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The Discrimination of Temporal Fine Structure in Call-Like Harmonic Sounds by Birds

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Thresholds for discriminating changes in the temporal fine structure of call-like, harmonic sounds were measured in zebra finches (*Taeniopygia guttata*) and budgerigars (*Melopsittacus undulatus*). Birds could detect changes in periods as short as 1.225 ms at near 100% accuracy even when spectral and envelope cues were identical, as in time-reversed stimuli. Humans performed poorly on such stimuli, paralleling results from previous studies. Bird thresholds were in the range of those reported in neurophysiological studies of the songbird high vocal center (HVC) to temporally modified conspecific songs. Taken together, these results show that birds can hear differences in temporal fine structure in their natural vocalizations that go beyond human capabilities, but whether these abilities have communicative relevance remains to be seen.

Keywords: temporal fine structure, vocalizations, bird's own song, complex sounds, auditory perception

Many species of birds learn to communicate with temporally and spectrally complex acoustic signals. Such signals often involve rapid modulations in amplitude and/or frequency (Lavenex, 1999; Suthers, 2005). Thus far, however, despite well-known differences in anatomy and physiology of the avian and mammalian auditory systems, birds have not been shown to be dramatically more sensitive on standard psychoacoustic tests than other vertebrates, including humans (Dooling, Lohr, & Dent, 2000). This finding is based on typical measures of temporal sensitivity such as maximum temporal integration, detection of gaps in noise, duration discrimination, and the detection of amplitude modulation (Dooling & Haskell, 1978; Dooling & Searcy, 1981, 1985; Klump & Maier, 1989). A common feature of these earlier temporal tests is that they used standard psychoacoustic stimuli, such as tones and white noise, and examined larger scale, overall changes in a stimulus waveform such as the amplitude envelope.

By contrast, more recent tests of temporal resolving power involving changes in the temporal fine structure of complex harmonic sounds now show considerable differences between birds and mammals. In tests that involved mistuning a single component of a harmonic complex (a manipulation that introduces changes to the temporal fine structure of a waveform), Lohr and Dooling (1998) found that small birds, especially zebra finches, were nearly an order of magnitude more sensitive than humans. Additional studies using harmonic sounds generated with the Schroeder-phase algorithm (Schroeder, 1970), which minimizes envelope cues, also showed that birds are highly sensitive to subtle temporal changes in a stimulus waveform, detecting changes in temporal fine structure on much shorter time scales than do mammals (Dooling, Leek, Gleich, & Dent, 2002). Related experiments that used these complex harmonic stimuli as maskers strongly suggest that avian and mammalian peripheral auditory systems differ dramatically with respect to certain temporal characteristics and traveling wave mechanics (Dooling, Dent, Leek, & Gleich, 2001; Lauer, Dooling, Leek, & Lentz, 2006; Leek, Dent, & Dooling, 2000). Taken as a whole, these more recent results of fine temporal processing using artificial harmonic sounds raise questions regarding the temporal resolving powers of birds with respect to the specific types of changes found in a bird's natural communication signals.

Zebra finch calls and songs provide an ideal test of whether sensitivity to temporal fine structure underlies species-specific perceptual specializations. Temporal modifications to vocalizations produced in nature may be subtle and, rather than involving envelope cues, may involve alterations occurring on a time scale within the duration of single periods. Zebra finches are the most popular avian model for laboratory studies of vocal learning, vocal production, and auditory perception. Their natural calls are spectrally and temporally complex (harmonically rich, rapidly modulated), they are easily trained in operant conditioning experiments, and neural recordings of auditory-motor regions in the zebra finch brain strongly suggest a particular, if not unique, sensitivity to the characteristics of conspecific songs. In anesthetized and sleeping zebra finches and in other species such as white-crowned sparrows and song sparrows, neurons in the high vocal center of the avian nidopallium (HVC; Jarvis et al., 2005; Reiner et al., 2004) respond

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strongly to the presentation of a bird's own song (BOS; see Jarvis, 2004; Margoliash, 1983, 1986; Margoliash & Fortune, 1992; Nealen & Schmidt, 2002; Theunissen & Doupe, 1998; Volman, 1996). The HVC is the central song production nucleus responsible for the motor control of singing behavior. Such BOS-selective responses are also observed in other portions of the song control motor pathway (Doupe, 1997), but this song selectivity is generally not characteristic of anterior forebrain sensory pathways leading up to the HVC (Lewicki & Arthur, 1996; Sen, Theunissen, & Doupe, 2001). Furthermore, changes in syllable ordering, as well as playing the song in reverse, can significantly reduce the response of HVC neurons (Lewicki & Arthur, 1996; Lewicki & Konishi, 1995; Margoliash & Fortune, 1992). A compelling question concerns how much of this selectivity may be reflected by properties of the auditory periphery.

