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Detection of Changes in Timbre and Harmonicity in Complex Sounds by Zebra Finches (*Taeniopygia guttata*) and Budgerigars (*Melopsittacus undulatus*)

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Thresholds for detecting alterations in the timbre and harmonicity of complex harmonic signals were measured in zebra finches, budgerigars, and humans. The stimuli used in this experiment were designed to have particular salience for zebra finches by modeling them after natural zebra finch calls. All 3 species showed similar abilities for detecting an amplitude decrement in a single component of a harmonic complex. However, zebra finches and budgerigars were extraordinarily sensitive to the mistunings of single harmonics and exhibited significantly lower thresholds compared with humans at 2 different fundamental frequencies, 570 Hz and 285 Hz. Randomizing relative phases of components in a harmonic stimulus resulted in a significant increase in threshold for detecting mistunings in zebra finches but not in humans. Decreasing the duration of mistuned harmonic stimuli resulted in higher thresholds for both birds and humans. The overall superiority of birds in discriminating inharmonicity suggests that birds and mammals may use different strategies in processing these complex harmonic sounds.

In spite of a long history of speculations to the contrary, including arguments from both anatomical and ethological perspectives (see, e.g., Pumphrey, 1961), carefully controlled psychoacoustic studies of hearing in birds over the last several decades have failed to find evidence of unusual temporal resolving power in birds. These traditional tests usually involve fairly simple sounds and include temporal integration (Dooling, 1979; Dooling & Searcy, 1985; Klump & Maier, 1990; Okanoya & Dooling, 1990b); duration discrimination (Dooling & Haskell, 1978; Maier & Klump, 1990); gap detection (Klump & Maier, 1989; Okanoya & Dooling, 1990a); and detection of amplitude modulation (Dooling & Searcy, 1981; Klump & Okanoya, 1991). Psychoacoustic tests with more complex stimuli such as vocalizations, however, frequently uncover evidence of perceptual specializations. We know, for instance, that auditory perceptual capabilities in birds are, in general, spectrally matched to the natural acoustic range of calls that a particular species produces, and there can be species specializations in perception beyond this level. For instance, zebra finches (*Taeniopygia guttata*), budgerigars (*Melopsittacus undulatus*), and canaries (*Serinus canarius*) each show an enhanced ability to discriminate among calls of their own species (Dooling, Brown, Klump, & Okanoya, 1992; Okanoya & Dooling, 1991).

The present experiments focus primarily on zebra finches and the harmonic vocalizations that they produce, and they examine the perception of synthetic, complex sounds modeled after these natural vocalizations. Zebra finches are small, colonial songbirds that are faced with the problem of learning and discriminating between the complex harmonic calls and songs of many conspecifics. Naturally occurring zebra finch calls consist of a series of tones of different amplitudes at integer intervals of a fundamental (see Figure 1). The zebra finch "distance" call is one of the longest, loudest, and most ubiquitous vocalizations given by these birds in captivity (Blaich, Kovacevik, Tansinsin, Van Hoy, & Syud, 1995) or in the wild (Zann, 1984, 1996). Synthetic complex harmonic stimuli provide a means of simulating the natural properties of harmonic bird vocalizations. Here we use this method to measure basic sensitivities to certain features of harmonic stimuli as a basis for later experiments examining the relation between production of specific features of natural vocalizations and species-specific perceptual processes.

Aside from offering insight into species-specific enhancements for the processing of bird songs, the present experiments also are relevant to historical issues of time coding in the auditory system. In the vertebrate auditory system, neural time codes are thought to be involved in a wide variety of sound qualities, such as pitch, music, phonetic identity, and timbre. There is a long history of theorizing on the ability of temporal discharges to convey information such as pitch and related percepts in both humans and animals (Evans, 1978; Licklider, 1951; Meddis & Hewitt, 1991; Schouten, 1940; Wever, 1949). Although the present

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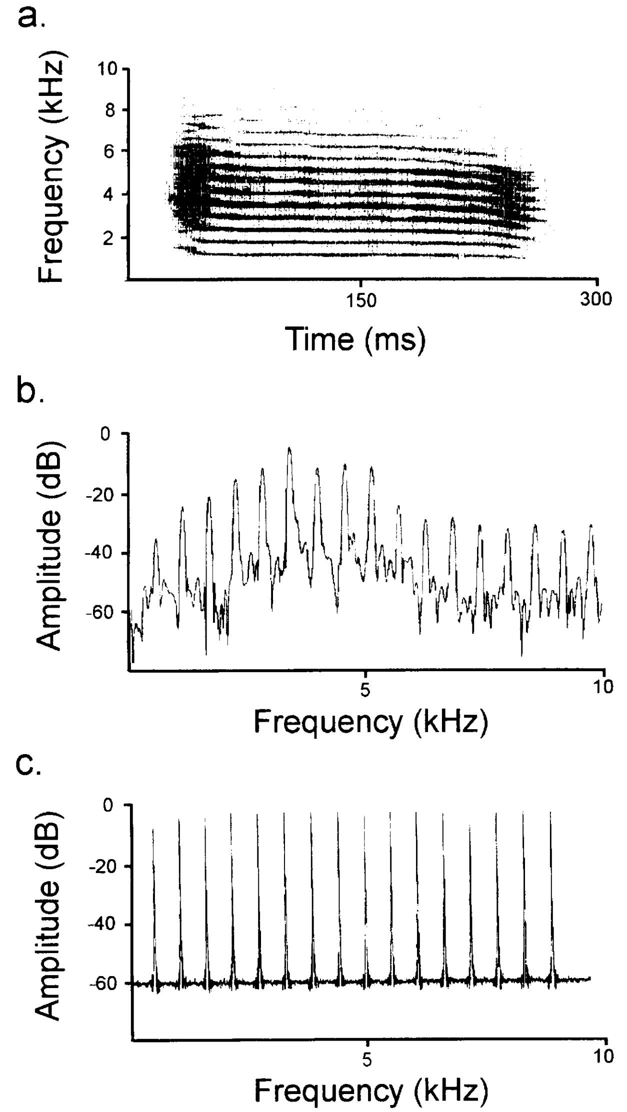

Figure 1. a. Sound spectrogram of female zebra finch distance call. b. Total power spectrum of female zebra finch distance call in Figure 1a. c. Power spectrum of complex harmonic tone used as a standard stimulus in these experiments. Note the general similarity of this stimulus to the spectrum of the natural zebra finch call.

experiments are the first to examine the perception of harmonicity in birds, the detection of changes in such tone complexes has been well-studied in humans (Green, 1988; Hartmann, McAdams, & Smith, 1990; Hillier, 1991; Moore, 1993). When discriminating "mistuned" harmonic complexes, human listeners may do so on the basis of a number of different cues (Hartmann, 1988). Listeners often report a mistuned harmonic as a separate entity to which they can assign a pitch (Hartmann, 1988; Moore, Glasberg, & Peters, 1986). Alternatively, they may identify a mistuned harmonic complex on the basis of several other cues, including a detection of "beats," "rolling," or "roughness" (Hartmann, 1988, 1997). The distinctions made between different types of cues depend on such features of the stimulus as harmonic frequency, amount of mistuning, and stimulus duration (Hartmann et al., 1990). These studies are very important in shedding light on the classic issue of spectral versus temporal processing in the vertebrate auditory system (Hartmann, 1996).

