PAPER

Perception of missing fundamentals in zebra finches and Bengalese finches

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Perception of missing fundamental is widespread in vertebrate animals but seldom it is discussed with the relationship with vocal signals used by the animals. We tested the perception of missing fundamentals in two species of closely related finches with widely different vocal signals. Zebra finches and Bengalese finches were trained, in a Go-Nogo operant task, to discriminate between two harmonic complexes that were constructed by adding integer multiples of a 400 Hz or a 652 Hz. Both stimuli produced the perception of missing fundamentals to human listeners. After the birds learned the task, 4 sine waves, the fundamental frequency of each of the training stimuli and the geometric average frequency of each, were presented as probe stimuli along with the original training stimuli. Both species responded more to the missing fundamental of the Go stimuli than to that of Nogo stimuli. However, both species of birds responded more to the geometric averages of the stimuli than to the missing fundamentals. Thus, in these birds, the perception of the spectral pitch is dominant over the perception of the periodicity pitch and this tendency was not dependent upon the types of vocalizations each species produced.

Keywords: Missing fundamental, Periodicity pitch, Songbirds, Zebra finch, Bengalese finch

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1. INTRODUCTION

The perception of the 'missing' fundamental is one of the most essential properties of the human auditory system (Green, 1976). When we hear a complex sound that is constructed by adding integer multiples of a fundamental frequency, our psychological pitch corresponds to the fundamental frequency even if that part is physically missing from the stimulus. This auditory mechanism gives us the constancy of perceptual pitch for musical sounds and human speech (de Boer, 1976).

Animal psychophysicists have been interested in whether or not animals perceive missing fundamentals. To date, the goldfish (Fay, 1970), cat (Heffner and Whitefield, 1976) and the starling (Cynx and Shapiro, 1986) have been shown to perceive missing fundamentals. Seldom, though, the results were discussed in relation to the vocal signals animals use in communication.

Songbirds heavily rely on acoustic signals for their communication (Kroodsma and Miller, 1996) and each songbird species has unique acoustical properties in their vocalizations. Since the perception of missing fundamentals has been studied only in the starling (Cynx and Shapiro, 1986), more species with different acoustic signals should be studied to discuss the relationship between pitch perception and vocal signals.

For this purpose, we tested pitch perception in

two songbird species with closely related phylogeny and very different vocal morphology. We selected the zebra finch (*Taeniopygia guttata*) and the Bengalese finch (*Lonchura striata* var. *domestica*), both belonging to the family Estrildidae. Most of elements in zebra finch vocalizations are made up by harmonic complexes (Williams *et al.*, 1989). On the other hand, only a part of elements have such structure in Bengalese finch vocalizations (Okanoya, 1997). This species difference in acoustic characteristics of the vocalizations should make the comparison interesting. Specifically, we predict that the zebra finch should rely more on the residual pitch than to the spectral pitch while the Bengalese finch should rely less to the residual pitch.

2. METHOD

2.1 Subjects

Birds were obtained from local pet suppliers and kept in an aviary under a fixed 14L10D cycle. Ambient temperature of the aviary was maintained around 24°C and relative humidity was around 60%. Four adult Bengalese finches (2 males and 2 females) were kept together in a cage (18 × 19 × 35 cm) while four adult zebra finches were each kept in a small cage (15 × 16 × 30 cm) to prevent fighting. Among these 8 birds, 6 birds (4 Bengalese finches and 2 zebra finches) were used in a previous operant experiment examining perception of species-specific distance calls (Okanoya and Kimura, 1993) utilizing a repeating background procedure (Okanoya and Dooling, 1988). During the week, birds were tested for six days and rested for one day. Food intake outside of experimental sessions was restricted to 60 min/day for Bengalese finches and 30 min/day for the zebra finches. This feeding schedule maintained birds at 85~90% of their free feeding weights. In addition to the birds, 4 humans (2 males and 2 females, 25–33 years old) participated in the experiment.

