Frequency discrimination in budgerigars (*Melopsittacus undulatus*): Effects of tone duration and tonal context

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Studies of frequency resolving power in budgerigars (*Melopsittacus undulatus*) have shown that this species has excellent discrimination abilities for both simple and complex sounds falling in the region of 2 to 4 kHz—the frequency range of their contact call. In four experiments, frequency discrimination by budgerigars of short tones similar to elements found in the contact call was examined. Frequency difference limens (FDLs) for simple pure tones at 2.86 kHz were constant for tone durations above 20 ms but higher for shorter tones. Budgerigars generally showed larger FDLs for shorter duration 1-, 2-, and 4-kHz pure tones. FDLs in budgerigars for 20-ms tones embedded in a sequence of six other tones were similar to FDLs measured for tones of the same frequency presented in isolation. Moreover, there was no effect of introducing trial-by-trial variation in the location of the frequency change in the seven-tone complexes for budgerigars, a condition for which humans showed a large decrement in performance. Taken together, these results suggest budgerigars possess enhanced spectral resolving power for short duration pure tones when they are embedded in contact call-like tonal patterns. © *2000 Acoustical Society of America.* [S0001-4966(00)00505-1]

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INTRODUCTION

Budgerigars (*Melopsittacus undulatus*) are small Australian parrots that show remarkable vocal plasticity and vocal learning throughout life. The dominant vocalization in their repertoire is a highly stereotyped, frequency modulated contact call about 150–200 ms in duration with most of the spectral energy concentrated in the region of 2–4 kHz (Dooling, 1986; Farabaugh and Dooling, 1996). Several experiments have described the important features that budgerigars use when listening to and discriminating among contact calls. These features are primarily spectral and include peak frequency, rate of frequency modulation, and concentration of spectral energy (Brown *et al.*, 1988; Dooling *et al.*, 1987). Budgerigars maintain nearly perfect performance on an identification task involving contact calls even when these calls are temporally or spectrally distorted (Park and Dooling, 1985, 1986), just as humans can recognize speech sounds under adverse conditions (French and Steinberg, 1947; Miller, 1981). These results on the perception and recognition of contact calls are supported by a variety of other experiments using simple sounds, which show that these birds have excellent frequency resolving power in the spectral region of 2–4 kHz (Dooling and Saunders, 1975; Okanoya and Dooling, 1987).

The experiments reported here further explored the ability of budgerigars to discriminate spectral changes in simple pure tones and contact call-like stimuli and compared these results with those from humans tested with similar procedures. In humans, a number of stimulus factors influence frequency discrimination abilities, and many of these stimulus characteristics are present in the budgerigar contact call. These include differences in durations, frequencies, and sequences of tones within patterns. By studying these factors in a particular frequency discrimination paradigm, we hoped to determine whether budgerigars have a particular species-specific advantage in perceiving small frequency changes in stimuli that closely resemble their contact calls. In a first experiment, frequency difference limens (FDLs) for pure tones at 2.86 kHz were measured at durations ranging from 5 to 160 ms. In a second experiment, FDLs were measured for very short tones at three additional frequencies between 1 and 4 kHz. Although FDLs for simple pure tones have been reported for budgerigars (Dooling and Saunders, 1975) and other birds (Gray and Rubel, 1987; Kuhn *et al.*, 1980; Langemann and Klump, 1992; Quine and Konishi, 1974; Sinnott *et al.*, 1980), the relation of FDL to duration has yet to be systematically examined in birds. In humans, there is an increase in FDL with decreasing tone duration for tones below 4–5 kHz (e.g., Moore, 1973). These results suggest that FDLs for low-frequency tones may be determined by temporal factors (for a review, see Moore, 1997). Since budgerigars excel in some aspects of temporal processing, they might show an enhanced ability to detect frequency changes, especially for tones of shorter duration (Amagai *et al.*, 1997; Dent *et al.*, 1999; Lohr and Dooling, 1998).

