The role of auditory feedback in the vocalizations of cats

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Summary. The vocalizations of deaf cats were compared with those of littermate hearing controls at 30 days, 50 days, 1 year and 3 years of age. At all ages, deaf cats called more loudly than hearing animals. At 30 days, 50 days, and 3 years, deaf cats called about twice as loudly as hearing animals while at 1 year the calls of the deaf animals were approximately 6 times louder than those of the hearing littermates. Analysis of variance revealed significant differences in call loudness between deaf and hearing animals at 30 days, 1, and 3 years. Deaf and hearing animals did not differ in rate of calling or in the duration of individual vocalizations at 30 days, 50 days, and 1 year. At 3 years, the calls of the deaf animal were shorter than those of the hearing control. The calls of deaf animals were less variable than those of hearing animals at 30 days, 50 days, and 3 years. There was a tendency for the fundamental frequency of the calls of deaf animals to be higher than that of hearing animals at 30 days, 50 days, and 1 year. These results document the importance of auditory feedback in the regulation of feline vocalization.

Key words: Auditory feedback – Audition – Animal vocalization

Introduction

Auditory feedback is crucial for the development of human speech and profoundly deaf children never acquire normal speech even with extensive training (Markides 1983; Monsen 1983). While the importance of auditory feedback in spoken language is clear, the neural mechanisms underlying this feed-

back are not well defined. For example, in discussing the conflicting results of experiments on the effects of delayed auditory feedback on vocalization, Siegel et al. (1980) argued that there may be a number of separate auditory feedback systems necessary for normal speech development. A major difficulty in understanding such systems is a lack of animal models which might be used to study the neural substrates involved in the control of vocalization. The lack of such models may be due, in part, to an assumption that the calls of non-human mammals are purely reflexive and do not depend upon hearing. Such an assumption, however, is based largely on indirect evidence since the role of auditory feedback in the development and maintenance of vocal behavior in nonhuman mammals has rarely been studied.

A few studies have attempted to determine if auditory feedback is necessary for the regulation of primate vocalization. Talmage-Riggs et al. (1972) deafened 3 squirrel monkeys and reported that the intensity of at least one call type, the trill, increased in the absence of auditory feedback. However, they noted no change in the quality of calls and concluded that, in general, vocalization in the squirrel monkey did not appear to be dependent on auditory feedback. Winter et al. (1973) reported that a squirrel monkey deafened early in the postnatal period developed normal vocalizations and also suggested that auditory feedback is not necessary for vocal development in this species. Sutton (1979) deafened three *M. nemestrina* newborns and reported a decrease in the variety and rate of vocalization over the first three months. The reports suggest that the importance of auditory feedback differed between the species studied. However, the varying results could be due to methodological differences, especially in the degree to which normal vocal behavior was defined and quantified.

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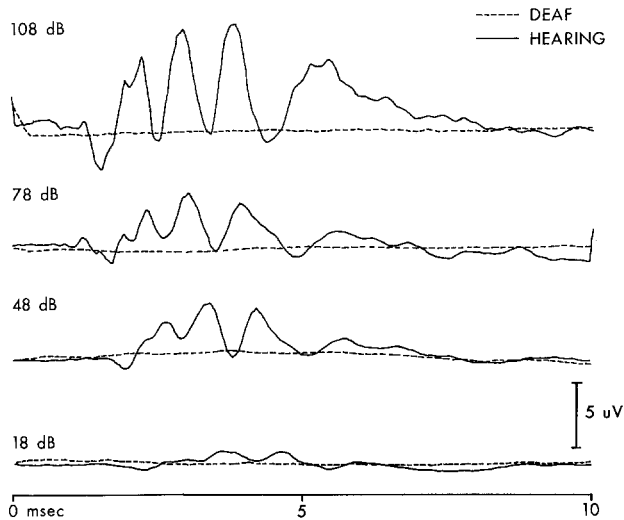
Fig. 1. Typical auditory brainstem responses (ABRs) from littermate deaf and hearing cats at 90 days of age. ABRs were not present at any age for the deaf animal