2.2 Apparatus

Birds were tested in a small wire cage attached on a panel placed in a sound proof room. A response panel consisting of two sensitive microswitches with attached light emitting diodes (LEDs; green and red) was mounted just above the food hopper opening. A wooden perch was placed in front of the food hopper opening. The bird could trip the microswitch by pecking the LED. Stimuli were generated by a digital-to-analog converter (DAC; Data Translation, DT2801A). The output of the DAC was lowpass filtered at 10 kHz for anti-aliasing, sent to a 1/3 octave graphic equalizer, amplified and transduced by a loud speaker mounted inside the sound proof room. Sound calibration was performed by placing a 1/2 inch microphone (ACO model 7012) attached to a preamplifier (ACO model 4012) which was connected to a measurement amplifier (ACO model 6020). The microphone was placed in front of the LEDs. That was the location occupied by the bird's head during the experiment.

Humans were tested in the same sound proof room using the same apparatus. Two push switches were inserted in parallel to the operant circuit to detect human responses.

2.3 Stimuli

Sine waves were synthesized digitally. Harmonic complexes, each 200 ms long, were constructed by adding several sine waves. One training stimulus was synthesized by adding 6, 7, 8, and 9th harmonics of a 400 Hz sinusoid (400 Hz missing fundamental complex; 400 MFC). The other training stimulus was constructed by adding 2, 3, 4, and 5th harmonics of a 652 Hz sinusoid (652 MFC). These two stimuli were the same as that used in Cynx and Shapiro (1986). These two stimuli had a wide range of overlap; 400 MFC ranged from 2,400 Hz to 3,600 Hz and 652 MFC ranged from 1,304 Hz to 3,260 Hz. In addition to the harmonic complexes, pure tones of 652 Hz (652 Hz fundamental; 652 F), 400 Hz (400 F), 2,158 Hz (the geometric average of the component frequencies of the 652 MFC; 652 GA) and 2,966 Hz (the geometric average of the component frequencies of the 400 MFC; 400 GA). All stimuli were gated by a 10 ms rise/fall. Narrowband (150 Hz) sound spectrograms of these stimuli are shown in Fig. 1.

The sound pressure level for the presentation of each stimulus was determined by considering the audiograms of the zebra finch and the Bengalese finch (Hashino and Okanoya, 1989; Okanoya, 1996). The two species have similar audiograms. Each of the stimulus components was set at 20–40 dB higher than the absolute threshold of the finches at that frequency, resulting in the sound pressure levels between 60 and 80 dB SPL.
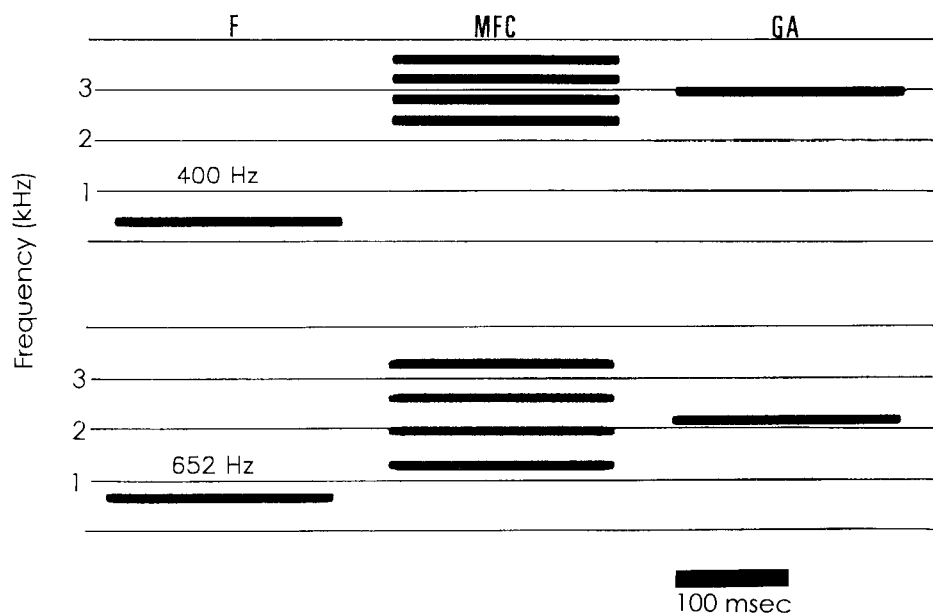
Harmonic distortion products of the 400 Hz and

