calculated across days, significantly smaller than those of isolated and normal animals with regard to call duration ($p < .05$), fundamental frequency ($p < .01$), and harmonic with maximum intensity ($p < .01$). Apparently, there is less variability among the calls of deafened kittens compared with those of normally hearing animals.

Discussion

Comparison with Other Studies on Kitten Calls

Some aspects of kitten calls have previously been described (Brown et al., 1978; Härtel, 1972, 1975; Haskins, 1979; Moelk, 1944) and a few quantitative data on call parameters are available which can be compared to our present results. Brown et al. (1978) analyzed calls from a condition similar to our condition, "alone." They found an average duration of 1 sec, which is longer than all our means from normal kittens (Fig. 8A), and a mean fundamental frequency of 1.2 kHz, which is lower than our means during the first 2 months (Fig. 8C). The differences between the two studies may be explained on the basis of how and on which days the samples of calls were taken—not described in Brown et al. (1978). In that study, calls were readily obtained up to 4 weeks of age, less frequently up to 2–3 months, and only from some kittens thereafter. This decrease of responsiveness to being alone closely corresponds to our finding of a reduction of call production in the alone situation after Day 32.

Härtel (1975) presents sonagrams of calls of "loneliness" from neonatal kittens that resemble those of Fig. 2A,B. The calls had fundamental frequencies between 1 and 2 kHz and durations between 0.3 and 0.5 sec with the maximum intensity usually at the first harmonic. In addition, Härtel (1972) found a reduction of the fundamental frequency from about 1.6 kHz to .8 kHz between juveniles and adults. These values come close to our means for these parameters. Haskins (1979) studied kitten vocalizations elicited by cold, restraint, and isolation during the first 6 weeks of age. He found that in the isolation situation, the mean fundamental frequency of the calls increased from about 1.3 kHz in the first week to about 1.65 kHz in the third week, and decreased again to about 1.45 kHz in the sixth week. The duration of the calls varied unsystematically between .44 and .66 sec. These values are in excellent agreement with ours from normal kittens in the "alone" condition (Figs. 3A,C; Fig. 8A,C). Haskins also found that in the restraint situation, calls were generally longer than in isolation, which agrees with our data if we compare being alone and picked up, with the latter representing a kind of restraint. In conclusion, our results on the structural characteristics of calls of young kittens in an "alone" situation agree well with available evidence from the literature. Calls from other situations cannot be compared because comparable data seem not to exist.

Up to Day 23, we observed calls with ultrasonic components (> 20 kHz) which occasionally reached as high as about 60 kHz. Calls with frequency components up to 100 kHz and pure ultrasounds, as mentioned by Härtel (1972), have never been recorded, although we looked for ultrasounds in the situations described by Härtel (1972). Therefore, the question, whether or not kitten can produce pure ultrasounds can be settled only in further tests.

Physiological and Motivational Bases of Call Development

The postnatal development of calls or call structures can be related to (a) the development of the vocal apparatus, including enlargement of vocal cords and resonance spaces, and improvement of motor control of the vocal cords and of muscles of the throat, mouth and nose area; (b) the development of hearing, which could serve as a feedback system for the proper adjustment of call parameters; (c) the development of emotions, motivational states, social relations, and situational experience which may all be linked with and signalled by certain kinds of call structures (compare Ehret, 1980).

By looking at the development of calls of normal kittens from different situations we can expect to find influences of physical development and to separate these from motivational influences. By comparing sounds of normal, isolated, and deafened kittens from one situation, we may infer influences of auditory and social feedback and experience on development. Although we clearly recognize that conclusions can be drawn only on a speculative level, we feel that they are justified on a conceptual and compared basis with other studies, as will be pointed out below.

Our present results indicate that the upper and lower frequency limits and therefore the frequency range of the calls are least influenced by call-releasing contexts, by deafness, or by social isolation from adults (Figs. 4B,C; 10B; 11B,C). The general development is always similar and, therefore, most probably reflects the physical development of the vocal apparatus. Thus we may use the respective curves as a basis for the interpretation of the development of the vocal apparatus. The increase of the upper frequency limit and frequency range during the first postnatal week may be due to an increase of the attainable air pressure under the vocal cords before the air is released. Such a pressure increase has been thought as a possible reason for the increase of fundamental frequency in human baby sounds during the first 4 months (Sheppard & Lane, 1968). Figure 9C shows that in kittens, the fundamental frequency averaged across situations also increases and parallels the increase of the frequency range during Days 1-9. Also, the harmonic with maximum intensity increases during the first week in normal kittens (Fig. 4A). Increases of fundamental frequency, upper frequency limit, and harmonic with maximum intensity all contribute to a marked increase of pitch of kitten calls during the first postnatal week. During this time, the air pressure under the vocal cords may increase by increasing air volume and breathing activity, but there is insufficient motor control of the vocal cords, which may not adjust their tonus. This suggestion is consistent with the finding of Levine, Hull, & Buchwald (1978) that motor development in kittens is very slow during the first postnatal week.