Cats have several types of vocalizations (Brown et al. 1978) and a number of studies have identified brain substrates involved in the production of these calls (e.g. Kelly et al. 1946; Molina and Hunsperger 1962; Kanai and Wang 1962; Skultety 1958, 1965; Altafullah et al. 1983). Thus, the cat is an attractive model for studies of the neural control of vocal behavior (Buchwald and Shipley 1985). However, little is known about the role of audition in feline vocalization. In an earlier study of hearing impaired kittens, calls of experimental animals were found to be louder than those of normal littermates and to have less variability (Shipley et al. 1981). This study argued that differences in loudness between deaf and hearing animals reflected active control of the intensity of calling by hearing animals. However, some of the experimental cats in this previous study were not completely deaf. In order to correct this possible source of artifact, the present study of the long-term relationship of hearing and vocalization in cats was carried out.

During the course of the present experiment, Romand and Ehret (1984) reported a study of the development of kitten vocalization that included two cats deafened at postnatal day 3 whose calls were studied across 170 days. The calls of these animals were compared to those of normal controls and to kittens that had undergone periods of isolation from the mother. One of the deafened animals was hand raised while the other was raised by its mother. Romand and Ehret found that the calls of deaf kittens were louder than those of the hearing controls at most ages, although this difference was not seen during the second and third month of development. Romand and Ehret also found that the calls of the deaf animals were less variable than those of hearing cats.

In the present study, the calls of normal cats were compared with those of littermates who had been deafened surgically at 14 days of age. Care was taken to insure that both deaf and hearing animals were maintained in identical social situations and were handled for equal amounts of time. Vocal behavior was studied in a number of kittens at 30 and 50 days; vocalizations produced at these ages consisted of "isolation" cries which kittens reliably give when separated from their mother and littermates (Buchwald 1981; Haskins 1979). Smaller groups of animals were also studied at one and three years of age in order to determine whether effects seen in kittens persisted into adulthood.

Methods

Ten kittens from 3 litters of a mongrel strain bred at the UCLA vivarium were used in these studies. Two experimental and two control animals were taken from each of two litters and one experimental and one control from a third. Within each litter, experimental and control animals were matched for sex. Experimental animals were anesthetized with Ketamine (45 mg/kg) and deafened by bilateral mechanical destruction of the cochlea at 14 days. In this procedure, the bulla was opened, and the bridge of bone separating the round and oval windows and the membranes covering the round and oval windows were removed. Subsequently, the cochlea was mechanically destroyed after which all tissue and fluid were aspirated by suction. Control animals underwent sham operations in which the bulla was opened bilaterally. Both experimental and control animals were handled equally during recovery from the surgery and throughout the course of the experiment. Kittens were allowed to recuperate from the deafening operation for two weeks before recording of vocalizations began. During this time the animals appeared to recover fully and both experimental and control animals were of equal weight at the time of first testing (448 ± 87 gm for deaf kittens versus 440 ± 38 gm for hearing) and maintained normal growth rates thereafter.

The results of the deafening procedures were monitored by recording auditory brainstem responses (ABRs) at 35 days, 55 days, 90 days and 1 year. Recording techniques were the same as have been used in previous studies of the ABR in kittens and adult cats (Shipley et al. 1980). Click trains of 10 pulses/s at intensities from 0 to 100 dB SPL (re 20 micro Pascal) were used in an attempt to elicit ABRs from the experimental animals. ABRs were not present in any experimental animal at any age. The evoked ABRs of control animals were normal and, in all cases, were present at a threshold of about 10 dB (Fig. 1).