Finally, the third and fourth experiments examine auditory pattern perception by budgerigars. In an approach modeled after a series of human experiments using word-length tonal patterns (Watson *et al.*, 1975, 1976), we examined how well budgerigars could ''hear out'' a small frequency change in specific temporal locations of contact call-length tonal patterns. Watson *et al.* (1975) reported that human listeners' discrimination of a small change in one tone embedded within a sequence of other tones was affected by the target tone's frequency and temporal position within the pattern, and the listener's knowledge of when the changes would occur. Specifically, frequency changes in targets low in fre-

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quency relative to the surrounding components, and in targets occurring at the beginning of the tonal pattern, were harder to discriminate than other target tones. Equally as important to discrimination performance, however, was the degree of the listener's knowledge about the target and the tonal pattern. High levels of uncertainty as to when the change in the target pattern would occur resulted in poor target-tone frequency discrimination (Watson *et al.*, 1976). Espinoza-Varas and Watson (1989) discussed the importance of central processes in the auditory-perceptual representation of sounds. They suggested that, for complex patterns, peripheral receptors probably do not impose the greatest limitations on performance. Rather, central processes such as attention, learning, and memory capacity play large roles in these discrimination abilities. Such central capacities may shed some light on auditory processing that differs between humans and birds.

In the present experiments, we compared budgerigars and humans on the discrimination of call-length tonal patterns under several conditions. First, tonal patterns were constructed where each tone was 2.86 kHz (the frequency of best hearing for the budgerigar). Next, tonal patterns were constructed with component frequencies varying from 1–4 kHz assembled in a random order. Subjects were tested under conditions in which the temporal location of the frequency change was the same from trial to trial (low uncertainty) and conditions where the location of the frequency change was randomized on a trial-by-trial basis (high uncertainty). Comparing the performances for budgerigars and humans in the low uncertainty and high uncertainty conditions provides some indication of the degree to which attention-like factors contributed to the thresholds reported here.

I. GENERAL METHODS

A. Testing apparatus

The birds were tested in a wire cage (23×25×16 cm) mounted in a sound-isolation chamber (Industrial Acoustics Company, IAC-3). A response panel consisting of two microswitches with light-emitting diodes (LEDs) was mounted on the wall of the test cage just above the food hopper. The microswitch was tripped by the bird pecking the LED. The left microswitch and LED served as the observation key while the right microswitch and LED served as the report key. The behavior of the animals during test sessions was monitored by a video camera system (Sony HVM-322).

An IBM 486 computer controlled test sessions. Pure tones were generated digitally at 20 kHz and output through Tucker-Davis modules to a speaker (KEF Electronics, Holliston, MA, model 80C) mounted 36 cm above the perch in the testing cage. Tones were output at an intensity of 65 dB SPL at the location of the bird's head. Stimulus calibration was performed using a General Radio (model 1982) sound-level meter. Stimulus intensities were measured with the microphone (1/2 in attached to the sound-level meter via a 3-m extension cable) in front of the response keys in the approximate position occupied by the bird's head during testing. Stimulus intensities were calibrated several times during these experiments to ensure that stimulus levels remained constant and the entire system was functioning appropriately.

B. Training and testing procedures

The birds were trained by a standard operant autoshaping program to peck at the left microswitch key (observation key) during a repeating background. After a random time interval of 2–7 s, a new stimulus was presented alternately with the background sound. If the bird pecked the right microswitch and LED (report key) within 2 s of this alternating pattern, the food hopper was activated for 2 s. A failure to peck the report key within 2 s of sound alternation was recorded as a miss and a new trial sequence was initiated. The dependent variable in these experiments was the percent correct responses on trials involving an alternating sound pattern. Thirty percent of all trials were ''sham'' trials in which the target sound was the same as the repeating background sound. A peck to the report key during a sham trial was recorded as a false alarm, and the lights in the test chamber were extinguished while the repeating background continued. The length of this time-out period was normally 5 s, but varied (up to 9 s) according to the bird's behavior. Longer time-out periods were instituted if the birds began developing higher false alarm rates. Sessions with a total false alarm rate of 16% or higher were discarded. About 10% of all sessions across birds were discarded for this reason.

Stimuli were presented according to the Method of Constant Stimuli (Dooling and Okanoya, 1995) in 5-Hz (experiments 1 and 2) or 10-Hz steps (experiments 3 and 4), with frequency values selected to bracket the presumed threshold. At the conclusion of testing, psychometric functions were constructed and thresholds were defined in several ways, including the frequency difference that the bird detected 50% of the time (unadjusted threshold), the frequency difference detected 50% of the time adjusted by the false-alarm rate (adjusted threshold; Hienz *et al.*, 1977; Sinnott *et al.*, 1980), and the frequency difference resulting in a d' of 1.5 (Dooling and Okanoya, 1995; Green and Swets, 1966; Penner, 1995). There was little difference between adjusted, unadjusted, and d' threshold values, so adjusted thresholds were used for all data analysis.

