Perception of the missing fundamental by cats*

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Two cats were tested on their ability to perceive the missing fundamental through the use of an avoidance technique. The animals were trained to discriminate between rising and falling pitch sequences first with single and then with multiple tones. They were then tested by presenting them with tone triads known to produce the perception of the missing fundamental in humans. In these traids the pitch of the frequencies composing the triad either remained the same or shifted in the direction opposite the shift of the missing fundamental. The results show that the animals' response to these triads was not in conformity with that expected from the direction of change of the component frequencies, but could be accounted for if it were assumed that the cats were responding on the basis of the missing fundamental. A further test given one of the cats indicated that this phenomenon declined progressively as the center frequency was raised, until at 6 kHz it was apparently completely absent. A similar decline in the strength of the fundamental pitch occurs over the same range in humans. Thus, there is reason to believe that cats perceive the missing fundamental.

Subject Classification: [43]65.75, [43]65.56, [43]65.54; [43]80.50.

INTRODUCTION

The phenomenon of the missing fundamental can be demonstrated with a complex tone made up of sinusoids with frequencies such as 1600, 2000, and 2400 Hz which, when presented to human subjects, gives rise to the perception of a "fundamental" tone of 400 Hz (e.g., Schouten, 1970; Schouten, Ritsma, and Cardozo, 1962). The missing fundamental has been considered to be one example of the more general phenomenon of periodicity pitch, in which the ear appears to assign pitch to the signal on the basis of the periodicity of its amplitude envelope (for a review, see Plomp and Smoorenburg, 1970).

Because of the importance of periodicity pitch to theories of hearing, it has become the subject of physiological investigations of auditory processing (e.g., Butler, 1972; Hind, 1972; Kiang and Goldstein, 1959; Small and Gross, 1962; Whitfield, 1970*a*, *b*). However, while behavioral investigations of periodicity pitch have been carried out with human subjects, the majority of physiological investigations have been carried out with animals. As a result, conclusions concerning the relation of neural activity and behavioral data have been limited.

In order to determine if animals could perceive pitch from such periodic stimuli, two cats were trained to respond to stimuli which in humans produce the perception of the missing fundamental. The results of this work have so far demonstrated that cats behave towards such stimuli much in the same way as do humans.

I. METHOD

The basis of the method is that if a tone triad A, A–D, A–2D (e.g., 2400, 2000, 1600 Hz) is replaced by the triad A, *A–E*, *A–2E*, where E > D (e.g., 2400, 1942, 1484 Hz), the apparent pitch—the "missing fundamental"—rises (from 400 to 458 Hz in our example). However, the actual stimulus frequencies either remain the same or fall. We train the animal to discriminate between rising and falling pitch sequences first with single and then with multiple tones. Finally, we present it with the above stimulus situation on the hypothesis that its response will depend on whether it is assigning pitch on the basis of the harmonics or of the "fundamental." In describing the detailed procedure, we propose to avoid the periphrasis "a pitch equivalent to that of a single tone of__Hz" and to speak simply of the "frequency" of the missing fundamental. This is merely a convenience and we are not addressing ourselves to the question of whether the perceived pitch does or does not have any equivalent frequency representation in the nervous system.

A. Subjects

Two cats were used in the experiment. The animals were maintained on dry food (Purina Cat Chow), and their individual daily water consumptions and drinking patterns were recorded. Following this procedure, the time during which the animals had access to water was restricted over a period of five to seven days until the animals had one hour to drink—a condition to which the animals rapidly adjusted. Once this procedure was completed, the cats were ready for introduction into the experiment.

B. Apparatus

The animals were tested in a rectangular cage, 30.5 cm long, 43 cm high, and 43 cm wide, which had a stainless-steel-bar floor and wire-mesh sides and top. A brass water cup (4 cm diam) was placed on the floor of the cage at one end and connected with rubber tubing to a water bottle via a solenoid water valve. The entire arrangement was placed in a soundproof chamber and monitored by closed-circuit television.