Fig. 1 Soundspectrograms of the stimuli used in this experiment. Abbreviations: MFC, missing fundamental complex; F, fundamental; GA, geometric average. Upper row: 400 F, 400 MFC, 400 GA. Lower row: 652 F, 542 MFC, 652 GA. Each stimulus is 200 ms long.

652 Hz stimuli were at most 40 dB lower than the original stimuli. Furthermore, none of the four probe stimuli (Fig. 1) had energy at fundamental frequencies significantly exceeding background noise levels and these levels were at most 40 dB lower than the original stimuli (measured by a RION NA-27 sound level meter with 1/3 octave band filter).

After final data collection was complete, another test session was repeated on one of the Bengalese finch subjects with the sound pressure level of each stimulus randomized by 10 dB for each presentation. This effectively removed the sound pressure level as a cue for the discrimination. The result was the same as when the level of each stimulus was fixed. Although no zebra finch subject was tested with this control, we at least know that zebra finches do not rely on sound pressure level under a task similar to the present one (Okanoya and Dooling, 1991).

2.4 Discrimination Training

A standard Go-Nogo procedure was used to train the birds (Okanoya, 1996). A trial was initiated by illuminating the green observation key. When the bird pecked the observation key, the key was immediately turned off. After 50 ms (an interval inserted to prevent possible masking of the stimuli by a key pecking noise), one of the harmonic complex was presented twice with a 200 ms inter presentation interval. If the subject bird pecked the key during presentation of the stimulus, the trial was aborted and the same trial was repeated. This procedure ensured that the bird listened to the stimulus in full length.

After the presentation of the stimulus, the red report key was illuminated for 2 s. If the sound presented was a 'Go' stimulus and the bird pecked the key during this interval, the key light was immediately turned off and the feeder and the feeder light was activated for 3 s (Hit). If, on the other hand, the sound presented was 'Nogo' and the bird pecked the key, all illumination in the sound proof room was immediately extinguished for 16 s (False Alarm). If no response occurred during the 2 s interval following the stimulus presentation, testing proceeded to the next trial.

The two harmonic complexes were presented in a random order with a restriction that the same stimulus was never presented for more than 4 trials in a row. One training session consisted of 50 presentations of the 'Go' stimulus and 50 presentations of the 'Nogo' stimulus. Either the 652 MFC or the 400

MFC was the 'Go' stimulus for each of the subject, with the stimulus and the sex of the subject counter balanced. A correct percent was defined as an average of a percent hit and a percent correct rejection (no peck for the 'Nogo' stimulus). Discrimination training was continued until the bird attained a level of performance of 90% correct for three successive sessions. For humans, only one training session was given and all humans attained more than 96% correct for the session.

2.5 Testing Procedure

Two test sessions, each consisting of 100 trials, were assigned. The first test session was conducted after the bird satisfied the training criterion. Before the second test session, training sessions were run until the 90% criterion was again satisfied.

A test session proceeded by a block of 10 trials. The training stimuli were delivered on 6 trials (3 Go, 3 Nogo) in a block of 10 trials with the same contingency as the training sessions. For the remaining 4 trials, the four sine waves were presented as probe stimuli. After the presentation of a probe stimulus, the response of the bird was recorded but no reinforcement contingencies were in effect (*i.e.*, no food presentation or no time-out). These 10 trials were randomized in each block and a total of 10 blocks were presented in a session.

For humans, only one test session was given and the session occurred immediately after the training session. The experimenter's instruction to human subjects was to respond when the stimulus was 'similar' to the Go stimulus. We did not specify what was meant by being similar.