II. EXPERIMENT 1

In the first experiment, FDLs were measured for pure tones of different durations. The frequency of all tones was 2.86 kHz, which is the frequency of best hearing in budgerigars.

A. Methods

1. Subjects

Three adult budgerigars (two males and one female) were used as subjects. The birds were kept on a normal day/night cycle correlated with the season at approximately 90% of their free-feeding weights. Three humans (one male, two females) were also tested in this experiment, to allow comparison with earlier studies using humans. None of the sub-

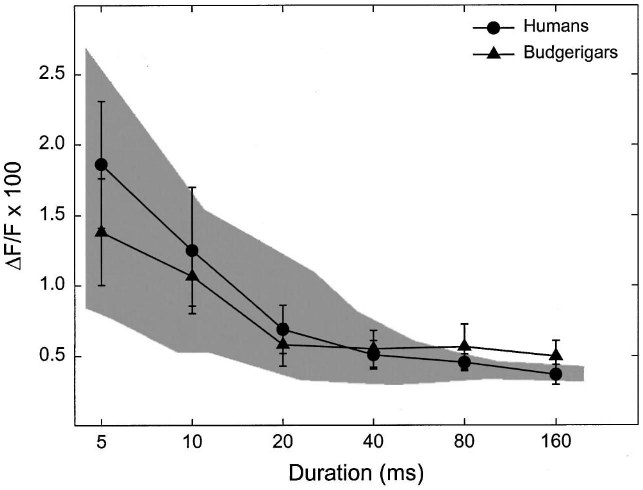

FIG. 1. Mean FDLs for three budgerigars (closed triangles) and three humans (closed circles) for 2.86-kHz pure tones of different durations. Error bars are standard errors. Each data point represents 200 trials and is plotted as Weber fraction ($\Delta F/F \times 100$) by duration (ms). The gray area represents the range of data on humans from previous experiments using slightly different stimuli and procedures (see text for references).

jects reported a history of hearing disorders, and all were researchers at the University of Maryland working in the laboratory at the time of the experiment.

2. Stimuli and procedure

All stimuli in this experiment were 2.86 kHz pure tones with 2-ms rise/fall times (shaped with a cosine function). The tones were 5, 10, 20, 40, 80, and 160 ms in duration (including the rise/fall times). FDLs were measured for a minimum of 300 trials at all durations in a random order, and a different random order was used for each bird. In a first set of tests, the tones were presented at a peak sound pressure level of 65 dB SPL as measured by the General Radio sound-level meter. In a second set of tests, the intensities of the pure tones of different durations were adjusted to be of equal energy according to the budgerigar's temporal integration function (Dooling and Searcy, 1985b).

Humans were tested with similar procedures as the birds, except that they listened to the stimuli over earphones (AKG type K-240 DF) and pressed keys on a hand-held control rather than hitting the LEDs attached to microswitches on the birds' response panel. Human subjects were tested for 100 trials at all tone durations. Tones were presented at a comfortable listening level (about 65 dB SPL) as measured by the General Radio sound-level meter.

B. Results and discussion

The data from the constant SPL and the energy-adjusted SPL experiments were not significantly different, $t(42) = 2.02$, $p > .05$, by a two-tailed paired t-test, so the results for both tests were combined for all subsequent comparisons. Figure 1 shows the mean FDLs as a function of tone duration for three budgerigars. These results are compared with the results from our humans tested using similar procedures used to test the birds and with the range of published data reported on humans tested by other investigators in other laboratories using different procedures (Freyman and Nelson, 1987; Hall and Wood, 1984; Hartmann *et al.*, 1985; Henning, 1970; Moore, 1973; Turnbull, 1944). The results for the humans in our experiments at all durations fall well within the range of results in other experiments on humans. For both humans and budgerigars, FDLs are relatively constant for tone durations longer than 20 ms but worsen considerably as tone duration decreases below 20 ms. A two-way repeated measures analysis of variance shows no differences between the FDLs of budgerigars and humans [$F(1,5) = 0.37$, $p > 0.05$]. For both species, there was a significant difference among durations [$F(5,25) = 27.73$, $p < 0.05$] with higher FDLs occurring at shorter tone durations. The interaction between the two factors was not significant [$F(5,25) = 1.65$, $p > 0.05$], and there were no differences between the budgerigars and the humans at any of the specific tested durations.

