Periodicity pitch perception and its upper frequency limit in cats

DAVID Y. CHUNG

Bioacoustics Laboratory, Eye and Ear Hospital, Pittsburgh, Pennsylvania 15213

and

FRANCIS B. COLAVITA

University of Pittsburgh, Pittsburgh, Pennsylvania 15213

We have established a procedure for behavioral assessment of periodicity pitch perception in the cat. This procedure requires the training of cats to make a differential response to two different pure tones, and then testing for the transfer of learning when complex stimuli known to produce periodicity pitch sensations in humans are substituted for the pure tones. Complex stimuli consisted of three to five harmonically related frequencies of the same amplitude and phase. Eight cats were the subjects of these experiments. Two of them were controls. It is demonstrated here that cats do perceive periodicity pitch. We also used this procedure to measure the upper frequency limit of periodicity pitch perception for two cats. The frequencies tested were 100, 200, 300, 400, 600, 800, 900, and 1,200 Hz. The data indicate that the upper frequency limit of periodicity pitch perception in the cat is on the order of 600 to 800 Hz. There is a trend of decreasing prominence of the perception of periodicity pitch as the component frequencies are increased. These results are parallel to the human psychophysical data.

The phenomenon of periodicity pitch perception has had a long history in human psychophysics (Bilsen & Ritsma, 1969). Periodicity pitch is a low-pitched percept experienced when listening to certain periodic complex tones comprising only higher frequencies. The existence region of periodicity pitch in human observers has been mapped by Ritsma (1962, 1963). He referred to it as residue pitch. A comprehensive review on the psychophysical aspects of this phenomenon can be found in Wightman and Green (1973). Several electrophysiological studies of periodicity pitch have been done on cats (Glattke, 1969; Goldstein, Ribanpierre & Yeni-Komshian, 1971). These studies assumed that cats perceive periodicity pitch, although at the time there was no behavioral evidence to support this assumption. Now, a recent experiment (Heffner & Whitfield, 1976) has apparently provided a behavioral demonstration of periodicity pitch in two cats.

The purpose of the present experiment was two-fold: first, to extend the observations of Heffner and Whitfield, using a larger number of animals and a different behavioral procedure, and second, given that our first purpose was achieved, to measure the upper frequency limit of periodicity pitch in the

cat in order to compare it with the upper limit in human observers.

METHOD

Subjects

Eight healthy adult cats with no obvious hearing loss were used as subjects for these experiments.

Behavioral Training

All behavioral training was carried out in a double-grill box shock-avoidance situation. Test stimuli were either pure-tone pairs or complex-tone pairs. Animals were trained to cross from one side of the double-grill box to the other side on hearing the tone or the complex with the higher pitch of the pair of tones or complexes which were to be discriminated. Failures to respond to the presented stimulus with the higher pitch resulted in the animal's receiving footshock through the bars of the box until a crossing response was made. Crossing responses made in the absence of the stimulus with higher pitch were also punished with footshock. Tonal intensities throughout training were varied to insure that intensity differences could not serve as a cue.

Stimuli

There were basically two kinds of stimuli. One kind was pure tones, and the other was complex tones. The complex tones consisted of three to five successive harmonics of the same phase and amplitude. The component frequencies of the complexes are shown in Table 1. A and B were the pure-tone pairs, and complexes L and H are known to produce periodicity pitch perception in human listeners corresponding to pure tones A and B, respectively. The complexes were generated digitally by a PDP-15 computer and a waveform generator (Wolf & Bilger, 1972). They were then recorded on tape for later use during the training of the animals. The spectra of the complexes were analyzed with a Hewlett-Packard 3581 A wave analyzer with a graphic display. The levels

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Table 1
Frequencies of the Components of the Complexes

	L ₁	H ₁	L ₂	H ₂	L ₃	H ₃	L ₄	H ₄
100	800	800	1800	1800	2800	2800	3800	3800
vs.	1000	1200	2000	2200	3000	3200	4000	4200
200	1100		2100		3100		4100	
	1200		2200		3200		4200	
200	1200	1200	2400	2400	3600	3600	4800	4800
vs.	1400	1500	2600	2700	3800	3900	5000	5100
300	1600	1800	2800	3000	4000	4200	5200	5400
	1800		3000		4200		5400	
400	2400	2400	3600	3600	4800	4800		
vs.	2800	3000	4000	4200	5200	5400		
600	3200	3600	4400	4800	5600	6000		
	3600		4800		6000			
	2400	2400	4800	4800				
600	3000	3200	5400	5600				
vs.	3600	4000	6000	6400				
800	4200	4800						
	4800							
900	3600	3600						
vs.	4500	4800						
1200	5400	6000						
	6300							