We investigated whether species-level and individual-specific advantages in perceptual processing are occurring at the level of temporal fine structure rather than at the level of the envelope of the sound. In other words, are the fine-scale changes occurring in complex communication signals discriminable to the birds that produce them? In Experiment 1, we tested whether birds could discriminate between natural and synthetic versions of species-specific zebra finch contact calls and whether response latency provided a measure of similarity in temporal fine structure. We compared response latencies when birds were discriminating between calls designed to match specific characteristics of a model stimulus. In Experiments 2A–2C, we tested several birds on a series of tasks asking more refined questions about temporal fine structure sensitivity. Here birds discriminated synthetic stimuli composed of repeated single periods taken from specific portions of natural zebra finch calls (see Experiment 2A), from the calls of different individuals (see Experiment 2B), and time-reversed versions of such stimuli (see Experiment 2C). In Experiment 3, we controlled for potential onset/offset cues and overall amplitude cues by measuring how many time-reversed periods were necessary for birds to detect a change between two synthetic complexes. In Experiment 4, birds discriminated between call-like stimuli, which differed in the phase characteristics between contiguous frequency bands to gradually reduce similarity of target calls from background models. These phase adjustments can be converted into time measurements that provide for an additional means of evaluating temporal resolution in the bird's auditory system on a fine scale, paralleling earlier physiological work (Theunissen & Doupe, 1998).

General Method

Subjects

A total of 11 zebra finches (*Taeniopygia guttata*; 4 male, 7 female), 7 budgerigars (*Melopsittacus undulatus*; 5 male, 2 female), and 6 human listeners (3 male, 3 female; ages 18–44) served as subjects in these experiments. One human subject (age 29) had her hearing tested and characterized as normal prior to participating in this study. As our results were similar across all human subjects for a given experiment, we presumed that all our human subjects had normal hearing. We housed birds in individual cages in a vivarium at the University of Maryland and kept them on a normal light–dark cycle correlated with the season. Zebra finches were offspring of birds obtained through commercial dealers. Budgerigars were first-generation captive descendants of wild Australian birds. We used yellow millet as a reinforcer during experimental sessions, and standard mixed finch or parakeet seed was available during free feeding times. We monitored the diet of the birds to keep them at about 90% of their free-feeding weight.

Stimuli

We constructed sound stimuli from natural zebra finch vocalizations. In Experiments 1–3 female zebra finch contact calls (i.e., long calls or distance calls; Zann, 1996) served as the models for our synthetic sounds. In Experiment 4 we tested birds on synthetic stimuli constructed by modifying portions of male zebra finch songs. Both female calls and male songs are broadband, spectrally complex sounds with substantial harmonic content (Blaich, Kovacevik, Tansinsin, Van Hoy, & Syud, 1995; Okanoya, Yoneda, & Kimura, 1993; Simpson & Vicario, 1990; Zann, 1984). We analyzed, decomposed, modified, and resynthesized vocalizations in different ways depending on the experiment, to test different aspects of the perception of temporal fine structure. We selected natural calls so as to represent the natural range of values for the temporal and spectral characteristics of these calls (for example, fundamental frequency and overall duration).

We recorded natural calls and songs of zebra finches in custom-built, anechoic chambers using a Realistic 33-3003 omnidirectional condenser microphone (RadioShack Corporation, Fort Worth, TX) and a Marantz PMD 740 analog tape deck (Marantz America, Inc., Itasra, IL). We used the SIGNAL/RTSD digital signal processing and synthesis software (Beeman, 2004) to create synthetic versions of female zebra finch calls. We modified stimuli for Experiment 4 from recordings of male song using proprietary software created to filter an original song into a set of adjacent narrowband signals, decompose the narrowband signals into amplitude and phase constituents using the analytical signal (Cohen, 1995), and recombine these signals after the introduction of a specified amount of Gaussian noise to the instantaneous relative phase across adjoining frequency bands (to within a given temporal resolution; Theunissen & Doupe, 1998). All stimuli were generated offline and stored as digital sound files on hard disk for playback during experiments using modules from Tucker-Davis Technologies (Alachua, FL).