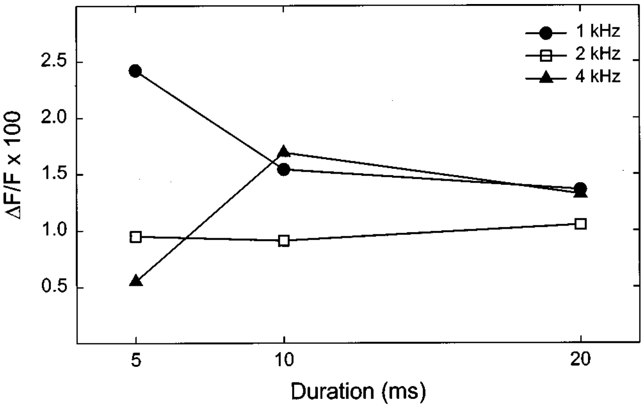

FIG. 2. Mean FDLs from budgerigars for pure tones of different durations and frequencies. Each data point represents a mean of two budgerigars and is plotted as Weber fraction ($\Delta F/F \times 100$) by duration (ms).

III. EXPERIMENT 2

The previous experiment showed that at their frequency of best hearing, budgerigars exhibit FDLs that worsen as a function of decreasing tone duration below 20 ms. Experiment 2 tested whether this result was typical of other frequencies within the budgerigar's range of hearing.

A. Methods

The specific methods and procedures were similar to those used in experiment 1. Two of the three budgerigars from experiment 1 (one male and one female) were used as subjects. The stimuli in this experiment were 1-, 2-, and 4-kHz pure tones. FDLs were measured for a minimum of 300 trials at each duration. The tones were 5, 10, and 20 ms in duration (including the 2-ms rise/fall times). FDLs were measured in a random order and a different random order was used for each bird. The tones were presented at a peak sound pressure level of 65 dB SPL as measured by the General Radio sound-level meter.

B. Results and discussion

Figure 2 shows mean FDLs for two budgerigars at three durations and three frequencies. In general, FDLs at 1 and 4 kHz are worse than FDLs at 2 kHz (and 2.86 kHz, see Fig. 1), consistent with previous results from this species (Dooling and Saunders, 1975). As tone duration decreases from 20 to 10 ms, FDLs increase at all three frequencies, similar to the results of experiment 1 for 2.86 kHz. For the 5-ms tone burst duration, however, the situation is somewhat more complicated. At 1 kHz, the mean FDL for the 5-ms tone is much worse than it is for the tone duration of 10 ms. For the 2-kHz tone burst, however, the mean FDL for the 5-ms tone is similar to the mean FDL at 10 ms. Surprisingly, for the 4-kHz tone burst, the mean FDL at 5 ms is much lower than the mean FDL for the 10- or 20-ms tone burst durations. In other words, FDLs improve with increasing frequency for short duration tones.

In humans, the effect of frequency on FDLs has been the subject of considerable investigation over the years (see, for example, Moore, 1973). In general, the discrimination of pitch may involve time-based mechanisms for frequencies below 5 kHz and place-based mechanisms at higher frequencies, with some perturbations evident in the transition from time-based to frequency-based mechanisms (Moore, 1973). In addition, there is the possibility that loudness cues influence FDLs measured at high frequencies where absolute sensitivity is decreasing at a rapid rate (Henning, 1966). In budgerigars, for instance, the budgerigar audiogram shows a loss of sensitivity of about 50 dB/octave at frequencies above 4 kHz. Finally, for very short duration tones (5 ms) where the rise/fall times (2 ms) are a significant fraction of the stimulus duration, there is always the possibility that small amounts of spectral splatter could influence thresholds differentially across frequencies. Since much less is known about the psychophysics of hearing in birds compared to humans, some or all of these factors may be relevant to the differences in FDLs across frequency at 5 ms for our birds.

In general, though, the results for budgerigars parallel those reported for humans at durations above about 10 ms. These results are important for understanding the design of the following experiments, where FDLs of short tones are measured in an acoustic context of other short tones—mimicking a natural contact call produced by this species.