An electronic circuit was connected to the water cup and grid floor in order to detect when the cat licked the bowl. A constant-impedance shock source was used to provide the electric shock, which was administered through the grid floor and controlled by a variable transformer.

The tones used were produced by either one or two

TABLE I. Stimuli used in the missing fundamental test.

	Oscillators				Direction of Change	
	A	B	Frequency	Missing fundamental	Frequency	Missing fundamental
(a)	342	···	342	None	Down	···
	400	···	400	None	Standard	···
	458	···	458	None	Up	···
(b)	342	1942	1600, 1942, 2284	342	Down	Down
	400	2000	1600, 2000, 2400	400	Standard	Standard
	458	2058	1600, 2058, 2516	458	Up	Up
(c)	342	2058	1716, 2058, 2400	342	Up	Down
	400	2000	1600, 2000, 2400	400	Standard	Standard
	458	1942	1484, 1942, 2400	458	Down	Up

independent oscillators and a balanced modulator. To produce the three-tone stimulus (triad), the output of oscillator A was added to and subtracted from the center frequency produced by oscillator B and all three frequencies were combined. The frequency of oscillator A thus determined the spacing of the three frequencies of the triad, and hence the frequency of the fundamental. By stepping the two oscillators through equal increments of frequency, either up or down and in the same or opposite directions, the four types of triad pairs set out below and in Table I could be produced.

The transducers were a 7.5-cm paper-cone speaker (used only in the initial stage of training) and an ionic loudspeaker (Ionophane 601, Fane Acoustics, Ltd.) which were placed 0.5 m in front of the animal and directed towards its head. The advantages of the latter speaker are that it has a linear response in the range of the frequencies used in this experiment and that there is no moving diaphragm to generate distortion products. In addition, it is matched to the air by a small horn such that the system has a high-pass characteristic, giving considerable attenuation for frequencies in the region below 1 kHz.

Sound measurements were made by placing a microphone (Brüel & Kjær $\frac{1}{2}$-in. model 4133) above the water cup in the position previously occupied by the cat's head and with its axis pointing directly at the loudspeaker. The sound level was measured with a Brüel & Kjær microphone amplifier (model 2604) and $\frac{1}{3}$-octave filter (model 1614). Readings for the 1600, 2000, 2400 Hz triad were 63, 70, and 65 dB with the filters centered on 1600, 2000, and 2500 Hz, respectively.

Because of their small separation, the three components of a triad are not completely resolved by the filter system, so that adjacent components contribute to each reading. The readings obtained would correspond to values for the respective components of about 62, 68, and 64 dB SPL. In general and on this basis, the intensities of the components of the various triads all fell within the range 65 ± 3 dB SPL. No output could be detected within the band 12.5–1000 Hz.

C. Stimuli

The stimulus pairs were composed of either single tones or triads in which the "standard" stimulus was followed by a "comparison" stimulus of either higher or lower frequency (Fig. 1). The tone pairs were presented at a rate of one pair/sec for 10 sec (290-msec duration, 20-msec rise–decay, with 10 msec between members of a pair and 410 msec between pairs). The stimuli used may be divided into three categories (cf. Table I).

(a) A standard tone of 400 Hz followed by a comparison tone of either 342 or 458 Hz [Table I(a)].

(b) A standard triad of 1600, 2000, 2400 Hz followed by a comparison triad of either 1600, 1942, and 2284 Hz or 1600, 2058, and 2516 Hz [Table I(b)]. In humans these triads produce the perception of a fundamental tone (the missing fundamental) of 400, 342, and 458 Hz, respectively. It is important to note that when the standard triad is paired with either of the two comparison triads, the frequencies of both the triad and the missing fundamental change in the *same* direction relative to the standard.

(c) A standard triad of 1600, 2000, and 2400 Hz followed by a comparison triad of either 1716, 2058, and 2400 Hz or 1484, 1942, and 2400 Hz [Table I(c)].