Calls were recorded by means of a Sony condenser microphone and a Uher Report 4000 IC tape recorder. The frequency response of this system was ± 3 dB in the range 200 Hz–10 kHz. Call duration and intensity were scored from a Tektronics storage oscilloscope (5103 n). Computer analysis of the acoustic parameters of vocalizations was carried out on a PDP 11/10 minicomputer. Calls were low pass filtered at 10 kHz to avoid aliasing, then digitized at a sampling rate of 20 kHz and stored on a magnetic
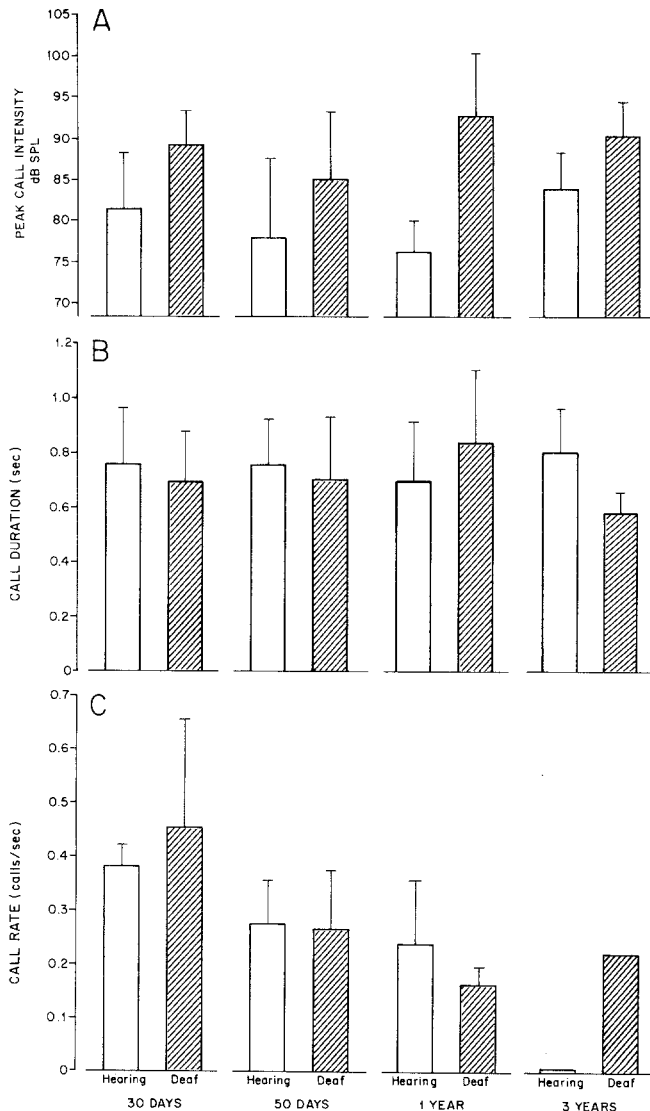
Fig. 2. Call intensity (**A**), duration (**B**), and rate (**C**), for deaf and hearing animals at 30 days, 50 days, 1 and 3 years

Table 1. Average intensity, duration and rate of calls for deaf and hearing cats at 30 days, 50 days and 1 year. For each parameter, the standard deviation is shown beneath the mean

	Intensity (dB)		Duration (s)		Rate (calls/s)	
	Deaf	Hearing	Deaf	Hearing	Deaf	Hearing
30 Days	89.2**	81.5	.70	.76	.45	.38
	±4.4	±6.6	±19	±21	±20	±04
50 Days	85.1	77.9	.71	.76	.26	.27
	±8.2	±9.6	±23	±17	±11	±08
1 Year	92.3**	76.2	.84	.70	.17	.24
	±5.1	±3.7	±27	±22	±03	±12
3 Years	90.4**	84.2	.59	.80	.22	< 0.01
	±4.1	±4.3	±.07	±.16	*	*

** deaf significantly different from hearing, $P < 0.05$
* No standard deviation given because only one rate was obtained at this age

identical to that used at 30 days. In order to determine if trends seen in these kittens persisted, one litter of two deaf and two hearing animals was tested at 1 year of age. Testing at this age was carried out with the cat isolated in the sound attenuated recording chamber. The cat was restrained in a canvas bag with its head 15 cm from the recording microphone and left in the room until it had given 30 spontaneous isolation calls. A deaf female and a matched normal female from this litter were also maintained until 3 years and two months of age (hereafter referred to as three years) when their calls were again recorded to determine if significant changes had taken place.