Birds are interesting subjects for studying comparative mechanisms of hearing because in tests with simple sounds they have shown many auditory abilities that are generally similar to those of humans (Dooling, 1982, 1991), yet there are substantial anatomical differences between the mammalian and avian cochleas (Manley & Gleich, 1992). The harmonic complexity of some bird songs and calls has been an obstacle to synthesis so that much less is known about the abilities of birds to discriminate changes in such sounds. Male and female zebra finches, for instance, produce different distance calls, and there is evidence that these differences involve learning and changes in neuronal control on the part of the males (Simpson & Vicario, 1990). Males that have received central lesions in song control nuclei produce female-like calls. Because of the relatively simple harmonic structure and elemental nature of the female call, we focused on this call as the standard for our harmonic stimuli, and we proceeded to test the bird's ability to discriminate among these stimuli.

In Experiment 1 we determined thresholds for detecting changes in amplitude of a single component of a complex harmonic stimulus for zebra finches, budgerigars, and humans. Budgerigars were used as a nonsongbird control and human subjects as a nonavian control. Further tests were performed to determine difference limens for frequency change in individual harmonics of a complex stimulus. These tests were performed at two different fundamental frequencies, one with a fundamental characteristic of zebra finch distance calls (570 Hz) and the other within the range of fundamental frequencies typical of human speech (285 Hz). In addition, Experiment 4 determined detection thresholds for stimuli with components at different relative phase angles and for stimuli of two different durations. Results from these experiments demonstrate the similarities and differences of the perceptual abilities in these different species.

General Method

Apparatus and Procedure

Birds were tested in a small-animal operant-conditioning chamber. The design and set up of this apparatus has been described previously (Dooling & Okanoya, 1995; Okanoya & Dooling, 1988, 1991; Park, Okanoya, & Dooling, 1985). In brief, birds were tested in a 25 cm × 25 cm × 25 cm wire cage mounted in a sound-attenuated chamber. One side of the cage was modified to accommodate a custom-built response panel consisting of two sensitive microswitches with light emitting diodes (LEDs) attached. The left microswitch served as an observation key, and the right microswitch served as a report key. Experimental events were controlled with an IBM 486/66 microcomputer.

Sound stimuli were generated digitally using the SIGNAL digital signal processing and synthesis software (Beeman, 1996) and stored on a hard disk. During an experiment these stimuli were output through a Tucker-Davis Technologies (Gainesville, FL)

DD1 stereo analog interface at 40 kHz, low-pass filtered at 8.5 kHz, sent through an amplifier and finally to a loudspeaker mounted 40 cm above the bird's head in the operant chamber. Stimuli were normalized to a level of 65 dB sound pressure level (SPL) root-mean-squared (RMS). Sound calibration was accomplished by placing the ½ inch microphone of a General Radio (Concord, MA) Model 1982 sound-level meter in the position normally occupied by the bird's head.

The birds were tested in the presence of a repeating background of the same sound. All stimuli were played at a rate of 1.67/s (cycle length of 600 ms). Birds were trained to peck one LED (observation key) repeatedly during the repetitive presentation of one sound (the background) until this sound was alternated with a new sound (the target). The birds were then required to peck the other LED (report key) when they detected this alternating sound pattern to obtain food. The initiation of the alternating pattern of target and background could not be predicted because it was randomized over 1–6 s following the first peck on the observation key. A peck on the report key within 2 s of this alternating stimulus pattern was defined as a correct response and was rewarded with a 2-s access to food. If the subject failed to peck at either the observation key or the report key within 2 s of the initiation of the alternating sound pattern, the trial was automatically ended and a new trial was begun.

Birds were tested in 100-trial sessions once or twice each day. Each block of 10 trials contained 7 target stimuli and 3 sham trials (during which the background stimulus was presented as a target). Targets consisted of incremental changes, or steps, of equal size. Responses during sham trials provided a measure of false alarm rate. A peck at the report key during a sham trial was punished with a 5-s timeout period during which lights in the test chamber were extinguished.

We used the method of constant stimuli for determining thresholds (Dooling & Okanoya, 1995; Gulick, Gescheider, & Frisina, 1989). Thresholds were defined as the stimulus value corresponding to a 50% correct, a corrected 50% correct, and a d' of 1.5 (Dooling & Okanoya, 1995; Gescheider, 1985). Thresholds corrected for false alarm rates were determined by $Pc^* = (Pc - FA)/(1 - FA)$, where FA = false alarm, Pc = percent correct, and Pc^* = corrected percent correct. In our experiments, false alarm rates were generally low (<20%), so there was little difference between these values. Sessions in which false alarm rates exceeded 20% were not included in our analysis. Therefore we used a 50%-correct value for our thresholds. Birds were tested repeatedly until threshold values showed no further improvement, defined as two successive 100-trial blocks in which the threshold was within ±⅓ the step size, typically resulting in a total of 500–600 trials per bird. These final two sessions were averaged for our threshold estimate.

The humans listened in the same sound field as the birds and were tested with a repeating background procedure similar to that described earlier. All subjects were tested using headphones with a General Radio 1982 sound-level meter recording directly off of a KEF 60S speaker mounted in the operant chambers. The microphone of the sound-level meter was placed in a position normally occupied by the bird's head in the chamber. The sound-level meter amplified the speaker signal and was connected by an AC output to an amplifier and the headphones. Two human subjects also were tested directly in the operant chambers used for avian subjects. Because results from these two procedures did not differ, only data acquired using the headphones are presented here.

Stimuli

Stimuli were modeled after characteristics of female zebra finch distance calls (Figure 1). In these experiments, the standard background stimulus was 280 ms in duration, with 10 ms rise–fall times, and it consisted of a harmonic series of tones: the first 16 harmonics of a fundamental at 570 Hz. These values represent average values for female zebra finch distance calls from our colony and from several other studies reported in the literature (Blaich et al., 1995; Okanoya, Yoneda, & Kimura, 1993; Simpson & Vicario, 1990; Zann, 1984). Even though natural zebra finch calls often are frequency modulated at the onset and offset, the modulation in female calls often is slight when compared with male calls (Simpson & Vicario, 1990; Zann, 1984). We did not frequency modulate our stimuli, in order to avoid other potentially confounding cues, and thus our stimuli model the internal portion of the female zebra finch call.