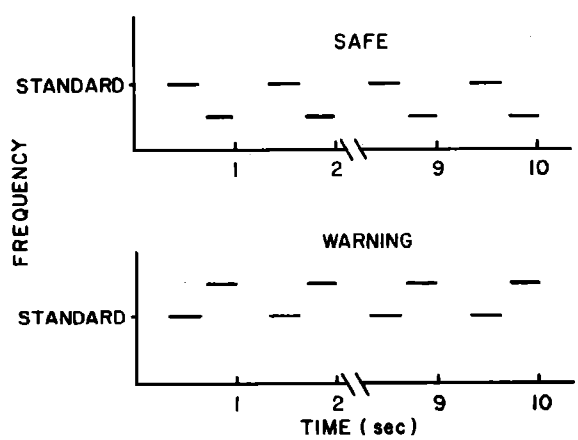

FIG. 1. Schematic representation of the tone pairs used in the missing fundamental test. The safe signal consisted of 10 tone pairs in which the second tone of each pair was of lower frequency than the first or standard tone. The warning signal consisted of 10 tone pairs in which the second tone was of higher frequency than the standard. The animals were trained to make an avoidance response upon presentation of the warning signal and to ignore the safe signal.

In this case, the frequencies of the triads and the missing fundamental produced by the triads change in the *opposite* direction relative to the standard. Thus, for example, a person who perceived the missing fundamental would say that the comparison tone of the pair was of higher frequency than the standard when in fact two of the tones in the triad were lower. This stimulus condition was therefore crucial in determining whether a subject perceived the missing fundamental.

During initial training, it was discovered that the cats tended to respond to changes in the absolute frequency of the tones as well as to the direction of the shift in pitch. To reduce the possibility of an animal responding to changes in absolute frequency, the settings of the two oscillators were randomly varied by as much as 10% for the stimuli listed in categories (a) and (b) [but not (c)]. This procedure also served to reduce the possibility that the task could be solved on the basis of changes in intensity which might have been associated with changes in frequency.

D. Procedure

Briefly, the cats were trained to maintain contact with the water cup for a water reward. After a reasonably steady rate of contact was attained, trials were begun which consisted of the presentation of one of two tone patterns for 10 sec. If the tone pattern had a *rising* pitch sequence, the cat had to cease licking within 3 sec of tone onset in order to avoid an electric shock which would otherwise be delivered to the animal's feet at tone offset. This conditioning procedure soon resulted in a cessation of contact with the cup during such a trial. However, if the tone pattern had a *falling* pitch sequence, it was never followed by shock and cats soon learned to maintain contact with the cup during these trials. Evidence that the cats had learned the discrimination was provided by demonstrating that the animals broke contact when a rising pitch sequence was presented and maintained contact when a falling pitch sequence was presented.

1. Details of training and testing

The cats were placed in the cage for a period of one hour and allowed to drink from the water cup. Water was delivered into the cup at a rate of 100 drops/min (0.025 ml/drop) as long as the animal maintained contact with the cup. If the animal broke contact with the cup for more than 0.25 sec, the flow of water was automatically stopped. As a result, the cats soon learned that steady contact with the cup would deliver the maximum amount of water.

Once the animal had learned to maintain constant contact with the water cup, a four-stage training and testing procedure was begun.

First stage: The 400–458-Hz tone pairs were presented for 10 sec and, unless the animal ceased drinking within 3 sec of tone onset, were followed at the end of the 10-sec period by an electric shock delivered through the grill floor. After several such tone–shock pairings, the cats learned to cease drinking when the "warning" stimulus came on and thus were usually able to avoid the shock. The warning stimulus was presented at random intervals varying in 15-sec blocks from 45 to 180 sec following the previous warning signal. Thus, there were generally 10 intervals in which a warning signal could occur (i.e., 45, 60, 75, ..., 180 sec) though longer intervals were occasionally inserted.