Results

Figure 2a presents comparisons between deaf and hearing animals for average intensity of vocalization at 30 days, 50 days, 1, and 3 years of age. The calls of deaf animals were louder than those of hearing controls at all ages (Table 1). At 30 days, 50 days, and 3 years, deaf cats called about twice as loudly as hearing animals while at 1 year the calls of the deaf animals were more than 6 times (15.6 dB) louder than those of hearing littermates. Analysis of variance revealed significant differences in call loudness between deaf and hearing animals at 30 days, 1, and 3 years. At 50 days, although call intensities were about twice as great (7 dB) for deaf as for hearing cats, the difference was not significant due to the large variability between calls.

At 30 days, 50 days and 1 year, the average call duration of deaf and hearing animals ranged from 0.7 to 0.84 s and did not differ significantly (Fig. 2b, Table 1). There was a tendency for the calls of deaf animals to be shorter than those of hearing animals at both 30 and 50 days but this trend was reversed at
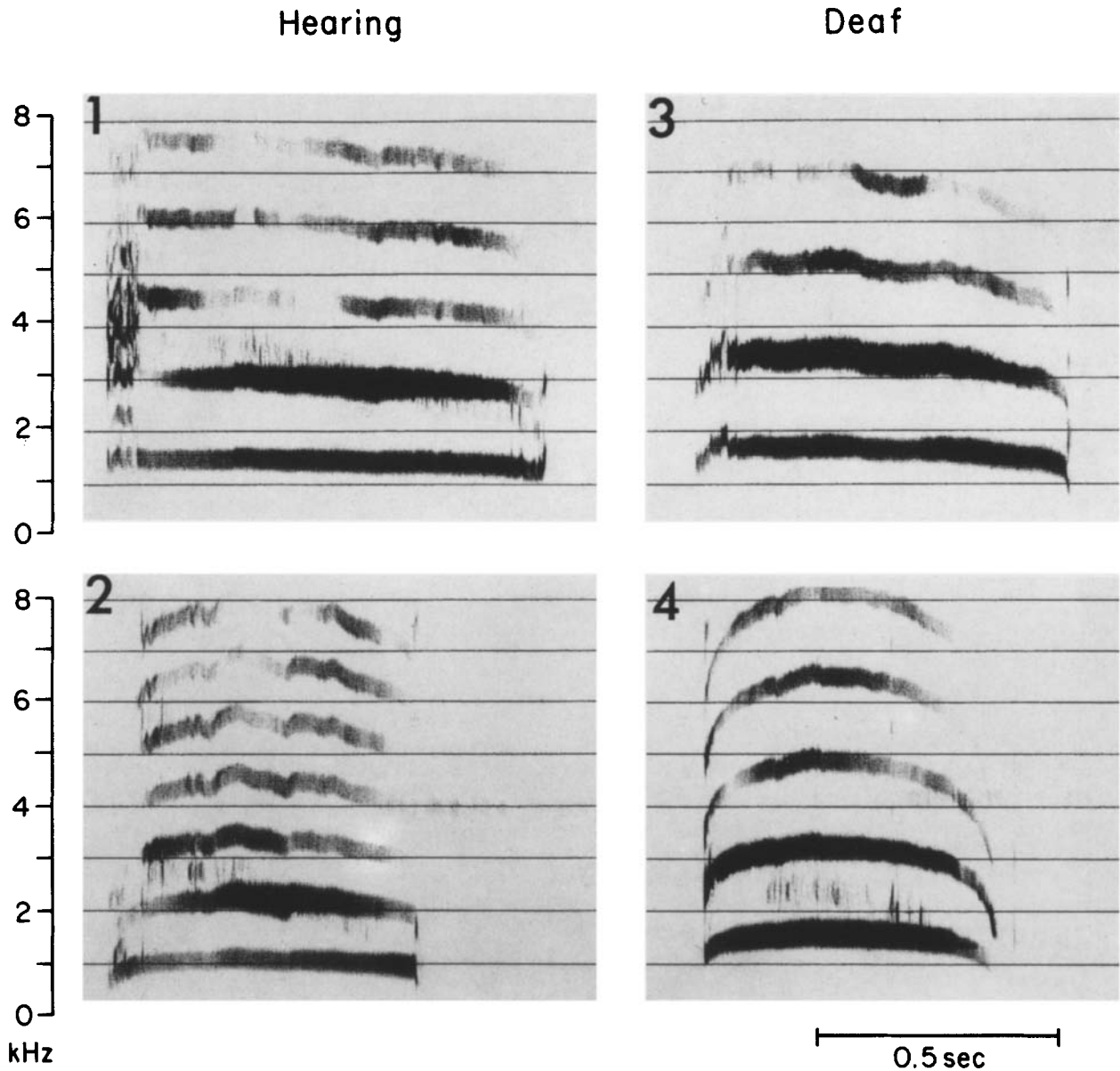
disk. The analysis programs employed a combination of linear prediction and Fourier transform techniques to measure call fundamental frequency. Digital techniques used for call analysis have been discussed in detail elsewhere (Carterette et al. 1979, 1984).