Apparatus

We tested birds in a small animal operant conditioning chamber, the setup and design of which has been described previously (Dooling & Okanoya, 1995; Okanoya & Dooling, 1988). Briefly, we constructed cages 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. Cages were made of wire ($23 \times 25 \times 16$ cm) and were mounted in an IAC-3 sound isolation chamber (Industrial Acoustics Company, Inc., Bronx, NY). We controlled all experimental events using Visual Basic programs on Windows-based microcomputers.

During an experiment, we delivered stimuli through a Tucker-Davis Technologies System 2 DD1 stereo analog interface (Tucker-Davis Technologies, Alachua, FL) at 20 kHz, low-pass filtered at 8.5 kHz, sent to a Crown D-75 amplifier (Crown International, Inc., Elkhart, IN), and finally to a KEF 60S speaker (KEF Electronics of America, Inc., Holliston, MA) mounted 40 cm above the bird's head in the operant chamber. Stimuli were normalized to a level of 65 dB SPL RMS using a Larson-Davis System 824 Sound Level Meter (A-scale, fast response; Larson-Davis, Inc., Provo, UT). We calibrated sound stimuli by placing the half-inch (1.27 cm) microphone in the position normally occupied by the bird's head in the chamber.

Procedure

We trained birds to peck one LED (observation key) repeatedly during the iterative 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 a food reward. The first peck on the observation key started a timer with a random interval of 2–6 s. After the end of this random time interval, the next peck on the observation key resulted in the presentation of a target. 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 scored as a miss, was automatically ended, and a new trial was begun.

We tested birds in 100-trial sessions. Each block of 10 trials contained 7 target stimuli and 3 sham trials (during which the background stimulus was presented as a target)—also referred to as *catch trials*. 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 time-out period, during which lights in the test chamber were extinguished. A failure to peck at the report key during a sham trial (the proper response) was scored as a correct rejection, at which time the trial was ended, and a new trial was begun.

We used the method of constant stimuli for testing discrimination (Dooling & Okanoya, 1995; Gulick, Gescheider, & Frisina, 1989). We defined thresholds as the stimulus value corresponding to a 50% correct value adjusted for false alarm rate (Dooling & Okanoya, 1995; Gescheider, 1985) using the formula $Pc^* = (Pc - FA)/(1 - FA)$, where FA = false alarm, Pc = percent correct, and Pc^* = corrected percent correct. The latencies to discriminate between two stimuli were also recorded. Misses were assigned the maximum 2-s latency.

Human subjects, who were laboratory staff members, listened in the same sound field as the birds and were tested with the same repeating background procedure. All subjects listened to test stimuli using AKG Model K240 DF headphones (AKG Acoustics, USA, Nashville, TN) with a Larson-Davis System 824 Sound Level Meter recording directly off of a KEF 60S speaker mounted in the operant chambers. We placed the microphone of the sound-level meter in the position normally occupied by the bird's head in the chamber. The sound-level meter was connected through an AC output to a TTE 411AFS amplifier (TKE, Inc., Los Angeles, CA) and the headphones. We also tested 2 human subjects directly in the operant chambers used for avian subjects. This was done by removing the test cage from the chamber and having the human listener stand with his or her head in the location of the test cage at a distance roughly corresponding to the distance between the bird and the speaker during testing. Because results for humans using these two procedures did not differ, only data acquired using the headphones are presented here.

Analysis

We compared mean threshold or latency data in the following tests directly, either across individuals, species, or in some cases, across phase condition or durations within a species. In some cases, data were log-transformed to fit the distributional assumptions of analyses of variance and *t* tests for comparisons of mean values.

Experiment 1

In Experiment 1 we tested the ability of zebra finches to discriminate natural stimuli from synthetic sounds designed to simulate overall spectral and temporal changes in the stimulus. All target stimuli differed from background stimuli in their temporal fine structure. One of three target stimuli preserved the frequency profile, period duration, and amplitude envelope of the original natural call, but other target stimuli differed in these features from the background stimulus.