Second stage: Once the cats had learned to avoid the 400–458-Hz tone pair, they were trained to ignore the 400–343-Hz tone pair, the "safe" signal [Table I(a)]. This was accomplished by presenting this tone pair during the 10-sec intervals in which a warning signal might have, but did not, occur. Thus, the cats were continuously presented with 10-sec tone pairs separated by 5 sec of silence, with the warning signal randomly interspersed among the safe signals. This stage of training was completed in approximately 20 sessions.

Third stage: When the cats had learned to discriminate reliably between the two signals, the triad pairs [Table I(b)] were introduced. The procedure used here was the same as in stage 2 in that the animals were trained to avoid the triad pair in which the pitch sequence of the component frequencies, as well as the missing fundamental, was rising and to ignore the triads in which the pitch sequence of the component frequencies and the missing fundamental were falling. Though the animals learned to perform this discrimination within three to five sessions, training was continued until the animals had received at least 20 training sessions.

Fourth stage: When the cats had learned to discriminate the triad pairs, they were presented with the test for the perception of the missing fundamental. This consisted of presenting "test" triad pairs [Table I(c)] in which the pitch sequence of the component frequencies was in the direction *opposite* the pitch sequence of the missing fundamental.

The test triads were presented by inserting them within sessions consisting primarily of the original triads with which the animals had been trained. Since the nature of these test triads (i.e., safe or warning) depended upon the cue the animal was using, these triads were never followed by shock regardless of the animal's response. Testing was complete once an animal had received 10 of each of the two test triads for a total of 20 test trials. For comparison, the performance of the cats on the original training triads was determined on the basis of the 60–80 trials which they received during the test sessions. A further test was given cat 2 to determine the range of frequencies over which the missing fundamental might be perceived. This test consisted of triads in which the center frequency was 3, 4, 5, or 6 kHz and the upper and lower frequencies were the center frequency plus and minus 400 Hz. To produce the comparison frequencies, the oscillator outputs were increased and decreased by 58 Hz, as in the 2-kHz center frequency test.

TABLE II. Performance on 2-kHz center frequency missing fundamental test. Low scores indicate a cessation of contact with the water cup in order to avoid electric shock. The letters "b" and "c" indicate the section of Table I from which the stimuli were drawn. Note that the animals showed avoidance behavior when the missing fundamental warned of possible shock even though the frequencies of the triad indicated no shock (c).

Condition		Score (in sec)	
Missing fundamental	Triad	Cat 1	Cat 2
(b) Safe	Safe	9.2	9.7
Warning	Warning	3.2	3.3
(c) Safe	Warning	9.6	9.7
Warning	Safe	4.8	3.0

2. *Analysis of behavioral data*

The amount of time that an animal maintained contact with the water cup during the safe and warning intervals was determined to the nearest 0.1 sec. Thus, the time or score for an individual trial could vary from 0 to 10.0. To reduce the effects of spurious pauses, the results of a trial were discarded if the animal broke contact during the 2 sec preceding a trial, though the trial was presented as usual. This procedure helped reduce variability by eliminating trials presented while an animal was pausing to groom or rest, as they occasionally did, without having to resort to modification of the randomized trial presentations sequence. Because this criterion was applied equally to safe and warning trials, it did not bias the results. The scores for the safe and warning trials were compared using the Mann-Whitney U test (Siegal, 1956) to determine the probability that the animals were successfully performing the discrimination.

To compare the performance of cat 2 as the center frequency was varied, a unitless measure of detection was chosen. This measure is a function of the length of time the animal maintained contact during the warning (W) and safe (S) signals and is computed as $(S-W)/S$. The values of the measure vary from +1 (indicating complete cessation of drinking during the warning signal) to 0 (indicating no cessation of drinking), with intermediate values interpreted as indicating that the warning signal was sometimes detected (e.g., Heffner, Heffner, and Masterton, 1971).