IV. EXPERIMENT 3

The previous experiments showed that for durations above 10 ms, budgerigars and humans show roughly similar patterns of FDLs across durations and across frequencies. In experiment 3, we explored the effects of a surrounding tonal context on discrimination of frequency change in a (24-ms) tone burst. In this experiment, the FDL was measured for short pure tones embedded in a pattern whose total duration was 198 ms. This is about the duration of naturally produced tonal contact calls of budgerigars.

A. Methods

1. Subjects

Two adult budgerigars (both males) and two humans (one male, one female) were used as subjects. Neither of the human subjects reported a history of hearing disorders, and both were working in the laboratory at the time of the experiments.

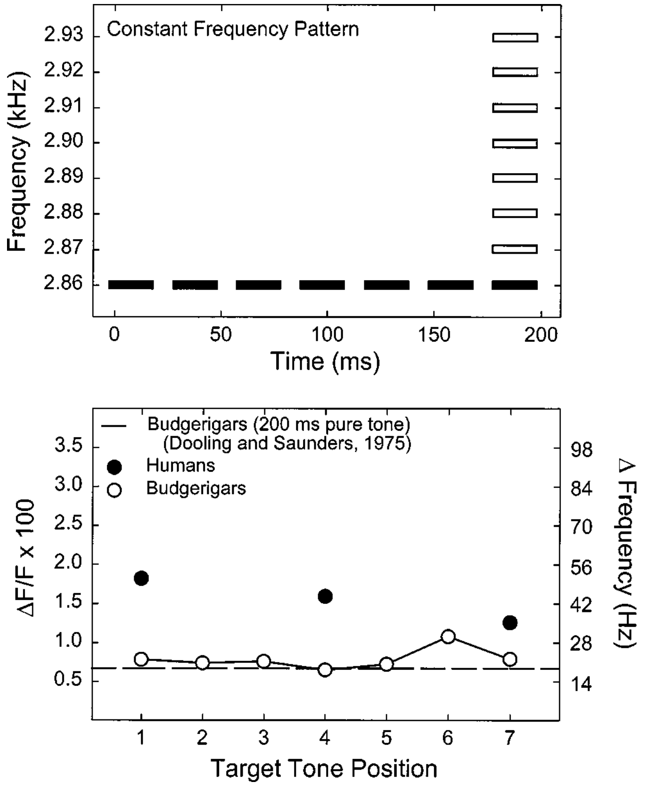

FIG. 3. The top panel is a schematic of a frequency-constant tonal pattern with examples of seventh position changes. The closed rectangles represent the constant frequency pattern. During a session measuring the FDL for the 7th position, the 7th tonal element is randomly replaced with one of the higher tonal elements (open rectangles) on any given trial. The bottom panel shows FDLs for a 2.86-kHz frequency tonal pattern. The mean of two birds (open circles) and two humans (closed circles) is represented by frequency in Hz (right axis) and Weber fractions (left axis). The dashed line represents budgerigar FDLs for a 200-ms pure tone of the same frequency in isolation (from Dooling and Saunders, 1975).

2. Stimuli and procedure

The stimuli in this experiment consisted of a sequence of seven 2.86-kHz pure tones, each 24-ms long (including 2-ms rise/fall times), with a 5-ms intertone silent interval. The birds' FDLs were measured for each tone in the seven-tone pattern. The patterns were presented at 65 dB SPL. Figure 3 (top) shows a schematic diagram of the fixed-frequency tonal pattern and an example of one tone selected as the target. In this example, seven target patterns are shown in which the frequency of the seventh component was changed in 10-Hz steps. FDLs were obtained for one component (position) in the pattern before another component was tested. This procedure was followed until all seven positions of the pattern were tested in a random order.

Humans were tested with similar procedures as the birds, except that they listened to the stimuli over earphones and pressed keys on a hand-held control rather than LEDs on the birds' response panel. The humans were tested on three positions of the fixed-frequency tonal pattern.