The general decrease after Day 9 of the upper frequency limit, of the harmonic with maximum intensity (only up to Day 19), and of the fundamental frequency may be explained by the development of motor coordination (Levine et al., 1978) and of the geometry of the vocal tract, i.e., by an increase of the length of the vocal cords and the size of the resonance spaces, as is suggested as the reason for the decrease of the fundamental frequency in human baby sounds after the first year (Kent, 1976). Our weight-increase curves (Fig. 1) support the suggested increase of resonance spaces after the first week, since they show an enhancement of growth after Day 7, compared to the first week.

A consequence of this physical development of the vocal apparatus also seems to become apparent in the change of FM and AM occurrence rates (Figs. 5, 6) in normal kittens during the first week. The drop of FM and AM occurrence from Day 1 to Day 3, which is equal to a reduction of the variability of the calls, may reflect the adjustment to breathing air after birth. The very low level of FM and AM occurrence up to Day 9 may be related to the reduced activity patterns of elements of the vocal tract because of lack of motor activity and control, as explained before. The rapid development of motor activity between Days 9 and 14 (Levine et al., 1978) might increase the flexibility of the vocal apparatus during vocalization and thereby the variability within calls expressed by FM and AM components. In conclusion, the physical development of the vocal apparatus is suggested as determining the major changes of upper frequency limit, frequency range, fundamental frequency, harmonic with maximum intensity, and FM and AM occurrence during the first 2-3 weeks and to affect calls from all situations in a similar way.

Three call parameters—duration, SPL, and noise contents—are not systematically influenced by the development of the vocal apparatus, since changes parallel to those of the

other parameters do not occur (Figs. 3A,B; 7A). Call duration, however, shows evidence for a developing influence of motivation, which is superimposed on physical development. During the first 2 weeks calls in "picked up" condition are longer than calls in the other conditions (Fig. 3A). A lengthening of calls often has been related to increased or prolonged stress or distress in the animals (Moelk, 1944; also compare Sebeok, 1977). During the first 2 weeks, therefore, distress at being picked up by the skin of the neck seems to be the greatest, while after Day 53, tail-pressing seems to cause the greatest distress. Around Day 19, calls from all situations are near a minimum duration, indicating that during this time, kittens experience the call-eliciting situations at least stressful. Consistent with that are data on general development. Around Day 21, kittens are able to actively move around and leave the nest area, and they start eating solid food (Moelk, 1979; Härtel, 1975); vision is operative (Moelk, 1979), and hearing has developed to normal sensitivity (Ehret & Romand, 1981) and high discrimination ability, so that sound qualities can be discriminated and differentially responded to (Olmstead & Villablanca, 1980). The achievement of advanced sensory and motor capacity around Day 21 could decrease the sensitivity to fear and stress and establish "emotional neutrality," with a strong tendency to use the new skills only for exploration and experiencing the environment. This emotional neutrality seems to be reflected in the SPL of the sounds, which is lowest at Day 19 (Fig. 3B), in the harmonic with maximum intensity, and the upper frequency limit and frequency range, which are lowest at Day 19 (Figs. 4A-C). Also, the high occurrence rates of FM and AM components during the second postnatal week have been reduced by Day 19 (Figs. 5A-C; 6A-C). If loud, long, high-pitched, and variable calls indicate high (di)stress (Moelk, 1944), then Day 19 calls, on the average, indicate just the opposite.

After Day 19, different developmental trends become obvious in calls from different situations with regard to call duration, fundamental frequency, harmonic with maximum intensity, and FM and AM occurrence rates. These differences, superimposed on general physical development, are suggested to be an expression of different motivational valuations of the situations of call release. In less distressful situations, i.e., being along (and being picked up) compared with tail-pressing, calls are generally shorter (Fig. 3A), show the stress on a lower harmonic (Fig. 4A), and contain less FM and AM (Figs. 5B,C; 6C). In these situations, the kittens also seem to use a shorter part of their vocal cords for call production, since the fundamental frequency is higher compared to calls after tail-pressing (Fig. 3C). In conclusion, motivation obviously is expressed in call parameters like duration and others, contributing to the timbre and variability of the calls.