Testing of vocal behavior was carried out on all animals at 30 days of age. Calls were elicited by holding the cat 15 cm from a microphone within a sound isolation chamber until thirty calls had been recorded. At the end of each recording session, an 80 dB SPL 2 kHz calibration tone of 30 s duration was played from a speaker placed in the same position as the cat and peak call amplitudes were measured relative to this calibration tone.

Different numbers of cats were tested at each age. One litter of 1 deaf and 1 hearing animal developed feline infectious peritonitis at 40 days of age. The control animal died at 48 days and the experimental, which was clearly ill at 50 days, died at 58 days. This litter could not be studied at 50 days. Eight kittens from the other two litters were tested at 50 days of age in a manner

Hearing

Deaf

Fig. 3. Representative call spectographs for one hearing cat (1 and 2) and a littermate deaf cat (3 and 4) at 30 days of age. Generally similar acoustic structure was seen in the calls of both deaf and hearing animals

1 year, the age at which the difference in intensity between the two groups was greatest. At 3 years, the calls of the deaf animal were significantly shorter than those of the hearing control.

Vocalization rate was computed from the total time taken to produce 30 calls (Fig. 2c, Table 1). These rates revealed no significant differences between deaf and hearing animals at 30 days, 50 days or 1 year of age. At 30 days, deaf animals tended to call somewhat faster than hearing animals while at 50 days and 1 year hearing animals tended to call more rapidly than deaf ones. At 3 years, the hearing

animal did not begin calling for more than 2 h and did not produce a total of 30 vocalizations until after almost 4 h. The deaf animal called at rates comparable to those seen at previous ages. For both deaf and hearing cats, the rate of calling tended to decline across age which may reflect a general tendency for the animals to be less distressed in the testing situation with increasing age. Isolation might be expected to be more stressful for a young, nursing kitten of thirty days than for one which, at 50 days, is close to being weaned or than for one, which at 1 or 3 years, is an adult.

Table 2. Average fundamental frequency, starting fundamental frequency, and sum of changes in harmonic ratio of calls for deaf and hearing cats at 30 days, 50 days, 1 year and 3 years. For each parameter, the standard deviation is shown beneath the mean

	Average fundamental frequency (Hz)		Starting fundamental frequency (Hz)		Sum of changes in harmonic ratio	
	Deaf	Hearing	Deaf	Hearing	Deaf	Hearing
30 Days	1360.7	1217.3	1319.4**	1065.3	1.75**	5.17
	95.2	20.9	45.0	09.6	1.49	7.68
50 Days	1121.7	1019.9	1150.7	1036.7	3.17**	5.53
	68.7	98.6	42.5	92.0	2.47	2.7
1 Year	564.5	480.3	645.41	552.2	15.501	15.94
	110.5	6.9	62.0	34.17	9.69	9.81
3 Years	424.9	445.4	518.0	400.2	4.65**	59.73
	18.5	112.2	94.4	47.1	4.08	19.75