Analysis

Mean thresholds in the following tests were compared directly, either across species or in some cases across harmonics, phase condition, or durations within a species. When data could be transformed to fit the distributional assumptions of parametric tests, we used analyses of variance (ANOVAs) and *t* tests for comparisons of thresholds. Paired *t* tests and repeated measures ANOVAs were used when making comparisons with the same set of subjects across different treatments. Otherwise, we used nonparametric Kruskal–Wallis ANOVAs to compare thresholds.

Experiment 1: Detection of Changes in Timbre

Differences in the relative amplitudes of different harmonics in human voices or the sounds of musical instruments are perceived as changes in the tonal quality of these sounds. This perceptual phenomenon is referred to as *timbre* (Plomp, 1976; Risset & Wessel, 1982). In zebra finches, as well, the term *timbre discrimination* has been used to describe the ability to detect differences between song syllables that vary in the relative amplitude of their frequency components (Cynx, Williams, & Nottebohm, 1990). Williams, Cynx, and Nottebohm (1989) demonstrated that although different song syllables in a zebra finch's repertoire varied widely in the relative amplitudes of different harmonics, relative harmonic amplitudes within individual syllables remained remarkably consistent across subsequent renditions of that syllable. They also showed that such consistency in the timbre of individual song syllables is learned and under neuronal control. Cynx et al. (1990), using natural song syllables as their test stimuli, were able to obtain a gross estimate of whether zebra finches could discriminate between syllables with different attenuated harmonics. Their birds detected a 5–10 dB change in amplitude of the second harmonic of a song syllable with a 615 Hz fundamental, with some birds showing a change in response latencies with attenuations as small as 2 dB. The purpose of Experiment 1 was to obtain a more precise determination of the bird's threshold for detecting a change in the intensity of a single harmonic.

Here we test the ability of zebra finches and budgerigars to detect changes in relative amplitude of the fifth harmonic in a standard harmonic stimulus with a 570 Hz fundamental. We focused on the fifth harmonic in this case for several reasons. This harmonic is in the range of best hearing for both the zebra finch and budgerigar, and it is one of the dominant harmonics in the female zebra finch distance call (Blaich et al., 1995; Zann, 1984). Additionally, the frequency of this harmonic is in the region of best spectral resolving power in budgerigars (Dooling, 1982; Okanoya & Dooling, 1987). Thus, the fifth harmonic in this stimulus should be relevant to the production and perception of the natural vocalizations of both these bird species.

This experiment resembles, to a certain extent, a class of studies with human subjects that generally are known as *profile analysis* (Green, 1988; Green, Mason, & Kidd, 1984; Kidd, Mason, & Green, 1986; Spiegel & Green, 1982; Spiegel, Picardi, & Green, 1981). In these experiments, investigators usually measure the ability to detect relative increases in the amplitude level of a tone embedded in a complex of background tones arranged along a logarithmic frequency scale. Here we measured the bird's ability to detect a decrease in the target harmonic in order to compare our results with those of Cynx et al. (1990) for zebra finch song syllables.

Method

Subjects. Three zebra finches (2 males and 1 female), 2 budgerigars (both female), and 3 humans (1 man and 2 women) served as subjects. Birds ranged in age from 2–5 years, humans from 25–35 years. The birds were kept on a normal light–dark cycle correlated with the season in a vivarium at the University of Maryland. The birds all were housed individually in the same room and kept at 90% of their free-feeding weight. Birds had free access to water and grit in their home cages and were food-deprived several hours prior to each training and testing session. Two of the zebra finches (the males) and both budgerigars had been used previously in psychoacoustic tests involving similar procedures with both tonal and harmonic stimuli and were thus familiar with the behavioral tasks. One zebra finch (the female) was naive and was trained to perform the operant procedure prior to the start of the experiment. Results obtained for this naive bird were similar to the results obtained for the previously trained zebra finches. One human subject had extensive musical training, while both of the other human subjects had some exposure to musical training at a more moderate level (musical instruction during high school).

Stimuli. Sound stimuli were generated using the SIGNAL sound synthesis and analysis software operating on a 486/66 microprocessor with a Data Translation (Marlboro, MA) DT-2823 input/output (I/O) board at a sample rate of 40 kHz. Stimuli were output through a Tucker-Davis Technologies DD1 stereo analog interface at 40 kHz, low-pass filtered at 8.5 kHz, sent to an amplifier, and finally to a KEF 60S loudspeaker mounted 40 cm above the bird's head in the operant chamber. All component tones were added in phase beginning at 0° sine phase. As in similar experiments on humans, the intensities of the background and target stimuli were roved randomly over a range of ±2.5 dB to minimize the possibility that birds might use overall amplitude between the background and target as cues. Target stimuli consisted of decrements in amplitude of the fifth harmonic (2850 Hz) of the background stimulus (Figure 2a). We defined the threshold as the amplitude decrement resulting in a 50% correct detection.

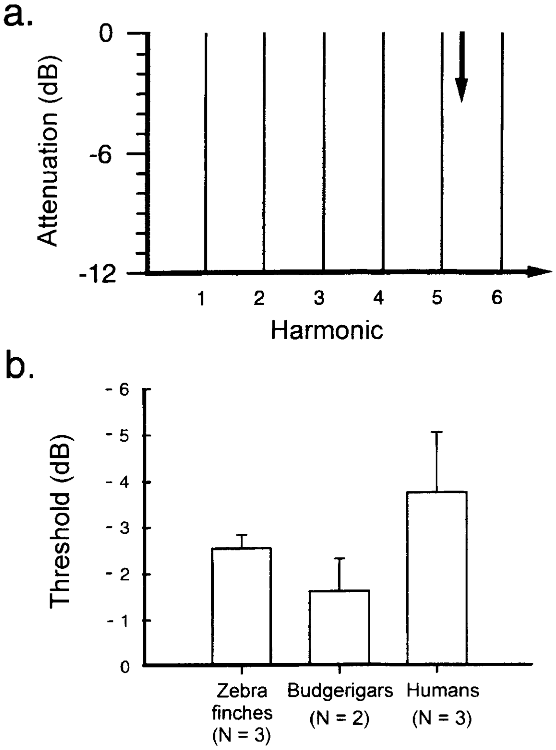

Figure 2. a. Schematic representation of background stimulus in Experiment 1 (fundamental = 570 Hz, duration of stimulus = 280 ms). b. Thresholds for zebra finch, budgerigar, and human subjects (*M* + *SE*).

Results and Discussion

Thresholds for detection of a decrease in amplitude of the fifth harmonic did not differ significantly between humans, zebra finches, and budgerigars, *F*(2, 5) = 1.224, *ns* (Figure 2b). Data were log-transformed prior to analysis to meet the distributional assumptions of an ANOVA. Thresholds ranged from 1–3 dB for avian subjects. These results suggest that birds can discriminate subtle differences in amplitude of single harmonics, well within the limits necessary to detect the differences in timbre that occur in natural song syllables and calls of zebra finches. Our data show a discrimination ability even better than that estimated by Cynx et al. (1990).