We can now try to transfer the conclusions drawn from the development of the calls of normal kittens to those of isolated kittens, which were deprived of social contact with the adults. During the first 9 days, significant differences between isolated and normal kittens occurred in the harmonic with maximum intensity (Figs. 10A; 11A) and in the rates of FM (Figs. 12A-C) and AM (Fig. 13C). The decrease of FM and AM occurrence rates after birth is delayed in isolated kittens and the increase of the harmonic with maximum intensity is delayed as well. A straightforward explanation is that the isolated kittens had delayed development in their vocal apparatus. Isolated kittens also do not reach the typical Day 19 patterns in many call parameters, which indicates—following the previous reasoning—that they may not reach "emotional neutrality" because they may be stressed by the lack of appropriate social interactions. A higher (di)stress level after Day 19 in isolated kittens is also indicated by longer calls and a different development of the harmonic with maximum intensity, compared with normal kittens. Newman and Symmes (1974) found that socially deprived rhesus monkeys developed structural abnormalities in certain call parameters of the "coo" calls, including temporal patterns,

FM occurrence, and harmonic with maximum intensity. On the one hand, these results resemble ours from the kitten, and indicate that social deprivation can change calls in a quantitative manner depending on the degree of change, probably of the motivational background of the animals. On the other hand, however, some structural change seemed to be present in all monkey coo calls, while in the kittens, structural changes of call parameters are only indicated by shifts of the means taken from many calls and are not necessarily present in every call. In another study on squirrel monkeys, Winter, Handley, Ploog, & Schott (1973) could not find consistent differences in call development between animals raised with their mothers and socially deprived ones. Isolated animals showed an apparently normal call repertoire. However, call parameters were not quantitatively evaluated in this study and shifts of the means of some call parameters, like those we found in isolated kittens, might have been overlooked.

The two deafened kittens studied showed a number of differences in the development of several call parameters compared to normal and isolated ones. First, their calls were louder between Days 9 and 23 and from Day 82 onward (Figs. 8B and 9B). Since auditory sensitivity increases rapidly between Days 6 and 10 (Ehret & Romand, 1981), we suggest that normal hearing animals control the SPL of their calls as soon as they have feedback via their auditory systems. The lack of feedback in deafened kittens may have changed the SPL of the calls, often to higher levels. A lack of auditory feedback may also be responsible for improper control of the vocal cords, causing lower fundamental frequencies in older kittens (Figs. 8C and 9C); of the resonance spaces, resulting in a different stress of the harmonics (mostly at lower harmonics up to Day 42 and at higher harmonics from Day 82 onward; Figs. 10A and 11A); and, in a different pattern of variability development (FM and AM), of the calls. In addition, calls of deafened kittens contain very few noise components (Figs. 7B and 10C), and the overall variability of the call parameters is less (SDs are smaller) than in normal and isolated kittens. Altogether, calls of deafened kittens sound, on the average, louder, more tonal and uniform, and lower pitched, up to Day 42, and higher pitched, from Day 82 onward, than those of normal hearing animals. We may conclude, therefore, that feedback through the auditory system is necessary for the adjustment of many call parameters to the normal average values. Deafened kittens may thus serve as mammalian models for studies of the physiology of auditory and vocal interactions in the brain during development of hearing and of call production. Finally, since the duration of deafened kittens calls most resembles that of the calls of isolated animals (Figs. 8A and 9A), the motivational background of deafened kittens in stress or distress situations seems to be closer to that of isolated than of normal animals.

Call development in kittens may be compared with the development of vocalization in birds, which has been studied in various species and various experimental conditions (e.g., Marler & Mundinger, 1971; Nottebohm, 1970). In species like the ring dove and the domestic fowl, social isolation or deafening during the first days of life had no influence on call development. This is similar to what we found in kittens, their calls being entirely within the normal range. However, looking at the mean values, especially from deafened kittens, several call parameters differed significantly from the normal averages, showing that auditory feedback plays a role in adjusting call production in a quantitative way. Apparently, vocal development in kittens follows a "self-centered strategy" rather than an "open and environmentally dependent" one (Nottebohm, 1970). The latter is found in many songbirds that depend on auditory feedback and/or have to learn from adults in order to develop a normal song pattern.

Notes

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