Method

We used 3 natural female zebra finch contact calls to generate synthetic zebra finch stimuli for this experiment. Calls were obtained from birds in our zebra finch colony, but not from individuals used as subjects in this experiment. Subjects were not familiar with these calls and had no prior experience with the individuals that produced them. We constructed synthetic calls by filtering and analyzing the fundamental frequency of each call, generating a sine wave signal matching the frequency profile of the fundamental frequency, and resynthesizing harmonics at average relative amplitudes based on measurements from the original calls (Beeman, 2004). We then superimposed amplitude envelopes extracted from each original call over the synthetic analogue. Synthetic stimuli thus differed from their natural analogues in temporal fine structure but not in period length, amplitude envelope profile, or overall duration. Stimulus durations ranged from 237–279 ms (see Figure 1).

A single natural call served as a background for each of 3 zebra finch subjects (2 males, 1 female), and target stimuli consisted of the synthetic analogue of the background call plus six other synthetic calls, for a total of seven different targets during each of 10 trials. Each subject received a different natural call as its background. We presented stimuli at a rate of 1.67/s (cycle length of 600 ms). We roved the intensity of the background and target stimuli randomly over a range of ± 1.5 dB to minimize the possibility that birds might use subtle amplitude differences between the background and target stimuli as cues, given the different overall amplitude envelopes of the background and some of the targets. Each bird ran a total of 300 trials.

Results and Discussion

There were no differences among birds or stimuli in terms of percent correct, as all three birds performed at or near 100% in detecting all target stimuli. We then examined response latency, which provides a finer measure of the difficulty of discriminating between stimuli (Dooling, Brown, Park, Okanoya, & Soli, 1987; Podgorny & Garner, 1979). We know from earlier work that longer response latencies reflect greater difficulty in discriminating between background and target sounds (Dooling et al., 1987). Figure 1 shows the latencies to discriminate a change between an alternating presentation of the synthetic target stimulus and the background call for each of the zebra finch subjects. The latency to discriminate between the natural call and its own synthetic analogue was longer than the latency to discriminate between the natural call and the synthetic analogues of the two other natural calls, $F(2, 87) > 3.03$, $p < .05$, η^2s > 0.065 for 2 birds, and $F(2, 87) = 2.41$, $p = .09$, $\eta^2 = 0.053$ for the 3rd bird, with data trending in the same direction. These results suggested a possible interaction between an individual's own call and the fine-scale features that were used to create synthetic models, as synthetic analogues differed principally in temporal fine structure (not in period length, amplitude envelope profile, or overall duration). Thus, Experiment 2 was designed to explore the perception of temporal fine structure in more detail.

Experiment 2

In Experiment 2 we designed test stimuli that controlled more precisely for the natural variation in spectral and temporal features of natural calls by creating synthetic harmonic complexes. By making changes only within single periods taken from natural zebra finch vocalizations, we could control for the effects of overall stimulus duration, changes in frequency profile over time, and relative harmonic amplitude. In other words, we excised single