The capacity to detect small changes in timbre is potentially important for information coding in many vertebrate communication systems, including those of the zebra finch and the human. Both zebra finches, across harmonics (Williams et al., 1989), and humans, across formants (Fry, 1979; Lieberman & Blumstein, 1988), produce harmonically complex sounds that contain consistent amplitude profiles. The consistency of such patterns may be used to maintain contact with and identify individuals, as well as to communicate complex information, as in the case of human speech (Lieberman & Blumstein, 1988).

Our human thresholds can be compared with a general class of experiments known as *profile analysis* tests. Humans in our tests tended to show similar to slightly poorer performance than those in a previous profile test involving increments in the level of a component in a harmonic stimulus (Zera, Onsan, Nguyen, & Green, 1993). Thresholds for increments in a similar component for a fundamental of 400 Hz in this study were approximately 2 dB (Zera et al., 1993). The most likely reason for this difference is that generally it is more difficult to detect a stimulus decrease than a stimulus increase (Ellermeier, 1996), even in birds (Hienz, Sinnott, & Sachs, 1980). Moreover, our human subjects were tested for only several hundred trials, whereas human psychoacoustic experiments typically report a continued improvement in threshold with training for human subjects up to several thousand trials (although most of this improvement seems to occur over the first 500–750 trials; Kidd et al., 1986).

Experiment 2: Detection of Inharmonicity (Fundamental = 570 Hz)

The zebra finches' colonial social system suggests that these birds are inundated with the communication signals of many conspecifics produced simultaneously (Immelmann, 1965; Zann, 1984). Presumably, the harmonic complexity of zebra finch vocalizations provides acoustic cues that convey important information about individual conspecifics in this highly social setting. The ability to discriminate efficiently among these cues would provide selective advantages to the listener, providing benefits in facilitating the ability to identify sex, breeding condition, and individual identity.

This experiment tested the ability of birds to resolve alterations in frequency of single components in a complex harmonic sound by determining thresholds for detecting that a single harmonic was mistuned from its "correct" frequency value. Such "inharmonic" complexes were formed by mistuning either the second, fifth, or seventh harmonic in a standard stimulus with a 570 Hz fundamental. (All subjects were tested on each harmonic in turn, in random order.) These harmonics were chosen because they fell within the range of best hearing for zebra finches and budgerigars. The fifth and seventh harmonics also are both dominant harmonics in female distance calls, whereas the second harmonic is less prominent (Figure 1b). None of the harmonics chosen is an integer multiple of any other, obviating concerns about periodic pitch perception (Cynx et al., 1990).

Mistuned harmonics produce a variety of sensations in human listeners, and recent literature (Hartmann et al., 1990; Moore, Glasberg, & Peters, 1985, 1986) has focused on the subjective pitch of these mistuned components, the perception of "roughness," and other specific cues to inharmonicity. In the present discrimination task, birds and humans were tested on their ability to detect any change from the repeating background rather than to report subjective qualities. This comparison of detection thresholds for mistuning among birds and humans is of interest when considering the problems that face these species while attending to their natural vocalizations, and as far as we know, it represents the first test of such discrimination abilities in birds.

Method

Subjects. Four zebra finches, 2 budgerigars, and 3 humans served as subjects. Subjects were the same as those used in the previous experiment, except for an additional naive female zebra finch trained prior to the beginning of this experiment.

Stimuli. Sound stimuli were generated using the SIGNAL sound synthesis and analysis software operating on a 486/66 microprocessor with a Data Translation DT-2823 I/O board at a sample rate of 40 kHz. Stimuli were sent through a Tucker-Davis Technologies DD1 stereo analog interface at 40 kHz, low-pass filtered at 8.5 kHz, sent to an amplifier and out to a loudspeaker in the operant chamber. All component tones were added in phase and began at 0° sine phase. As before, the standard background stimulus consisted of a series of tones: the first 16 harmonics of a fundamental at 570 Hz. All stimuli were 280 ms in duration with 10 ms rise–fall times. The intensities of the background and target stimuli were roved randomly over a range of ± 1.5 dB to prevent subjects from using amplitude cues. Target stimuli consisted of incremental increases in frequency of the second, fifth, or seventh harmonic (1140 Hz, 2850 Hz, or 3990 Hz, respectively) of the background stimulus. The threshold of detection was defined as the frequency change resulting in a 50%-correct detection. Figure 3 shows the average psychometric function for the zebra finches in Experiment 2 and the stimulus values corresponding to a 50%-correct detection, a stimulus value corrected for false alarm rate (Pc*), and a stimulus value corresponding to a d' of 1.5.

Results and Discussion

Birds were much better than humans at detecting the mistuning of single components in a harmonic complex: $Fs(2, 6) > 33.8$, $ps < .001$, for all three harmonics. Data were log-transformed prior to analysis. Post hoc tests with Bonferroni-adjusted probabilities revealed that both bird species performed significantly better than humans for all three harmonics. Zebra finches also performed better than

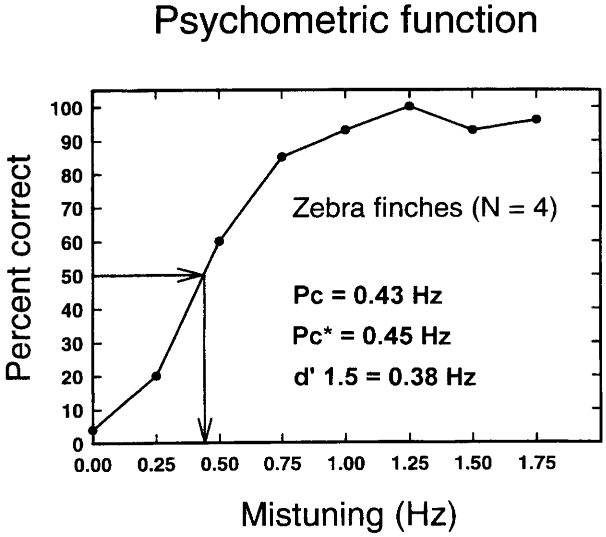

Figure 3. Average psychometric function for zebra finches in Experiment 2. Thresholds were defined as the stimulus value corresponding to a 50%-correct detection rate (Pc), a corrected 50% correct (Pc*), and a d' of 1.5.

budgerigars at detecting mistunings of the second and seventh harmonics (Figure 4). Budgerigars exhibited their lowest thresholds when discriminating alterations of the fifth harmonic (average threshold = 0.70 Hz).