B. Results and discussion

Mean FDLs for the two budgerigars are shown for all seven temporal positions (Fig. 3, bottom). FDLs for these short tones embedded within a sequence of like-frequency tones are as good as FDLs for simple tones of the same overall duration (i.e., 200 ms) (Dooling and Saunders, 1975). Weber fractions ($\Delta F/F\times 100$) for the budgerigar have a mean of 0.7 across all positions. In fact, Weber fractions for 20-ms pure tones of the same frequency presented in isolation (see experiment 1) are the same as those for the 20-ms tones embedded in the patterns used in this experiment. The results for the humans differ from those of the budgerigars, but the trends are similar to those from earlier experiments. Watson and his colleagues found that thresholds for discrimination of tones earlier in a (mixed-frequency) tonal pattern were higher than those occurring later in the pattern (Watson *et al.*, 1975). Here, humans tested on tonal patterns had Weber fractions ranging from 1.6 to 2.3, depending on the position of the change. Experiment 1 showed that FDLs for humans tested on tones of 2.86 kHz with a duration of 20 ms had Weber fractions ranging from about 0.3 to 1.2. FDLs for tones embedded in the tonal patterns were higher than those for simple pure tones for humans but not for budgerigars.

V. EXPERIMENT 4

The previous experiment showed that budgerigars were as good at discriminating frequency changes in pure tones embedded in complex tonal patterns as they were at discriminating frequency changes in tones presented in isolation. This experiment measured FDLs for pure tones embedded in tonal patterns again, but this time the tonal patterns were further modified to mimic some of the spectral characteristics of the contact calls of this species. That is, the components of the patterns were now varied in frequency, and the target tone to be discriminated was embedded within this varying-frequency pattern. Further, FDLs were measured for each component of tonal patterns where the position of the target tone varied from trial to trial to assess the role of experimental uncertainty and possible attentional factors in these experiments.

A. Methods

1. Subjects

The budgerigars and humans in this experiment were the same as those used in experiment 3.

2. Stimuli and procedure

The stimuli in this experiment consisted of a sequence of seven pure tones, each 24-ms long (including 2-ms rise/fall times), with a 5-ms intertone interval. The seven-tone patterns were constructed so that each tone was of a different frequency, ranging from 1 to 4 kHz, in 500-Hz steps, and arranged in a random order (see Fig. 4). The frequency spacing of the tonal components exceeded the critical bandwidth of the budgerigars at all frequencies (Dooling and Searcy, 1979; Saunders *et al.*, 1979). Each bird was tested on three different variable tone patterns (to account for positional and frequency effects of the tonal components), each with a different random temporal ordering of the seven tones. FDLs were measured for each tone in these patterns in random order, in both a low uncertainty and a high uncertainty condition. Thresholds for each frequency were obtained by averaging across all three variable tone patterns.

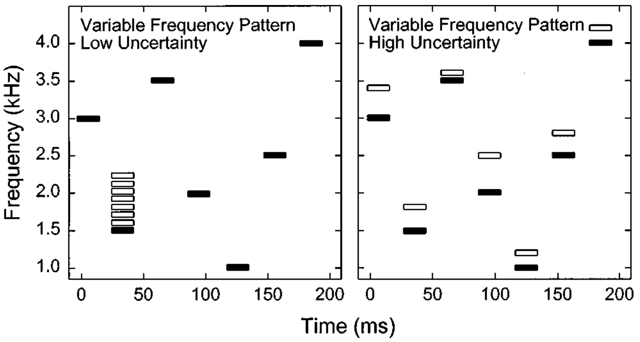

FIG. 4. Schematic of a variable frequency tonal pattern in the low uncertainty (left panel) and high uncertainty (right panel) conditions (closed rectangles). During a low uncertainty session measuring the 2nd position FDL, the second tone is replaced by a tone of higher frequency (one of the open rectangles). During the entire low uncertainty session, changes will occur only at that position. Examples of seven possible changes in a high uncertainty session are shown by the open rectangles in the right panel. Here, the change can occur in any of the positions (open rectangles, right panel) from trial to trial in the session.

In the low uncertainty condition (Fig. 4, left), FDLs were measured for a single component within the pattern in each session. By repeatedly testing the bird with the stimulus change occurring in the same temporal and spectral location, the bird could know ''where to listen'' for a frequency change in the repeating tone pattern. In other words, since trial-to-trial changes occurred in the same location in the tonal pattern, the birds should be able to focus on a particular segment and a particular frequency. Humans listening in a similar low uncertainty stimulus condition are thought to use their knowledge of the target location to focus their auditory attention and reduce interference from surrounding tones (Watson *et al.*, 1976). On the other hand, in the high uncertainty condition (Fig. 4, right) the location of the frequency change in the pattern varied on a trial-by-trial basis. Watson *et al.* (1976) suggested if a listener cannot know from one trial to the next where in a multitone pattern a change is going to occur, they cannot focus attention on a specific location within the pattern, and instead must distribute attention across all components. A comparison of FDLs in low and high stimulus uncertainty conditions should reveal the role of ''attention'' in complex pattern perception in these birds.