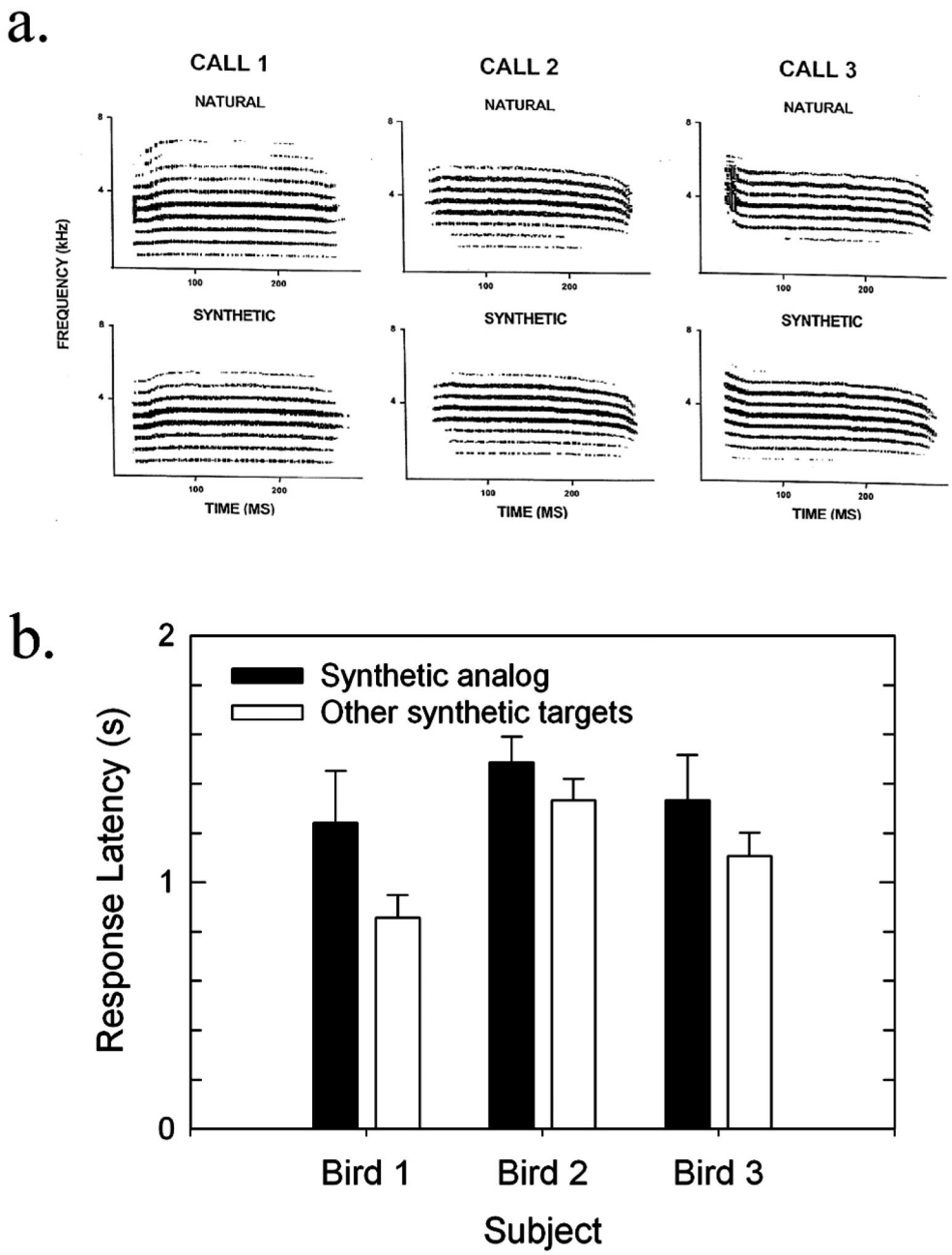

Figure 1. a: Spectrograms of three natural zebra finch calls and corresponding synthetic stimuli designed for Experiment 1 using parameters measured from each natural call. b: Response latencies (mean ± 95% confidence limits) for each subject to detect synthetic calls against a background of each natural call ($N = 30$ trials per bar). A different natural call served as background for each subject: Call 1 (279 ms) was for Subject 1, Call 2 (275 ms) was for Subject 2, and Call 3 (237 ms) was for Subject 3.

periods of natural zebra finch calls and replicated them to create a stimulus that simulated natural calls in terms of the waveform within an individual period, but having a flat envelope and no variation across periods in temporal fine structure (i.e., with no overall AM or FM). Three types of comparisons were tested with these stimuli: (a) periods taken from within the same call, (b) periods taken from the calls of different individuals, and (c) identical call periods played forward and backward.

Method

We generated synthetic stimuli using single periods of natural female zebra finch calls (see Figure 2). All natural call stimuli came from individuals in our colony not used in this experiment, and no subject had any experience with individuals from which the natural calls were recorded. Single periods were isolated, copied, and concatenated to create a 200-ms call. These synthetic calls were given a constant envelope with 10-ms