We were interested in whether budgerigar thresholds were better for the fifth harmonic (2850 Hz) than for the other two harmonics. For each of the two budgerigars in the experiment, we used a repeated measures ANOVA averaging 50-trial blocks over the last 200 trials. Thresholds for the fifth harmonic were significantly lower for both subjects, $Fs(2, 6) > 20.9$, $ps < .01$. A repeated measures ANOVA for zebra finches and humans showed that thresholds did not differ across different harmonics within a species in either case, $F(2, 6) = 0.90$, *ns*, and $F(2, 4) = 3.13$, *ns*, respectively. Thresholds for our human subjects would be similar to those reported by Moore, Peters, and Glasberg (1985) if extrapolating to a higher fundamental frequency and a duration of 280 ms.

These results are surprising because there is known to be a general similarity between birds and humans on many basic hearing measures (Dooling, 1982, 1991). In particular, frequency difference limens for birds tested on pure tones in isolation are similar or even slightly worse than those reported for humans between approximately 2–6 kHz (Fay, 1988). Clearly, spectral resolution alone cannot account for our mistuning thresholds in birds. On the other hand, budgerigars show lower thresholds for detecting inharmonicity in the fifth harmonic (2850 Hz) rather than the second (1140 Hz) or seventh harmonic (3990 Hz), a pattern of results consistent with the fact that budgerigars show peak spectral resolving power around 2860 Hz (Dooling, 1982; Okanoya & Dooling, 1987). That budgerigars approach the level of sensitivity shown by zebra finches only at 2850 Hz is consistent with the hypothesis that the zebra finch might enjoy an enhanced sensitivity to alterations in the harmonic structure of these sounds.

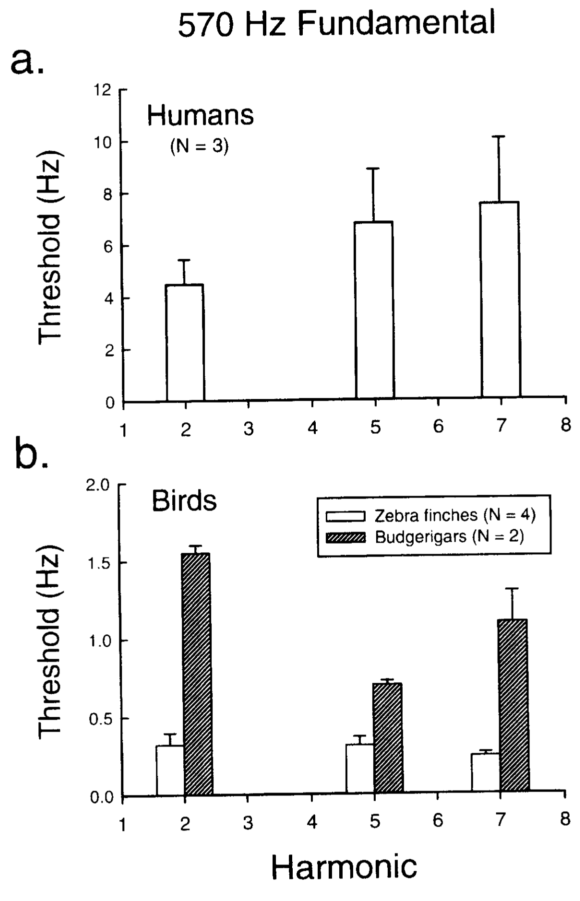

Figure 4. a. Thresholds for human subjects in Experiment 2 (*M* + *SE*, fundamental = 570 Hz, duration = 280 ms) for the second, fifth, and seventh harmonics. b. Thresholds for zebra finches and budgerigars in Experiment 2.

Experiment 3: Detection of Inharmonicity (Fundamental = 285 Hz)

The previous experiment used a harmonic series with a fundamental of 570 Hz. This might bias the detection of inharmonicity in favor of birds. This experiment tested the ability of birds to resolve alterations in frequency of single components in a harmonic complex with a 285 Hz fundamental. (All subjects were tested on each harmonic in turn, in random order.) Because the fundamental was lower, these stimuli fell more closely within the frequency range important for human speech than the range of zebra finch calls (Lieberman & Blumstein, 1988). Also, using a fundamental frequency that is half that used in previous tests allowed us to duplicate the frequency of a harmonic and thereby make a comparison based on frequency (the fourth harmonic of this fundamental is the same frequency as the second harmonic of 570 Hz) or harmonic number. Again, thresholds were determined for detecting that a single harmonic was mistuned from its "correct" frequency value. Such "inharmonic" complexes were formed by mistuning the second (570 Hz), fourth (1140 Hz), fifth (1425 Hz), or seventh (1995 Hz) harmonic in a standard stimulus.

Method

Subjects. Four zebra finches, 2 budgerigars, and 3 humans served as subjects. Subjects were the same as those used in the previous experiment.

Stimuli. The standard background stimulus in this experiment consisted of the first 16 harmonics of a fundamental at 285 Hz. Sound stimuli were generated using the SIGNAL digital signal processing and synthesis software, as in the previous experiment. Stimuli were sent through a Tucker-Davis Technologies DD1 stereo analog interface at 40 kHz, low-pass filtered at 8.5 kHz, and then sent to an amplifier and out to a loudspeaker in the operant chamber. Again, all component tones were added in phase and began at 0° sine phase. All stimuli were 280 ms in duration with 10-ms rise–fall times. The intensities of the background and target stimuli were roved randomly over a range of ±1.5 dB to prevent subjects from using amplitude cues. The birds were trained to discriminate increases in frequency of the second, fourth, fifth, or seventh harmonic (570 Hz, 1140 Hz, 1425 Hz, or 1995 Hz, respectively) of the background stimulus.

Results and Discussion

Thresholds among species differed for detection of mistuning of single components in a harmonic complex (Figure 5). For the second and fourth harmonics, log-transformed data met the distributional assumptions of an ANOVA, and these tests showed significant differences between species, $Fs(2, 6) > 7.5$, $ps < .05$, for both harmonics. Post hoc tests showed that human thresholds were significantly higher than those for both bird species, as in the previous experiment. Because log-transformed data for Harmonics 5 and 7 were not normally distributed, we used a Kruskal–Wallis one-way ANOVA to compare species. For the seventh harmonic, there was a significant difference between species (Kruskal–Wallis test, $H = 6.3, p < .05$). Results for the fifth harmonic did not differ significantly between species (Kruskal-Wallis test, $H = 5.5$, $p = .064$). Post hoc comparisons for the seventh harmonic showed a human threshold significantly higher than those for both bird species (which did not differ). Although thresholds for the fifth harmonic were not significantly different among species, the data were in the same direction, with human thresholds higher than those for both bird species. As in previous experiments, the thresholds for our human subjects were similar to those reported by Moore, Peters, and Glasberg (1985), using different methods.