Humans were tested with similar procedures as the birds, except that they listened to the stimuli over earphones and pressed keys on a hand-held control rather than LEDs on the birds' response panel. The humans were tested on all positions of one of the variable frequency patterns under both the low and high uncertainty conditions.

B. Results and discussion

Discrimination of the variable-frequency tonal patterns was more difficult than discrimination of the fixed frequency patterns for both birds and humans, under both low and high uncertainty conditions. For birds, Weber fractions were somewhat larger below 2 kHz and relatively constant between 2.5 and 4 kHz (see Fig. 5), which is similar to the

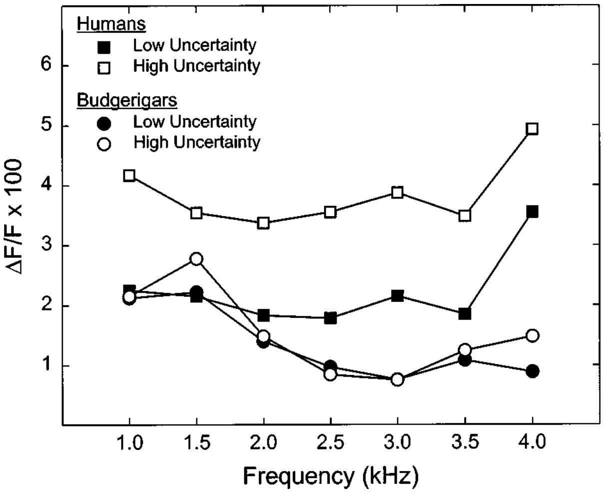

FIG. 5. Mean FDLs for the variable frequency tonal patterns are plotted as Weber fractions by frequency (kHz) for two birds and two humans. The budgerigars ran on three different variable frequency tonal patterns under both the low uncertainty (closed circles) and high uncertainty (open circles) conditions. The humans ran on one variable frequency tonal pattern under both the low uncertainty (closed squares) and high uncertainty (open squares) conditions.

results from Watson *et al.* (1975) in humans. The humans in this study had Weber thresholds that were generally larger than those of budgerigars with thresholds that were relatively constant at the lower frequencies but somewhat higher at 4 kHz (a result opposite of that reported by Watson *et al.*, 1975).

A two-way repeated measures analysis of variance compared results from humans and budgerigars at the low and high uncertainty conditions. Both the species factor $[F(1,52)=15.82,\ p<0.05]$ and the level-of-uncertainty factor were significant $[F(1,52)=4.54,\ p<0.05]$. That is, budgerigars were significantly different from humans and the low uncertainty condition was significantly different from the high uncertainty condition. A subsequent two-tailed, paired sample *t*-test on the individual species at each condition showed that budgerigar FDLs between the low uncertainty and high uncertainty conditions were not significantly different $[t(13)=0.74,\ p>0.05]$, while the human FDLs were significantly different between the two conditions $[t(13)=4.28,\ p<0.05]$. Thus not knowing where the change was going to occur from trial to trial affected a human's but not a budgerigar's ability to discriminate frequency changes in a single component of these complex tonal patterns.

VI. GENERAL DISCUSSION

Experiments 1 and 2 showed that the frequency discrimination abilities of budgerigars for simple pure tones were similar to those found in humans. The FDLs were relatively constant for long duration pure tones above 20 ms and increased as tone duration decreased below 20 ms. The FDLs reported here for both budgerigars and humans fell within the range of data from humans previously tested using different procedures (Freyman and Nelson, 1987; Hall and Wood, 1984; Hartmann *et al.*, 1985; Henning, 1970; Moore, 1973; Turnbull, 1944). The best frequency discrimination for short tones was in the region of 2–3 kHz for budgerigars, and similarly in humans, the lowest FDLs were at 2 kHz (Moore, 1973).