** deaf significantly different from hearing, $P < 0.05$

Acoustic structure

Cat isolation calls of the type recorded in this study consist of a fundamental frequency (Fo), which reflects the activity of the vocal folds, and a group of regularly spaced harmonics which are integer multiples of the fundamental. Some of these harmonics may be enhanced by resonances of the vocal tract so that they have greater acoustic energy than the fundamental. Figure 3 presents representative sound spectrographs of the calls of deaf and hearing littermates at 30 days of age. Inspection of spectrographs such as these revealed that, despite differences in average intensity of the calls, the general acoustic structure of vocalizations from deaf and hearing animals was similar at both 30 and 50 days of age. Vocalizations at 1, and 3 years sometimes showed individual idiosyncracies as is discussed below.

In order to study differences in the acoustic structure of the vocalizations in detail, a digital analysis of the fundamental frequency of the first 6 calls from each animal at 30 days, 50 days, 1 year, and 3 years was carried out. Analysis was restricted to the first 6 calls in an attempt to avoid the possibility of including calls whose acoustic properties reflected strain of the larynx (hoarseness) on the part of the deaf animals who were calling from 2 to more than 6 times as loudly as the hearing animals. Calls were digitized and the fundamental frequency from successive 12.8 ms segments of each call was determined by Fourier analysis and linear prediction techniques. Summary statistics taken from the analy-
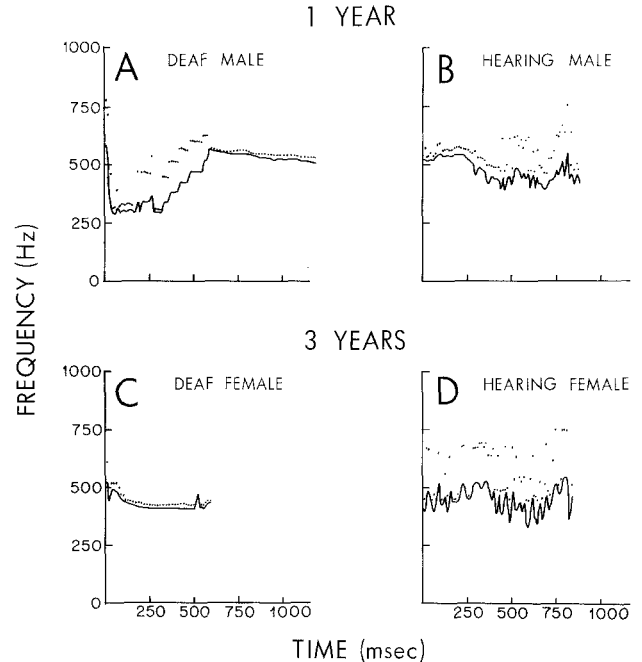

Fig. 4A–D. Average fundamental frequency functions with standard deviations (indicated by dots above the function) for deaf and hearing cats at 1 year and 3 years. All cats are from the same litter. Each function is an average of the first 6 calls made by the cat in the standard testing situation

sis of Fo values at all ages are presented in Table 2. Calls of deaf animals tended to have higher Fo than those of hearing littermates at 30 days, 50 days, and 1 year. Significant differences were present for the starting pitch at 30 days, which was about 250 Hz greater for deaf than for hearing animals. The apparently consistent tendency for increased Fo in deaf animals may be a direct result of the increased intensity of their calls. As subglottal air pressure increases, fundamental frequency should also tend to increase because of Bernoulli forces acting on the vocal folds (see, for example, Borden and Harris 1984).