Thresholds did not differ across different harmonics within a species for either budgerigars or humans, $F(3, 3) = 9.06$, *ns,* $F(3, 6) = 0.08$, *ns,* respectively, although this result is only marginally insignificant for budgerigars ($p = .052$). However, zebra finch thresholds did differ depending on the harmonic being mistuned, $F(3, 6) = 13.92, p < .01$. Zebra finches exhibited their lowest thresholds when discriminating alterations of the fifth and seventh harmonics (average threshold = 0.32 Hz), with the threshold for the second and fourth harmonics significantly higher (average threshold = 0.82 Hz).

Comparisons across species based on harmonic number or harmonic frequency for the two different fundamentals of Experiments 2 and 3 did not yield any interesting patterns. Across all three species, results for Harmonics 2 and 4 of Experiment 3 (285 Hz and 570 Hz) exhibited a more similar pattern than either did with Harmonic 2 of Experiment 2 (570 Hz; compare Figures 3 and 4). Our human detection thresholds were relatively constant across all harmonics in both experiments in terms of absolute frequency change necessary for discrimination. This pattern is consistent with results from previous experiments with human subjects (Hartmann, 1988).

Zebra finches had similar thresholds for all three harmonics of a 570 Hz fundamental and the higher harmonics (fifth and seventh) of a 285 Hz fundamental, but they showed higher thresholds for the two lower harmonics of the 285 Hz fundamental. These two lowest harmonics fall at frequencies (285 and 570 Hz) that are not the most prominent in the natural vocalizations of this species (Blaich et al., 1995; Williams et al., 1989; Zann, 1984). Budgerigars, on the other hand, exhibited their lowest thresholds in this experiment (285 Hz fundamental). In Experiment 2, the only comparable threshold for budgerigars is that for the fifth harmonic. There is no immediate explanation for the budgerigars' superior performance at frequencies below 2000 Hz with a lower fundamental.

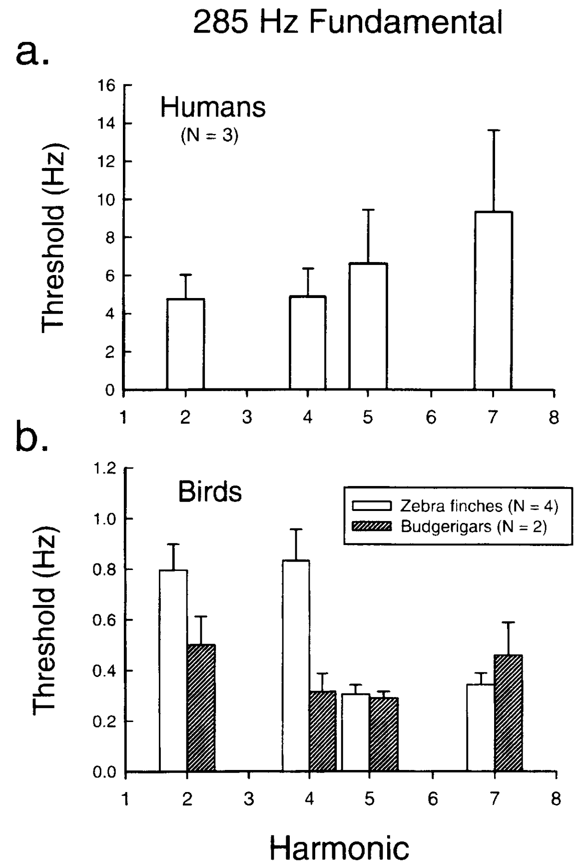

Figure 5. a. Thresholds for human subjects in Experiment 3 ($M + SE$, fundamental = 285 Hz, duration = 280 ms) for the second, fourth, fifth, and seventh harmonics. b. Thresholds for zebra finches and budgerigars in Experiment 3.

Figure 6a compares our results with data from Moore, Peters, and Glasberg (1985). Thresholds are shown as a percentage of harmonic frequency and show the same pattern of decreasing threshold with increasing harmonic number. Mean thresholds as a percentage of harmonic frequency for zebra finches and budgerigars are shown in Figure 6b. The most obvious difference between this curve and the preceding one for human subjects is the scale of mistuning, which is an order of magnitude lower for birds. However, the overall pattern of results is relatively similar to that of the human subjects, suggesting that this is not specific to a particular frequency range but may be a more general process (at which birds are better than humans). As a percentage of harmonic frequency, the best thresholds of all species were exhibited by zebra finches at 570 Hz.

Experiment 4: Detection of Inharmonicity (Effect of Phase and Duration)

If birds are more sensitive to phase information that occurs with mistuning, then using stimuli whose compo-

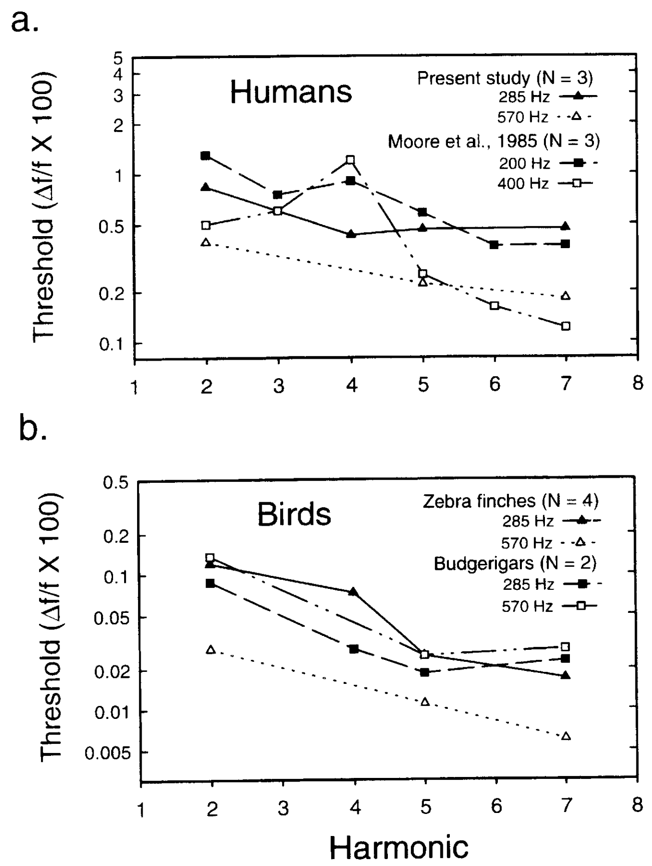

Figure 6. a. Thresholds for detecting inharmonicity in humans. Data from Moore, Peters, and Glasberg (1985) are included as a comparison. Mistuning threshold is plotted as a percentage of each harmonic frequency on a log scale. b. Comparative thresholds for detecting inharmonicity in birds plotted as percentage of harmonic frequency (log scale). There is an overall similarity of the pattern of these curves to the previous data for human subjects. Note, however, that the scale of the ordinate for bird thresholds is nearly an order of magnitude lower than that for humans. The best thresholds were exhibited by zebra finches at a fundamental of 570 Hz.

nents vary in relative phase with each new stimulus presentation might cause an increase in thresholds for birds. The relative phase angles of components in a harmonic complex can have an effect on the perception of inharmonicity (Hartmann, 1988), and studies on humans have used harmonic stimuli with a variety of relative phase relationships among components (Hartmann, 1988; Hartmann et al., 1990; Lee & Green, 1994; Moore, Glasberg, & Peters, 1985, 1986). We constructed harmonic stimuli with components having random phase angles to ask the question of whether prior thresholds for detection of mistuning were dependent on having all components in sine phase (starting at a positive-going zero crossing).