II. RESULTS

The performance of the two cats during the test sessions is shown in Table II. When both the missing fundamental and the component frequencies of the triad were safe signals [Table II(b)] the animals generally continued to drink from the water cup with little or no pause. Indeed, though on the average the animals broke contact with the cup for less than 1 sec, the cats showed no break in contact at all on over half of the safe trials. Thus, the animals had learned not to respond to a falling pitch sequence. In contrast, when both the missing fundamental and the component frequencies indicated shock, the animals ceased drinking from the water cup in an average time of 3 to 4 sec. In addition, the median score for each animal was less than 3 sec, so that on most of the warning trials the animals did not receive a shock at the end of the 10-sec trial. Thus, the distribution of the animals' scores indicated that they had learned to distinguish a rising from a falling pitch sequence ($p<0.0001$, one-tailed distribution).

The scores for the trials in which the direction of the pitch sequence of the missing fundamental was opposite to that of the component frequencies are shown in Table II(c). Note that both animals maintained contact when the missing fundamental indicated a safe trial and broke contact when it indicated a warning trial ($p<0.002$, two-tailed distribution). Indeed, the performances of the animals were so consistent that the distributions of the safe and warning scores did not overlap. This result suggests that the cats were not responding to the component frequencies of the triad and may have been responding to the missing fundamental.

The investigation of the missing fundamental in humans has suggested that the phenomenon does not occur for center frequencies above about 5 kHz (Schouten, 1970). To further explore the ability of cats to respond to these signals, cat 2 was tested using triads with center frequencies of 3, 4, 5, and 6 kHz.

Figure 2 shows the performance of the animal when the missing fundamental and the triad signaled the same condition (i.e., both indicated safe or warning) and when they signaled opposite conditions. The decline in performance in the latter condition indicates that whatever cue the animal was relying on at 2 kHz (the missing fundamental in our hypothesis) is progressively lost as the center frequency is raised, until at 6 kHz performance is not above chance. There was a parallel decline in performance when the missing fundamental and triad indicated the same condition, suggesting

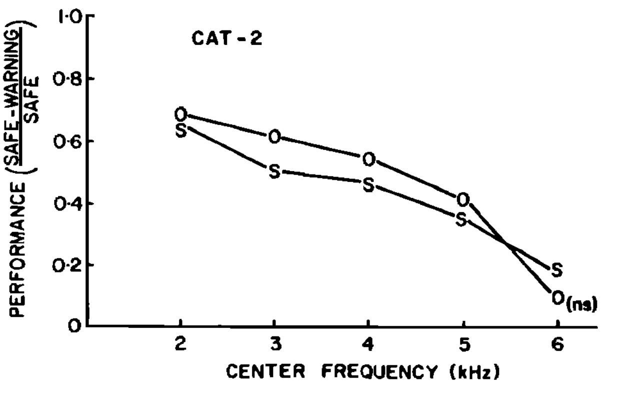

FIG. 2. Performance of cat 2 on the missing fundamental test using center frequencies of 2, 3, 4, 5, and 6 kHz. Scores were obtained under two conditions: the missing fundamental and the frequencies composing the trials shifting in the *same* (S) and *opposite* (O) directions. Note that performance in both conditions declines as center frequency is increased. (ns indicates that performance was not above chance, $p>0.05$.)

that the animal does not switch to using the component frequencies when the fundamental cue disappears.

III. DISCUSSION

The results of this study strongly suggest that cats experience something similar to, if not identical with, the perception of the missing fundamental in humans. The response of the animals in the test condition was not in conformity with that expected from the direction of change of the component frequencies of the triads, since, contrary to other training, the animals avoided when the direction of the test signal was down and failed to avoid when it was up. However, their performance could be accounted for if it were assumed that the cats were responding on the basis of a phenomenon in which the direction of pitch change was that of the missing fundamental.

The additional tests given to cat 2 show a further parallel with results in humans. In the "opposition" situation where a correct response requires attention to the missing fundamental cue, performance declined progressively as the center frequency was raised, until at 6 kHz it was apparently completely absent. In humans there is a similar decline in the strength of the fundamental pitch over about the same range (e.g., Schouten, 1970).