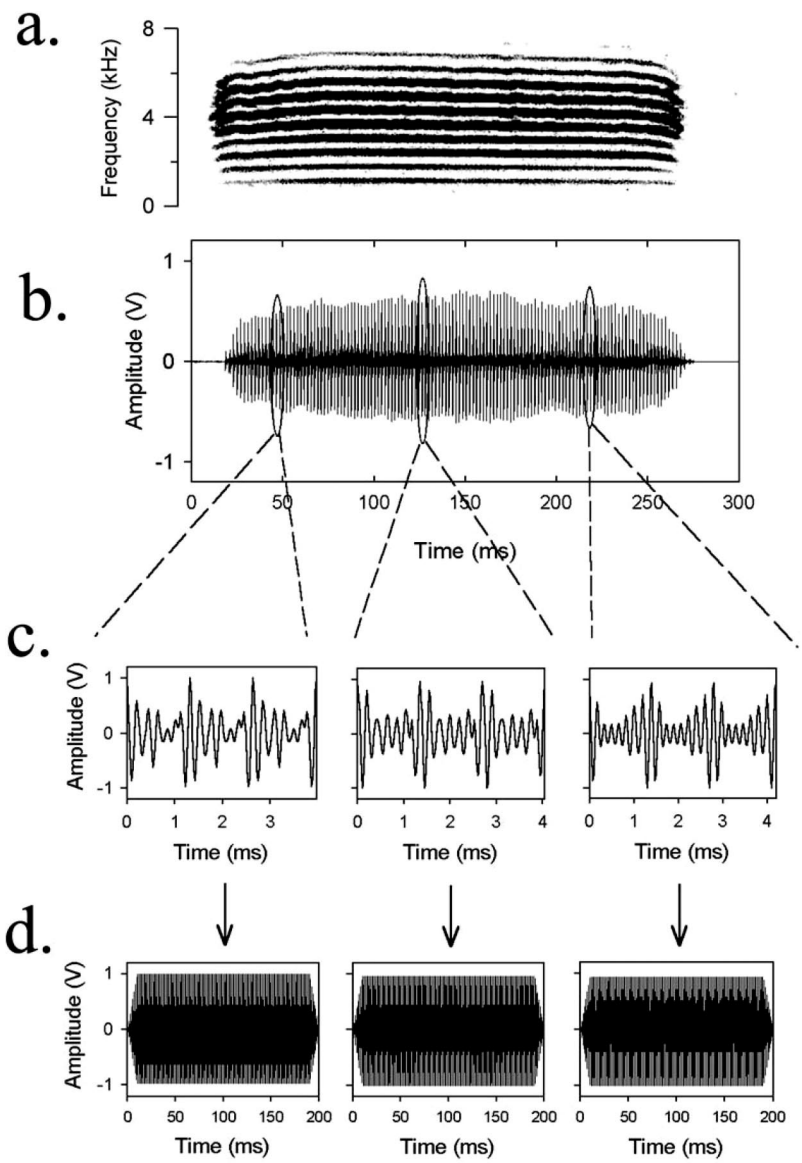

Figure 2. Schematic for the generation of synthetic harmonic calls used in Experiment 2. a: Sound spectrogram of female zebra finch contact call. b: Time waveform of spectrogram indicating regions selected for excision of single periods: Single periods were taken at random from the first 50 ms, central 50 ms, and final 50 ms to create synthetic calls. c: Expanded regions of the time waveform showing temporal fine structure of single periods. d: Synthetic calls reconstructed by replicating the individual periods.

linear onset/offset ramps. During stimulus presentation, we presented synthetic calls at a rate of 2/s (cycle length of 500 ms).

A: Period discrimination within the same call. Each test stimulus in this phase of the experiment was constructed from a single period taken randomly from around the beginning, middle, or end of a natural female zebra finch call, with each period replicated an appropriate number of times to produce a 200-ms synthetic call. Call periods chosen for this phase of the experiment ranged in duration from 1.325 ms to 1.400 ms, producing stimuli that ranged in fundamental frequency from 714 Hz to 755 Hz (see Table 1).

Birds were tested on their ability to detect a target stimulus composed of periods from a different part of the same call than the background. Two zebra finches (both female) and 2 budgerigars (1 male, 1 female) served as subjects in this part of the experiment. Each subject was tested on all of the following pairwise comparisons with one sound being the background and one the target: beginning/middle, beginning/end, middle/end, and middle/beginning. We ran birds for 100 trials for each of the two background stimuli (beginning and middle), giving a total of 70 possible targets and 30 sham trials in which the background and target stimuli were the same. Thirty targets consisted of one of the other call sections, 30 targets consisted of the remaining call section, and 10 targets were a heterospecific (canary, *Serinus canaria*) call. Order of presentation of the background stimulus (beginning or middle call periods) was randomized among individuals.