Experiments with humans also have shown that an increase in duration results in an improvement in thresholds for detecting inharmonicity (Hartmann et al., 1990; Moore et al., 1986; Moore, Peters, & Glasberg, 1985). In theory, increasing stimulus duration provides subjects with more information (Hartmann, 1988). Here we also tested whether zebra finches show a similar tendency for a decrease in threshold with an increase in stimulus duration.

Method

Subjects. Four zebra finches and 3 humans served as subjects. Subjects were the same as those used in the previous experiments.

Stimuli. In this experiment, to guard against birds memorizing specific examples, we used 5 exemplars of each target mistuned stimulus and 10 exemplars of the background, all with components having different randomly assigned relative starting phases, again generated using the SIGNAL sound synthesis software. Stimuli were stored digitally, sent through a Tucker-Davis Technologies DD1 stereo analog interface at 40 kHz, low-pass filtered at 8.5 kHz, and then sent to an amplifier and out to a loudspeaker in the operant chamber. Background and target examples of each stimulus were played out in random order. Within a species, each subject received a different set of random starting phases for the target stimuli. Background stimuli consisted of the first 16 harmonics of a fundamental at 570 Hz. The intensities of the background and target stimuli were roved randomly over a range of ±1.5 dB to minimize amplitude cues.

Target stimuli consisted of incremental increases in frequency of the fifth harmonic (2850 Hz) of the background stimulus. Thresholds were measured for two stimulus durations, 280 ms and 140 ms, with onset–offset ramps of 10 ms.

Results and Discussion

Zebra finches showed significantly lower thresholds for discriminating mistuning than did humans at 280 ms, $t(5) = 2.23$, $p<.05$, and 140 ms, $t(5) = 3.16$, $p < .05$, for the harmonic series with a fundamental at 570 Hz by a one-tailed t test (Figure 7). Data were log-transformed prior to analysis. The thresholds for random-phase stimuli in this experiment were similar to those for sine-phase stimuli from Experiment 2 for humans but not for zebra finches. In other words, thresholds for human subjects did not differ significantly for stimuli with all components in sine phase and for stimuli with components beginning at randomly selected phases, $t(2) = 1.49$, *ns*. Interestingly, zebra finches had significantly higher thresholds for stimuli with components beginning at random starting phases, $t(3) = 4.11$, $p < .05$ (Figure 7a). In this case, tests were two-tailed because we had no *a priori* expectations regarding the direction of any differences. Both zebra finches and humans also showed significantly higher thresholds for stimulus durations of 140 ms compared with 280 ms by a one-tailed t test, $t(3) = 3.37$, $p < .05$; $t(2) = 2.95, p < .05$, respectively (Figure 7b).

Taken together, our results suggest that both relative phase angle and other temporal cues play a role in the discrimination of mistuned harmonics in zebra finches. Changing the relative phases of harmonic components had no effect on our human subjects (but see Hartmann, 1988, for phase effects in stimuli having shorter durations). These results suggest that birds are more sensitive than humans to the relative phases of harmonics in a complex tone. On the other hand, longer stimulus durations result in lower thresholds, just as in humans. One interpretation is that birds, like humans, detect temporal cues related to "beats" or "rolling" in these mistuned stimuli. Hartmann et al. (1990) have proposed that if thresholds are based on time-dependent features, the "dephasing" of a mistuned component with respect to other harmonics would provide the most salient temporal feature of the waveform. A threshold for detecting such dephasing would necessarily depend on stimulus duration.

General Discussion

The objectives of this study were threefold. First, we wanted to produce synthetic versions of natural harmonic stimuli as are found in some animal vocalizations, such as those of zebra finches. Second, we wished to compare the ability of humans and birds, especially zebra finches, to discriminate among versions of these stimuli. Third, we wanted to compare the ability of zebra finches (a species whose repertoire is made up primarily of such stimuli) with budgerigars (a species whose repertoire generally consists of more tonal vocalizations; Dooling, 1986) to discriminate changes in these harmonic complexes. The purpose of this last objective was to determine whether zebra finches attend preferentially to or discriminate more efficiently the cues in such stimuli.

Many naturally produced sounds follow a harmonic series and contain energy at multiple integer intervals of a fundamental frequency (Fletcher, 1992). Using modern digital synthesis methods, it was not difficult to construct a harmonic series that approximated that found naturally in the zebra finch distance call. Organisms that produce complex harmonic sounds as communication signals should have the ability to partition the components of one complex signal from those of another when presented with more than one such sound simultaneously (Hartmann et al., 1990; Moore & Glasberg, 1990; Moore, Peters, & Glasberg, 1985). Indeed, there is a rich literature describing the ability of human listeners to segregate a single mistuned harmonic component from an otherwise periodic harmonic complex (Hartmann et al., 1990; Lee & Green, 1994; Moore et al., 1986; Moore, Peters, & Glasberg, 1985), although the specific mechanisms used to make such perceptual judgments still are not known.

In comparison with humans, zebra finches and budgerigars are especially sensitive to alterations in the frequency of single components of complex harmonic stimuli. In fact, our results show one of the largest species differences measured to date in the acoustic perceptual capabilities of birds compared with that of humans (Fay, 1988). Like zebra finch vocalizations, human speech is rich in harmonic complexity. The fundamental of human speech, however, is lower in frequency than zebra finch calls and song syllables, with average fundamentals ranging from 120 Hz to 265 Hz for adults and up to 500 Hz for children (Fry, 1979). Our birds still outperformed humans when tested on a harmonic series with a fundamental in the range of human speech. These results suggest that an enhanced ability to detect inharmonicity may be a more general phenomenon characteristic of all birds.