2.6 Data Analyses

2.6.1 Sessions required to reach criterion

The number of sessions required to reach the criterion was compared between Bengalese finches and zebra finches with a *t* test. Alpha smaller than 0.05 with two-tailed probability was required for the statistical significance.

2.6.2 Responses to the probe stimuli

Over the course of two test sessions, each sine wave probe was presented 20 times. Thus response rate to each of the probe stimulus was determined as a 5% precision. For the probe stimuli, response rates were compared between the fundamental (F) stimuli based on Go and Nogo stimuli, and between the geometric average (GA) stimuli based on Go

and nogo stimuli. For the comparisons, the paired *t* test was used. Alpha was originally determined to be 0.05, but since two *t* tests were run for each animal species, alpha was adjusted using a Bonferroni criterion to be $0.05/2 = 0.25$ (two-tailed probability).

2.6.3 Species comparisons

For each of the probe stimuli, performance of each animal was described by an index of detectability, or, d' based on the signal detection theory (Green, 1976). In doing so, we defined that 'hit' rate to be the Go response rate to the stimulus based on the Go stimulus and 'false alarm' rate to be the Go response rate to the stimulus based on the Nogo stimulus. Difference in d' was compared between Bengalese finches and zebra finches for each types of the stimuli by an independent *t* test. Two *t* tests were run for the two types of the probe stimuli. Thus alpha was set to be 0.025 (two-tailed).

3. RESULTS

3.1 Discrimination Training

On average, Bengalese finches required 20.75 sessions (range 15–26 sessions) and zebra finches required 16.00 sessions (range 10–21 sessions). Bengalese finches and zebra finches learned these discriminations with a similar degree of efficiency ($t = 1.306$, $df = 6$, $p = 0.120$).

3.2 Probe Testing

The response tendency of the humans is depicted in Fig. 2. For missing fundamentals, humans re-
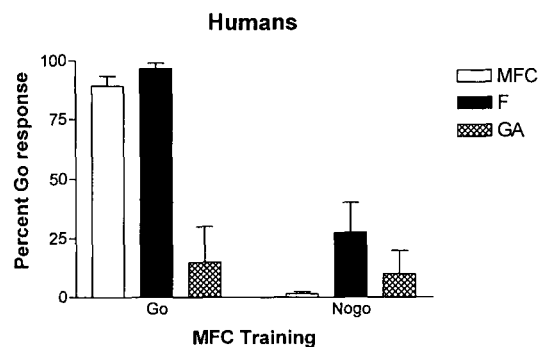

Fig. 2 Four human subjects' performance on the test sessions. Graph compares Go responses to each probe stimulus and training stimulus. Abbreviations are the same as Fig. 1.

sponded more to the stimulus based on the Go stimulus than that based on Nogo stimulus (97% versus 28%; $t=6.537$, $p=0.004$). For geometric averages, response rates were below 20% for both of the stimuli and the difference was not significant ($t=1.000$, $p=0.197$).

Figure 3 shows the data of the Bengalese finches. For missing fundamentals, Bengalese finches responded more to the stimulus based on the Go stimulus than that based on Nogo stimulus (55% versus 10%; $t=3.669$, $p=0.018$). For geometric averages, response rates were larger for the stimulus based on the Go stimulus (75% versus 50%), but the difference was only marginally significant ($t=1.704$, $p=0.094$).

The data obtained from zebra finches are described in Fig. 4. For missing fundamentals, zebra finches responded significantly more to the stimulus based on the Go stimulus than that based on Nogo stimulus (55% versus 22%; $t=3.286$, $p=0.022$). For geometric averages, response rates were above 50% for both of the stimuli and the difference was not significant ($t=0.174$, $p=0.436$).

3.3 Species Comparisons

For fundamental frequencies (Fs), Bengalese finches had higher d's than zebra finches (1.678 and 0.895 ; $t=1.749$, $p=0.065$). Also for geometric averages, Bengalese finches had a higher d' than zebra finches (0.849 and 0.005 ; $t=1.555$, $p=0.085$). But these differences were only marginal.