B: Period discrimination across different calls. In this part of the experiment, we tested birds on their ability to discriminate synthetic stimuli made from single periods of different zebra finch calls. In this case, we used periods taken near the middle of each of four different female zebra

Table 1
Period Duration and Fundamental Frequency (F0) for Stimuli Used in Experiment 2

Experiment and stimuli	Period (ms)	F0 (Hz)
Experiment 2A		
Beginning	1.325	755
Middle	1.350	741
End	1.400	714
Experiment 2B		
Background 1	1.450	690
Background 2	1.350	741
Target 1	1.225	816
Target 2	1.475	678
Experiment 2C		
Stimulus 1	1.450	690
Stimulus 2	1.475	678
Stimulus 3	1.450	690
Stimulus 4	1.225	816

finch calls to construct the background and target synthetic calls (see Figure 2b). Two stimuli served as the background sounds for subjects in this part of the experiment. We assigned each subject randomly to one of the two stimuli, with the stipulation that half the individuals of each species receive one background stimulus, half the other. The three remaining test stimuli not used as the background for a given subject served as targets. Call periods used in this part of the experiment ranged in duration from 1.225 ms to 1.475 ms, producing stimuli that ranged in fundamental frequency from 678 Hz to 816 Hz (see Table 1).

We tested 6 zebra finches (2 male, 4 female), 6 budgerigars (5 male, 1 female), and 2 human subjects (1 male, 1 female; ages 18 and 26) on these stimuli. Two zebra finches and 2 budgerigars were subjects in Phase A of this experiment. We ran birds for 100 trials giving a total of 70 possible targets (and 30 sham trials). We presented each of the 3 targets 20 times, with the 10 remaining targets consisting of a heterospecific (canary) call. As an additional control, we also tested 4 of the budgerigars (all male) and 4 of the zebra finches (2 male, 2 female) with background and target stimuli that were roved in intensity randomly over a ±1.5 dB range.

C: Discrimination of time-reversed periods. In this experiment, we tested birds on their ability to detect a time-reversed version of each stimulus. Such stimulus pairs have identical spectra and envelopes and differ only in the within-period temporal fine structure of the waveform. Both forward and reversed versions of the stimuli served as backgrounds and targets. Stimulus testing order was randomized across individuals. We ran subjects for a total of 200 trials, 100 trials each with forward and reversed versions of the same stimulus as background. Final performance measures were taken as the average value across these 200 trials for each individual. Call periods chosen for this part of the experiment ranged from 1.225 ms to 1.475 ms, producing stimuli having fundamental frequencies ranging from 678 Hz to 816 Hz, respectively (see Table 1).

We tested 6 zebra finches (2 male, 4 female), 6 budgerigars (5 male, 1 female), and 4 human subjects (2 male, 2 female; ages 18–44) on these stimuli. All avian subjects had previously been tested in Phase B of this experiment. As in Phase B, we tested 4 of the budgerigars (all male) and 4 of the zebra finches (2 male, 2 female) with background and target stimuli that were roved in intensity randomly over a ±1.5 dB range as a comparison with subjects that received constant-amplitude test sounds. For each species in each condition (0 dB rove or ±1.5 dB rove), no 2 individuals received the same background stimulus; assignments were made to specific subjects within each species and condition at random.

Results and Discussion

In general, subjects performed well on tasks involving synthetic calls made by replicating single periods from natural zebra finch contact calls with percent correct discrimination performance approaching 100% in many cases. The ease with which subjects were able to discriminate differences in some of these stimuli is instructive in terms of the differences in their general properties.

A: Period discrimination within call. Though birds showed some difficulty discriminating stimuli made from the beginning and middle of the call, most birds performed very well, reaching close to 100% correct discrimination on beginning/end and middle/end comparisons (see Figure 3a). We averaged results for the beginning/middle comparison, as synthetic calls made from beginning and middle periods served as both background and targets. Although the synthetic stimuli used in this experiment had identical envelopes and came from the same zebra finch call, they differed in period duration (and therefore fundamental frequency) and in timbre (or relative amplitude of different harmonics), as well as in temporal fine structure. Because these stimuli came from the same call and female zebra finch calls are relatively unmodulated in frequency, period durations and fundamental frequencies between stimuli did not differ as much as in the other phases of this experiment (see Table 1).