Note—Numbers are in Hertz. L and H are the low- and high-pitched complexes, respectively.

of the complexes were kept below 50 dB SPL, as measured in the 24 locations in the double-grill box by a Bruel and Kjaer sound-level meter, Type 2203, with an octave filter, Type 1613. The levels of the pure tones were kept below 65 dB SPL. The stimuli were presented in sets of four pulses. Each pulse was 1.5 sec in duration with a 1.0-sec interpulse interval. The rise and fall time was 25 msec. The intertrial interval was varied from 5 to 10 sec. Ten of each of the two stimuli were presented haphazardly in each session over a KLH Model 14B speaker placed beside the double-grill box. Both the double-grill box and the speaker were located in a sound-shielded room (Industrial Acoustics Corporation).

Procedure

Experiment 1: Periodicity pitch perception in cat. Cats were initially trained to cross from one compartment of the double-grill box to the other on hearing a train of four pulses of a 300-Hz tone. Failures to cross were punished with footshock. Animals were given 20 trials per session, and were trained until they reached a criterion of 90% correct or better. They were then trained to remain in one compartment in the presence of a train of four 200-Hz tone pulses, but to make a crossing response in the presence of a train of four 300-Hz tone pulses. Failures to respond to the 300-Hz pulses were punished with footshock, as were any crossing responses made in the absence of 300-Hz pulses. The above training was carried on at the rate of 2 sessions/day until the cats reached criterion for two successive sessions. Then the complexes L₁ and H₁ were substituted for the 200- and 300-Hz pure tones, respectively. After the performance on the L₁ and H₁ discrimination was assessed, the animals were tested with L₂ and H₂. It was felt that the degree of transfer shown between training on the pure tones and testing with the complex tones would provide a behavioral measure of periodicity pitch perception. Two additional cats, Joseph and Tino, were first given avoidance training on the L₁ vs. H₁ and L₂ vs. H₂ complex-tone pairs and then tested for response transfer to pure tones. After being tested on the 200- vs. 300-Hz pure tone discrimination, Joseph was trained on 600 vs. 1,000 Hz and Tino on 100 vs. 200 Hz. This was done as a control procedure to see whether any transfer of

learning would occur to novel tone pairs as a function of original training.

Experiment 2: Upper frequency limit of periodicity pitch perception in cat. Two cats were tested in this part of the study. Their periodicity pitch perception was tested by the same procedure described in the above section for frequency pairs 100 vs. 200 Hz, 200 vs. 300 Hz, 400 vs. 600 Hz, 600 vs. 800 Hz, and 900 vs. 1,200 Hz. The component frequencies of the complex stimuli that generated periodicity pitch corresponding to the frequency pairs are shown in Table 1. The two cats were first trained to discriminate A and B. After they reached criterion, they were tested for the transfer of learning from A vs. B to L₁ vs. H₁, L₂ vs. H₂, and so on until the complex pair with the highest frequencies shown was reached. For example, for the 100- vs. 200-Hz pure-tone pair, the transfer of learning was tested first for L₁ vs. H₁, then for L₂ vs. H₂, L₃ vs. H₃, and finally L₄ vs. H₄.

RESULTS

Positive transfer of the discrimination was demonstrated in all eight cats. This transfer is consistent with the cats responding on the basis of the periodicity pitch of the complex tones. The results can be seen in Table 2. It is clear that there are considerable savings in training the cats to discriminate the complex-tone pairs after they were trained to discriminate the pure-tone pairs. The amounts of savings in percentages are also shown in Table 2. Tino and Joseph were control animals. The sequence of the stimulus pairs for discrimination training for these control cats was L₁ vs. H₁, L₂ vs. H₂, and A vs. B. The percentage of savings in the control cats was calculated from the number of trials for L₁ vs. H₁ and the number of trials for A vs. B.