Acoustic analysis of calls at 1 and 3 years of age was complicated by the occurrence of rapid shifts in Fo for some animals, presumably reflecting changes in the mode of vibration of the larynx. Figure 4 shows average fundamental frequency functions with standard deviations for deaf and hearing males at 1 year of age (A and B), and for deaf and hearing females at 3 years (C and D, all cats whose calls are shown in Fig. 4 are littermates). In the calls of the deaf male at 1 year, Fo started high, fell quickly, then nearly doubled in the first half of the call and was quite stable thereafter. Changes in Fo were abrupt in individual calls which is reflected in the step-like changes in the average shown in Fig. 4A. The calls of

some littermates also contained instabilities in pitch (indicated by relatively large SD points in the average Fo function of the hearing male) but they were not as pronounced. A possible explanation for the shifts in Fo seen in the calls of the deaf male is the high intensity of the calls, which were generally from 5 to 10 times (14 to 20 dB) louder than the calls of the hearing control. It is possible that the very high rates of air flow at the beginning of these intense calls forced a different mode of vibration of the larynx than that seen in softer calls. This explanation might also account for the relative stability of Fo in the later stages of the calls since air flow (as measured by RMS) typically decreases during the latter half of the call. In support of this explanation, relatively soft calls made by this animal at this age were not characterized by the extreme changes in Fo seen for louder calls.

Data from the male cats at one year shown in Figs. 4A, B suggests that deaf cats produce more variable calls than hearing cats. However, data from other animals did not support this conclusion as can be seen in the average Fo functions from deaf and hearing females at 3 years presented in Figs. 4C, D. Both of these females displayed rapid Fo shifts in their calls but these shifts were much common for the hearing animal. These rapid shifts in Fo have also been reported in children where the phenomenon has been termed biphonation (e.g., see Keating 1980). Acoustic reasons for biphonation are not clear. Biphonation-like shifts in Fo were much more common for the hearing than for the deaf animal at 3 years as is indicated in the average standard deviation of the Fo function which was 112.19 Hz for the hearing versus 18.55 Hz for the deaf cat. This difference in the stability of Fo was not present for these two animals at 1 year of age when few rapid shifts in Fo were seen for either animal (standard deviations were 37.77 Hz for the hearing and 32.68 Hz for the deaf animal at this age).

As Fig. 4 indicates, extensive variability was sometimes seen in the acoustic structure of the calls of both deaf and hearing animals. This variability could be reflected in the form of the harmonic structure of calls as well as in the fundamental frequency. Harmonic structure is extremely important in considering call stability since, in almost all feline vocalizations in this study a harmonic of the fundamental, rather than the fundamental itself, was the most intense frequency in the call (such a harmonic is somewhat analogous to a formant in a human vowel).

In an attempt to develop a general measure of the stability of the acoustic structure of the isolation call, we computed a ratio of the frequency of the har-

monic with maximum energy to the frequency of the fundamental for each analysis frame in the call. This ratio, termed the harmonic ratio, thus reflected both the major resonance of the vocal tract (which might vary, for example, as a function of mouth opening) and the activity of the larynx. The harmonic ratio could vary from a value of 1 (when the fundamental contained the maximum energy in the analysis frame) to 5 or 6 (when the fifth or sixth harmonic contained the maximum energy), but was usually between 2 and 4. If the acoustic structure of a call remained constant across time, the harmonic ratio would also be constant. Thus, the number of changes in this ratio was used as a measure of overall call stability.

The third pair of columns in Table 2 presents the average total change per call in the harmonic ratio for deaf and hearing animals at each age. The calls of deaf animals displayed fewer changes in the harmonic ratio at all ages and this difference was significant at 30 days, 50 days, and 3 years. At one year of age, the extensive instability present in the fundamental frequency of the very loud calls of the deaf animals produced a large number of changes in the harmonic ratio leading to an average variability similar to that seen for the hearing animals.