The entirely similar decline in performance by cat 2 when the triads and the missing fundamental moved in the same direction suggests that the animal was unable to switch from the fundamental to the triad frequencies as the former declined. This further suggests that the animals were not using the triad frequencies in any of the experimental situations, but that they always heard the pitch in the earlier experiments as corresponding to that of the missing fundamental.

It is necessary, of course, to consider the possibility that while there was no detectable external signal below 1 kHz, the animals could have been responding to an intra-aurally generated difference tone. Plomp (1965) found that in man a difference tone of 400 Hz in the missing fundamental situation was just detectable when the intensity of the harmonics forming the complex reached a level of about 70 dB SPL, there being a good deal of scatter between subjects. It is, however, begging the question to use human data in this context and some internal evidence is to be preferred. We suggest that this might come also from the experiments with higher center frequencies. Had the animals been responding to difference tones, they might well have been expected to do so whether these were generated with a 2- or a 5-kHz center frequency. To account for their actual behavior in such circumstances, it would be necessary to postulate that the way the cat ear generates difference tones happens to decline with generating frequency in just the same way that the missing fundamental declines in man. A more realistic conclusion is that the animals were not able to use difference tones to solve the problem.

The discovery that cats may be able to perceive the missing fundamental is encouraging for the study of auditory processing, because it suggests that the auditory system of cats is similar in this respect to the human auditory system. As a result, it may be possible to compare the extensive data concerning periodicity pitch gathered through psychophysical studies on humans with the physiological data concerning the auditory system obtained in the cat. Such comparisons can then be used to determine the physiological mechanisms which underlie the psychological phenomena of hearing. Though further investigation is needed to establish that the phenomenon observed in cats is identical in every respect to that in man, we have at this time no reason not to believe that cats do indeed perceive the missing fundamental.

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Butler, R. A. (1972). "The auditory evoked response to stimuli producing periodicity pitch," Psychophysiology 9, 233–237.

Heffner, R., Heffner, H., and Masterton, B. (1971). "Behavioral measurements of absolute and frequency-difference thresholds in guinea pig," J. Acoust. Soc. Am. 49, 1888–1895.

Hind, J. E. (1972). "Physiological correlates of auditory stimulus periodicity," Audiology 11, 42–57.

Kiang, N. Y-S., and Goldstein, M. H. (1959). "Tonotopic organization of the cat auditory cortex for some complex stimuli," J. Acoust. Soc. Am. 31, 786–790.

Plomp, R. (1965). "Detectability threshold for combination tones," J. Acoust. Soc. Am. 37, 1110–1123.

Plomp, R., and Smoorenburg, G. F., Eds. (1970). *Frequency Analysis and Periodicity Detection in Hearing* (Sijthoff, Leiden, The Netherlands).

Schouten, J. F., (1970). "The residue revisited," in *Frequency Analysis and Periodicity Detection in Hearing*, edited by R. Plomp and G. F. Smoorenburg (Sijthoff, Leiden, The Netherlands), pp. 41–54.

Schouten, J. F., Ritsma, R. J., and Cardozo, B. L. (1962). "Pitch of the residue," J. Acoust. Soc. Am. 34, 1418–1424.

Siegel, S. (1956). *Nonparametric Statistics* (McGraw-Hill, New York).

Small, A. M. R., and Gross, N. B. (1962). "Response of the cerebral cortex of the cat to repetitive acoustic stimuli," J. Comp. Physiol. Psychol. 55, 445–448.

Whitfield, I. C. (1970a). "Neural integration and pitch perception," in *Excitatory Synaptic Mechanisms*, edited by P. Andersen and J. K. S. Jansen (Universitetsforlaget, Oslo), pp. 277–285.

Whitfield, I. C. (1970b). "Can nerve impulse periodicity be used for pitch perception?" in *Ciba Foundation Symposium on Sensorineural Hearing Loss*, edited by G. E. W. Wolstenholme and J. Knight (Churchill, London), pp. 213–223.