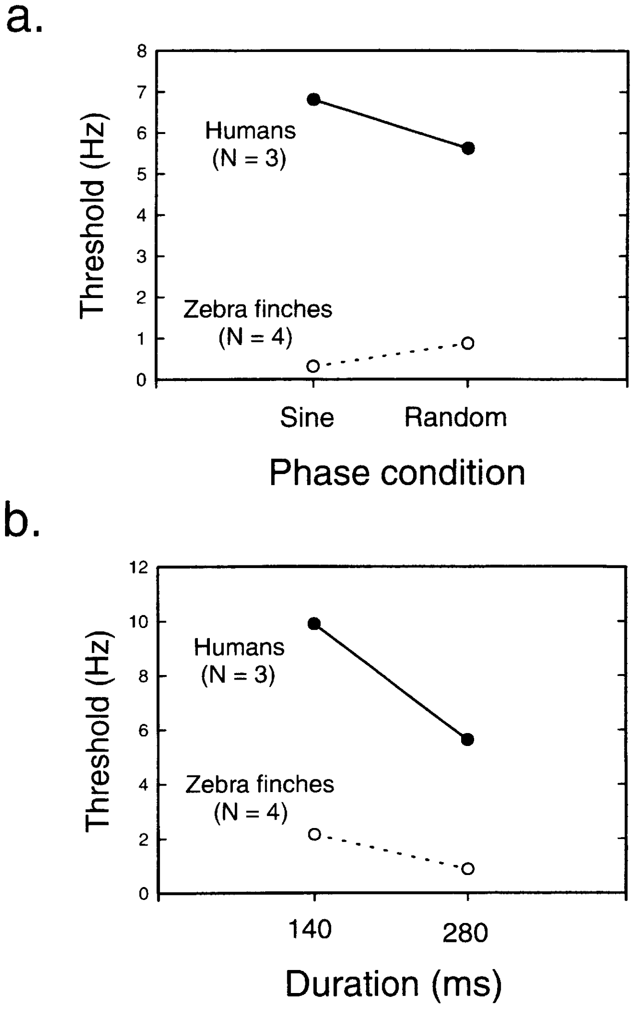

Figure 7. a. Comparison of human and zebra finch thresholds for mistunings of the fifth harmonic of complex stimuli in two different phase conditions. Stimuli consisted of the first 16 harmonics of a fundamental of 570 Hz with components in zero sine phase versus components having randomized relative phases. All stimuli had a duration of 280 ms. Zebra finch thresholds with randomized phase stimuli were significantly higher than with zero sine phase stimuli, suggesting that birds may be especially sensitive to relative phase information. Human thresholds in the two different phase conditions did not differ significantly. b. Thresholds for humans and zebra finches in the randomized relative phase condition for two stimulus durations, 280 ms and 140 ms ($M + SE$, fundamental = 570 Hz). This study's results for both species were similar to previous results with humans, showing an increase in threshold with a decrease in duration. In the case of zebra finches, this increase is significant. These results are consistent with detection of mistuning mediated by temporal cues related to "beats" or "roughness" (Hartmann, 1988; Hartmann et al., 1990; Lee & Green, 1994).

In contrast to zebra finches, the vocalizations of budgerigars are predominantly pure-tonal, although their repertoire also includes some harmonic sounds (Brockway, 1969; Dooling, 1986; Farabaugh, Brown, & Dooling, 1992).

Budgerigars do less well than zebra finches at the higher fundamental but come closest to the thresholds of zebra finches in the region of the fifth harmonic (2850 Hz). This is very close to their frequency of best spectral sensitivity and also is the characteristic frequency of budgerigars' "contact" calls (Dooling, 1986; Farabaugh, Linzenbold, & Dooling, 1994). This result is consistent with an enhanced spectral sensitivity in this frequency region. Interestingly, budgerigars show low thresholds at all harmonics tested for a fundamental of 285 Hz. This low fundamental is more characteristic of human speech than the vocalizations of small birds.

One of the promising aspects of these complex stimuli is that pitch correlates of such sounds almost always are considered in the framework of temporal rather than spectral coding mechanisms in the vertebrate auditory system. A compelling case can be made for a temporal coding mechanism underlying pitch perception in humans (Meddis & Hewitt, 1991; Patterson, 1987; Yost, Patterson, & Sheft, 1996) and animals (Cariani & Delgutte, 1996a, 1996b; Simmons & Buxbaum, 1996). It is not clear whether exclusively temporal or spectral coding mechanisms underlie inharmonicity detection in humans or birds. But the difference between bird and human thresholds in our experiments suggests that birds may be using different mechanisms for detecting inharmonicity in complex stimuli. Because human thresholds for detecting inharmonicity are distinctly poorer than those of birds, there is a strong possibility that nonspectral cues are used by birds for detecting mistuned harmonics. But human subjects also are known to use a variety of different cues for discriminating such stimuli (Hartmann, 1988), and a number of explanations based on temporal coding mechanisms have been proposed (Hartmann, 1996; Hartmann et al., 1990). It is also logically possible, though we consider it unlikely, that birds may be memorizing particular stimulus examples. Such an ability, however, would still require that the birds detect differences in mistuned harmonic stimuli to begin with.

To return to issues raised earlier, it also may be possible that, rather than implicating different mechanisms, our superior bird thresholds simply may reflect an enhanced ability of birds to discriminate the same cues used by humans. There is a long history of speculation about the superior temporal resolving power of birds, although it has yet to be demonstrated in psychoacoustic tests (Dooling, 1991; Pumphrey, 1961). It also may be that humans and birds attend to a variety of cues at the same time (Hartmann, 1988). The variety of sensations that humans experience when hearing a mistuned harmonic complex depend on the duration of the stimulus and the degree of mistuning. At short durations (less than approximately 70 ms), humans use a shift in the pitch of the complex tone as a principal cue for detecting inharmonicity. At longer durations, the cue may be a separate, segregated tone formed by the mistuning (Hartmann et al., 1990; Moore et al., 1986) or a "rolling" or "roughness" that may be the result of changes in the envelope of the waveform (Hartmann, 1988). These complex harmonic sounds, then, may afford a means for exploring mechanisms related to a variety of perceptual sensations.

Zebra finches performed best at detecting changes in the fundamental and harmonic frequencies characteristic of the dominant frequencies in their natural calls and song (Blaich et al., 1995; Williams et al., 1989; Zann, 1984). The subtle perception of mistuned harmonics may be contingent on controlled, relatively noise-free laboratory conditions. However, zebra finches, at least, use their vocalizations over relatively short distances in the wild (Hall, 1962; Zann, 1984), and small differences in the characteristic envelopes, relative phases, or time-dependent features of the waveform may provide important identifiable cues in social contexts. Such cues could provide essential information for individual, group, or species identity, as well as information concerning the motivational state of the individual.

Patterns of amplitude or frequency structure are distinctly different in different zebra finch song syllables and may produce distinctive features in the waveform. Furthermore, these differences are maintained with remarkable consistency by individuals (Williams et al., 1989). Well-developed abilities to detect subtle changes or distinctions in the acoustic features of natural calls may manifest themselves in enhanced thresholds for detecting inharmonicity. In aggregate, the superior performance of zebra finches over budgerigars at 570 Hz would seem to argue for the zebra finches having enhanced abilities related to its species-specific vocalizations. It would be interesting to test other avian species on these complex sounds. Such experiments may not only illuminate species-specific coding mechanisms but also shed light on underlying mechanisms involved in the abilities of birds in general to recognize subtle yet important communicative cues.

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