Discussion

The present results confirm our previous findings that auditory feedback plays an important role in regulating the loudness and variability of kitten isolation calls and extend these results to demonstrate that the effects of deafness persist into adulthood. Differences in the intensity of the calls of deaf and hearing animals appear to reflect active control of call loudness by the hearing animals who, presumably, were physically able to make much louder calls than they did. Humans are known to control the intensity of their vocalizations to account for differing conditions of background noise, raising the intensity of speech in the presence of competing background noise and reducing it when background noise is relatively low (e.g. Siegel et al. 1982; Lane and Tranel 1971). Similar behavior has been reported for the Japanese monkey and the quail (Sinnott et al. 1975; Potash 1972). The present results suggest that active modulation of call intensity is carried out by cats as young as 30 days of age. Hearing animals apparently lowered the intensity of their calls, perhaps reducing call intensity because of the low background noise present in the sound attenuation chamber in which vocalizations were recorded, while this control was not exercised by deaf cats. Many species communicate largely through graded vocali-

zation systems in which variations in the intensity of a call can convey subtle differences in meaning, especially about the emotional state of the animal (e.g., Rowell and Hinde 1962; Green 1975). If such a system is used by cats, modulation of intensity would have clear importance for communication in this species.

The finding that the calls of deaf animals tended to be less variable than those of hearing animals also suggests the presence of active modulation of call structure by hearing cats. The possible behavioral significance of such modulation is not clear. Leyhausen (1979) has documented a variety of social situations in which cats vocalize, and it is possible that active modulation in the acoustic structure of vocalization is important within or across these situations.

While experimental animals in the present study had received some exposure to sound before deafening, this experience was quite limited and unlikely to have affected the results seen. Deafening was carried out at 14 days in order to insure that experimental animals would recover quickly from the surgery, would maintain a normal growth curve, and would not require hand feeding which might influence the results. In neonatal kittens airborne acoustic stimulation is either totally absent or quite restricted for some time after birth (Shipley et al. 1980) because the middle ear is filled with fluid, the external ear canal is filled with mesenchyme and the external auditory meatus is closed with the ear flattened over it. Over a period of 10–14 days (Villablanca and Olmstead, 1979) postnatally, the middle ear and external canal gradually clear and the meatus opens.

The results of the present experiment are in general agreement with those of Romand and Ehret (1984) who found that the intensity of the calls of dear kittens was significantly greater than that for hearing controls between days 5 and 23, not between days 26 and 60, and again between days 82 and 135. Our finding of significant differences in loudness at 30 days, not at 50 days, and again at 1 and 3 years suggests a similar pattern. Although Romand and Ehret did not see significant differences in loudness between deaf and hearing cats at days 42, 46, 53, and 60 days, the average intensity of the calls of deaf animals was greater than that of the normal controls at each of these days except for day 42 (Romand and Ehret 1984, Fig. 9). These results are similar to our finding that the calls of deaf animals were louder at 50 days even though this difference did not reach significance. The fact that the present study found a significant difference in loudness at 30 days while the difference that Romand and Ehret saw at 26 days did not reach significance could easily be due to

methodological factors, such as the number of subjects, rearing conditions, and the exact recording protocol, all of which differed in the two studies.

The calls of deaf cats showed characteristics which are consistent with commonly reported features in the speech of hearing impaired humans. Excessive loudness is a frequently cited problem of deaf speakers (Nickerson 1975) which is most pronounced in cases of complete sensorineural deafness (Carhart 1970, Miller 1968), a degree of impairment analogous to that of the experimental animals in this study. Deaf speakers also tend to have higher fundamental frequency than do hearing speakers and even have been reported to speak in falsetto voice (Boothroyd et al. 1975; Forner and Hixon 1977). A similar tendency for increased Fo was seen in the deaf cats of this study. Horii (1982) has attributed the elevated Fo of deaf speakers to increased vocal effort, which may be directly comparable to the increased call amplitude seen for deaf cats. The finding that the calls of deaf animals tend to be less variable than those of hearing animals is consistent with reports of decreased variability in the intonation patterns of some deaf speakers (Monsen 1979, 1983). The finding that deaf animals vocalize at rates comparable to or even greater than hearing controls through 3 years of age agrees with a study by Stark (1983) showing that the spontaneous vocalizations of deaf children continue at high rates for several years after birth. Taken together, these similarities suggest that auditory feedback may function comparably for both cats and humans in the regulation some aspects of vocalization.

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