4. DISCUSSION

The present study demonstrated that the two species of finches perceived the missing fundamental. However, despite the differences in vocal signals, we did not find any species differences in the perception of residual and spectral pitches.

4.1 Hearing and Vocalizations in Zebra Finches

Vocalizations of the zebra finch are rich in harmonics (Williams *et al.*, 1989). Often the fundamental of their vocalizations are very weak or totally missing (Williams *et al.*, 1989). Since fundamental frequencies utilized by zebra finches are relatively low (0.5~1.2 kHz ; Okanoya *et al.*, 1993 ; Simpson and Vicario, 1990), and such low fundamental is difficult to hear (Dooling, 1982) and produce for a small bird (Greenwalt, 1968), actual fundamental frequencies could be an irrelevant information for zebra finches. Thus, zebra finches might not use the residual pitch in making discrimination among different vocal signals. However, our present data suggest that this is not the case ; the present data could most well be understood that zebra finches are listening to the missing fundamentals when discriminating between two harmonic complexes with missing fundamentals. There are several evidences that zebra finches are able to discriminate between two harmonic complexes that had different harmonics attenuated. This suggests that they are able to hear differences in timbres (Cynx *et al.*, 1990 ; Okanoya, 1997 ; Willimas *et al.*, 1989). The present study also suggested, in addition to the timbre information, zebra finches might rely upon the spectral pitch as evident from the response to probe stimuli.
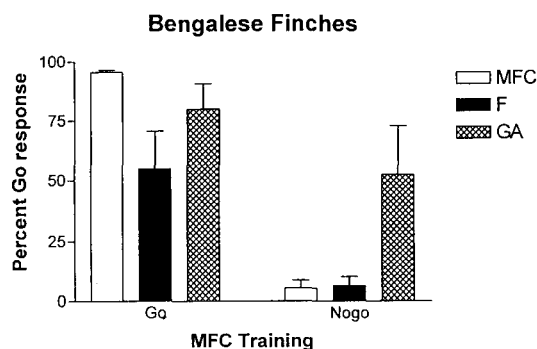
Bengalese Finches

Fig. 3 Performance of Bengalese finches on the test sessions. Graph compares Go responses to each probe stimulus and training stimulus. Abbreviations are the same as Fig. 1.
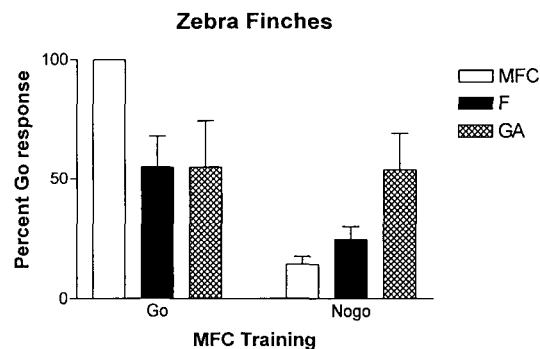
Zebra Finches

Fig. 4 Performance of zebra finches on the test sessions. Graph compares Go responses to each probe stimulus and training stimulus. Abbreviations are the same as Fig. 1.

4.2 Hearing and Vocalizations in Bengalese Finches

In a recent investigation (Okanoya and Kimura, 1993) we revealed that Bengalese finches may be using 'difference tone' in discriminating among distance calls of conspecific females. Although distance calls of the female Bengalese finch do not contain harmonic structures, these vocalizations have two spectral peaks. In an operant discrimination task Bengalese finches classified female distance calls according to the differences of the two peaks. Of course, this demonstration does not directly leads to the conclusion that Bengalese finches are perceiving the missing fundamental in their distance calls, since the perception of missing fundamental and difference tones do not share common mechanisms (Green, 1976). Our present data simply suggest that in addition to difference tones, Bengalese finches also perceive missing fundamentals.

5. CONCLUSION

In conclusion, species differences in the acoustics of the vocal signals did not lead to the species differences in the perception of missing fundamentals. Perception of missing fundamentals may rather be one of the most fundamental properties of the vertebrate auditory system that is independent of the acoustic patterns of species-specific vocal signals.

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