The results show that the savings for all animals for the transfer of learning from A vs. B to L₁ vs. H₁ were 50% or above. Savings were as high as 86% for Scotty. At first glance, the savings for the transfer from L₁ vs. H₁ to L₂ vs. H₂ appear to be difficult to interpret. In comparing the percentages shown in Table 2, it can be seen that the two cats, Scotty and Glen, which had -50% and 0% in savings, respectively, also took only 40 trials and 60 trials to reach criterion in the L₁ vs. H₁ discrimination. Since

Table 2
Number of Trials to Reach Criterion and Percentage of Savings from Transfer of Learning

Cat	Number of Trials to Criterion			% of Savings	
	A/B	L ₁ /H ₁	L ₂ /H ₂	A/B-L ₁ /H ₁	L ₁ /H ₁ -L ₂ /H ₂
Jerzy	540	160	20	70%	88%
Russell	560	280	180	50%	36%
Scotty	280	40	60	86%	-50%
Glen	320	60	60	81%	0%
Barney	480	140	100	71%	29%
Caesar	400	180	0	55%	100%
Tino*	60	380	60	84%**	84%
Joseph*	80	380	40	79%**	89%

*Joseph and Tino are control animals.

**Percentages were calculated on savings from L₁/H₁ to A/B instead of that indicated.

there is a certain amount of timbre difference between L_1 vs. H_1 and L_2 vs. H_2 , the transfer of learning is not expected to be instant. Taking three additional sessions (60 trials) for them to reach criterion for L_2 vs. H_2 after learning L_1 vs. H_1 seems to be reasonable. The savings in learning from L_1 vs. H_1 to L_2 vs. H_2 in Tino and Joseph, however, reflect more in savings due to pitch identity than to differences in timbre. The savings were 84% and 89% for Tino and Joseph, respectively. These values are significantly higher than the average of the savings in transfer of A vs. B to L_1 vs. H_1 in the other six cats. The average is 69%. This is consistent with the fact that the timbre between the complexes themselves is not as different as the timbre differences between the complexes and the pure tones as judged by human observers.

The percentages of savings in the transfer of learning from the complexes to the pure tones in the control animals were calculated from the number of trials of L_1 vs. H_1 to the number of trials of A vs. B. For these control cats, pure-tone discrimination training for other frequency pairs was run after testing for 200 vs. 300 Hz. Joseph was tested with 600 vs. 1,000 Hz, while Tino was tested for 100 vs. 200 Hz. After training for 160 trials, Joseph was still at chance level, and Tino took 260 trials to reach criterion. These data appear to eliminate the possibility that rapid new learning was the source of the savings seen in the other animals. Since rapid new learning is unlikely to be the cause of the savings in transfer, it can reasonably be assumed that the savings are due to the identity in pitch between pure tones and complexes. The mean savings in the column "A/B- L_1/H_1 " of Table 2 is 72%. In testing this with the t test, a significant difference is obtained with $p < .01$.

Two of the eight cats were used to test for the upper frequency limit of periodicity pitch perception. These results are summarized in Table 3. The results in this part of the study confirm those of the first part. There were tremendous savings in the transfer of learning from pure-tone pairs to complex-tone pairs. This is evident in Table 3 for frequency pairs

100 vs. 200 Hz and 400 vs. 600 Hz. For the 600- vs. 800-Hz pair, there was savings in learning in Glen, but no transfer in Tino from pure-tone pair to complex-tone pair. However, in the transfer of L_1 vs. H_1 to L_2 vs. H_2 for Tino, there seems to have been some slight but definite transfer. When the frequency pair was 900 vs. 1,200 Hz, transfer was absent in both animals. After 220 trials on the L_1 vs. H_1 pair, Glen still showed no improvement, although he had required only 180 trials to reach criterion for the original pure-tone discrimination. Tino definitely showed no periodicity pitch perception for the 900- vs. 1,200-Hz pair. After more than twice the number of trials as in the pure-tone pair, he was still at chance level for the L_1 vs. H_1 pair. This means not only that there is no transfer of learning, but also that it is difficult to discriminate the difference in any way between the two complexes. This supports the above statement that some transfer of learning occurred from L_1 vs. H_1 to L_2 vs. H_2 for Tino (L and H corresponded to 600 and 800 Hz, respectively). Notice, from Table 3, that there was a trend of increasing number of trials required to reach criterion as the component frequencies of the complexes were increased. If periodicity pitch was as prominent in L_4 and H_4 as in L_1 and H_1 , the cats should take less trials to learn L_4 vs. H_4 than L_1 vs. H_1 or, for that matter, for L_2 vs. H_2 or L_3 vs. H_3 . The trend here would imply that the periodicity pitch is getting less and less prominent as the component frequencies are increased. This is particularly noticeable for the L_4 vs. H_4 pair.

The results indicate that these cats were not capable of discriminating between the complexes which have periodicities of 900 and 1,200 Hz. If periodicity pitch was perceived at 900 Hz and not 1,200 Hz, the cats should easily respond correctly to the two complexes. Glen's performance showed obvious transfer of learning at periodicities of 600 and 800 Hz. Tino showed a lower limit than Glen, but the perception was in the same region. It therefore seems reasonable to put the upper frequency limit on periodicity pitch perception somewhere between 600 and 800 Hz.