Experiment 3 showed that as the complexity of the experimental situation increases, humans showed decrements in performance while the birds were much less affected. In this minimal uncertainty pattern perception task, the context of the components being measured did not change from trial to trial (all tones were the same duration and frequency) and neither did the temporal position of the target. In budgerigars tested under these conditions, FDLs for pure tones embedded in a sequence of like-frequency tones were the same as FDLs for simple short tones presented in isolation.

Humans, on the other hand, may have experienced some temporal masking in this situation because they were not able to discriminate changes in these tones embedded in the patterns as well as they could for the same tones presented in isolation. There is evidence that considerably less masking occurs for budgerigars in nonsimultaneous masking experiments where birds demonstrate a much greater frequency selectivity than humans (Dooling and Searcy, 1985a). Although these experiments involved detection, the same mechanisms may also be affecting discrimination abilities and this may explain why the budgerigars were not as affected as the humans were by the complexity of this frequency discrimination task.

Experiment 4 added another level of task complexity. This experiment tested birds and humans on tonal patterns consisting of tones of different frequencies. This increased the uncertainty levels but only slightly increased the thresholds compared to experiment 3. The similar thresholds in experiment 4 clearly show that the context of the tones has only a minor effect on frequency discrimination in budgerigars. When the surrounding context varies along the same dimension as the dependent variable, budgerigars have only slightly more difficulty ignoring the context. Moreover, the tasks in experiment 4 ranged from low uncertainty, where the FDL being measured was always in the same position from trial to trial, to high uncertainty, where the FDL being measured could be in any position from trial to trial. Surprisingly, the budgerigars, in contrast to humans, were completely unaffected by the manipulations of uncertainty level.

One interpretation of the present results is that budgerigars can listen in an analytic mode even under high uncertainty conditions where humans cannot. For instance, Espinoza-Varas and Watson (1986) suggest that one effect of increasing the level of uncertainty in humans is that they switch from an analytic mode of listening (focusing attention on specific components while ignoring others) to a synthetic mode of listening (a multiple-channel mode of listening where the listeners focus on how the components are related). Perhaps budgerigars do not switch listening modes in the same way as humans.

Another interpretation for the species differences in these experiments comes from results of several studies on humans, which suggest that different processes mediate frequency discrimination in low- versus high-frequency regions. Temporal coding may be more important at low frequencies, while tonotopic organization is more relevant at higher frequencies (see Prosen *et al.*, 1989 for a review). Coding in birds is somewhat less certain than in mammals, but recent experiments suggest that some aspects of temporal processing in birds may be better than that found in humans (Dooling *et al.*, 1999). For instance, budgerigars show an enhanced ability to discriminate between two harmonic complexes with identical envelope shapes that differ only in temporal fine structure (Dent *et al.*, 1999). As another example, in discriminating silent temporal gaps in sinusoidal markers, budgerigar performance was relatively unaffected by a frequency change in the tonal marker following the gap, while humans show large decrements in performance as the separation between the markers exceeds the critical bandwidth (Amagai *et al.*, 1997). Finally, both budgerigars and zebra finches are much better than humans at detecting the mistuning of single components in a harmonic complex (Lohr and Dooling, 1998). If the transition from temporal to tonotopic coding is different in budgerigars, and they do have better temporal resolution than humans, then perhaps this may account for their superiority in discriminating complex patterns.

Yet another interpretation of the species differences in these experiments comes from auditory perception experiments in humans. Speech sounds represent extraordinarily familiar complex sounds with which humans have had extensive experience from an early age. Similar context effects have been reported in the visual domain as well. The ''word superiority effect'' refers to the fact that humans are better at visual letter perception when letters are presented in context of a word (for examples, see Johnston and McClelland, 1980; Reicher, 1969; Wheeler, 1970). Birds could be hearing these tonal patterns as a whole, perhaps like humans hear words. If this is so, then the species differences reported here may be due to the roles of learning strategies or differences in the focusing of auditory attention. Such factors have been shown to be important contributors to human performance in similar listening tasks (Leek and Watson, 1984, 1988). Following the lead of work on complex pattern perception in humans, these results suggest a useful future direction for experiments on the perception of species-specific vocal signals in birds. This direction would be to move beyond studies of the limits of resolution and begin to focus on attentional and memory processes that are recruited in the special processing of complex acoustic communication signals.

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