Table 3
Number of Trials to Reach Criterion for the Different Stimulus Pairs

	Tino					Glen				
	A/B	L_1/H_1	L_2/H_2	L_3/H_3	L_4/H_4	A/B	L_1/H_1	L_2/H_2	L_3/H_3	L_4/H_4
100/200	260	0	40	80	140	140	80	40	60	120
200/300	100	20	0	60	100	320	60	60	60	80
400/600	300	100	100	140		340	0	60	100	
600/800	360	380	240			220	0	20		
900/1200	300	>620				180	>220			

Note—Only two animals, Tino and Glen, were run in this experiment. The numbers at the left column show frequencies of the pure-tone pairs for discrimination.

DISCUSSION

The data in the present study strongly indicate that cats perceive periodicity pitch. Such a finding permits comparison between human psychophysical data and electrophysiological findings on animals. The low sound levels used in the present study preclude the possibility of the perception of difference tone that is generated at medium and high levels, based on human psychophysical data (Hall, 1972). Although there is a possibility that cats have a lower level for the generation of difference tone than humans, it is highly unlikely that it could be so prominent that the cats could use it as a cue and could respond to it accordingly at such a high percentage of savings. The intermodulation distortion product measured for each complex at the fundamental frequency was 40 dB down from the primary components as measured by a wave analyzer. This means that the distortion product is at most 10 dB SPL. This is below the threshold of the cat at frequencies less than about 300 Hz (Neff & Hind, 1955). To further eliminate the remote possibility that difference tone or distortion products were serving a cue function, a masking experiment was done on two cats. The idea is that, if transfer of learning is due to the perception of either the difference tone or intermodulation distortion product due to the equipment system, then the cats should not be able to respond correctly if a low-frequency noise band is introduced at the region of the fundamental frequency, while the introduction of a high-frequency band of noise at the region of the primary frequencies should not change the correct response of a trained cat to the complex tones. Tino and Glen were trained to respond to both 300 Hz and the H_1 complex which was composed of 1,200-, 1,500-, and 1,800-Hz tones. After they were trained, a masking noise was introduced. There were two different masking noise bands. One was from 125 to 375 Hz, and the other was from 1,000 to 2,000 Hz. The low noise band should mask the 300-Hz pure tone, and the high noise band should mask the H_1 complex. Using the signal-to-noise ratio at masked threshold given by Watson (1963), the noise level required for masking was calculated. It was found that for both cats, when a high band of noise was the masker, they did not show any response for signal H_1 , but responded when the low noise band was used as masker. The reverse happened for the 300-Hz tone. These data support our assertion that cats perceive periodicity pitch.

In this study, there was a trend of increasing number of trials necessary to reach criterion as the component frequencies of the complexes were increased. This trend implies that the periodicity pitch was getting more and more obscure as the component

frequencies were increased. In this respect, the cat's data are consistent with the human data. However, the center frequency of 4,000 Hz for 100-Hz periodicity pitch and 5,000 Hz for 200-Hz periodicity pitch were somewhat higher than those found to produce periodicity pitch in human subjects (Ritsma, 1962). This might have been due to species differences or differences in the kinds of stimuli used. Ritsma used AM complexes, which when compared with the stimuli used in the present study, seemed weaker in the effect of generation of periodicity pitch.

Our upper frequency limit of periodicity pitch perception was in good agreement with the human data. The 600- to 800-Hz limit in cat is definitely close to the limit of 800 Hz reported by Ebata, Sone, & Nimura (1974) in humans. A finer resolution of frequency limit could be obtained if more frequency pairs in smaller frequency difference were employed. However, this would require thousands of trials more. The close correspondence between the cat behavioral data and the human psychophysical data is enough to lead one to believe that the cat does, in fact, perceive periodicity pitch in much the same way that human observers do.¹

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NOTE

1. As can be seen in Table 1, the L and H complexes contained different numbers of components. Thus it is possible that our cats were

discriminating L from H on this basis, and not on the basis of pitch differences. To test this possibility, we attempted to train one animal to discriminate between two complexes having a different number of components, but both producing a periodicity pitch of 400 Hz. After more than 600 trials, the animal was still performing at a chance level. This suggests that our cats were not respond-

ing on the basis of number of components in the L and H complexes. We are grateful to Dr. Irwin Pollack for pointing out this problem in our original procedure.

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