B: Period discrimination across calls. Again in this phase, birds performed very well; in almost all cases discrimination rates were at or near 100%. Results for Experiment 2B are shown in Figure 3b. Results across amplitude condition (roved vs. unroved) did not differ and thus are pooled here. Because synthetic stimuli were constructed from the calls of several individuals, there was a larger range of period durations and fundamental frequencies (see Table 1). Therefore, it is not surprising that subjects, including humans, performed well on these stimulus comparisons. As in Phase A, target stimuli differed from background stimuli in period duration and timbre, as well as in the temporal fine structure of individual periods.

C: Discrimination of time-reversed periods. In this phase, budgerigars and zebra finches outperformed human listeners. The stimuli and results for Experiment 2C are shown in Figure 3c as the mean values across all trials. A ±1.5 dB rove in intensity of the background and targets (total rove range of 3 dB) reduced performance in budgerigars and zebra finches, but not to the level of humans in the 0 dB rove condition. The stimuli in this phase of Experiment 2 differed from the earlier phases in that time-reversed stimuli differed only in temporal fine structure; envelope cues, frequency profile, period duration, and the spectral structure or harmonics were the same for background and target stimuli. In other words, the birds could use only cues pertaining to the time scale of single periods in the zebra finch call to discriminate these stimuli. Period durations for some of the test subjects were as brief as 1.225 ms (see Table 1).

By using single periods of natural zebra finch calls to create our stimuli, we were able to control for the effects of overall stimulus duration, changes in frequency profile over time, and relative harmonic amplitude. We found that birds were generally very good at discriminating differences in fine structure of periods as brief as 1.225 ms, especially when compared with human subjects.

Experiment 3

Experiment 3 further explored the discrimination of these time-reversed stimuli. In the previous experiments, the total length of a test stimulus was 200 ms, which we constructed by concatenating

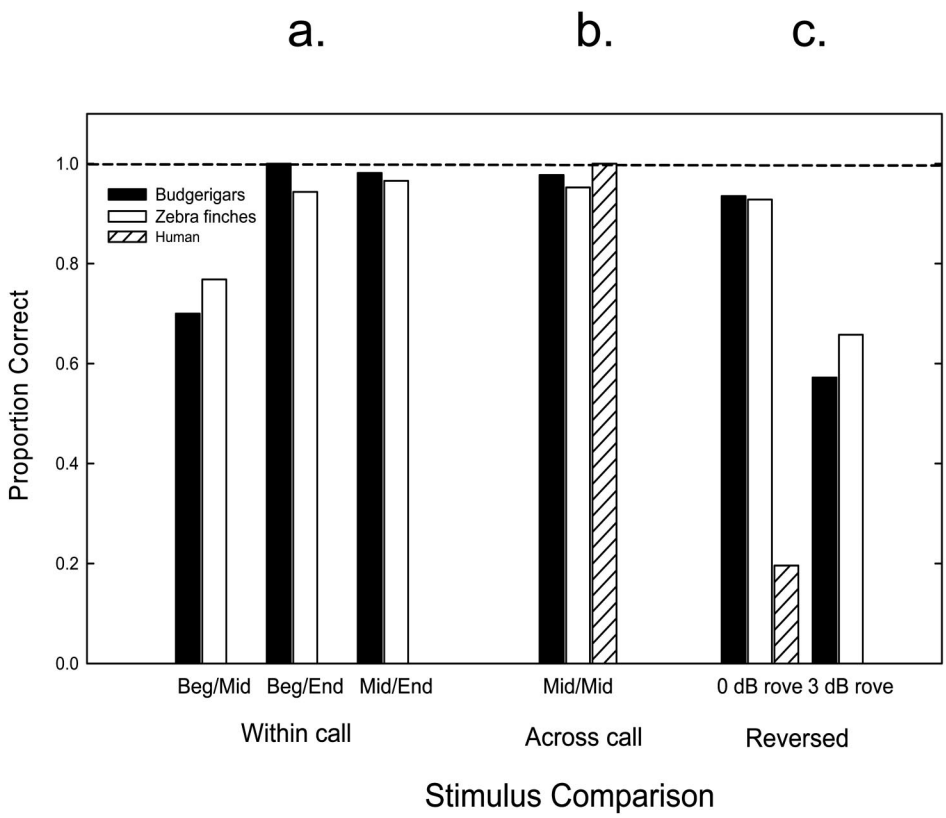

Figure 3. Thresholds for the detection of synthetic calls generated from single periods of natural female zebra finch contact calls in Experiment 2. a: Experiment 2A results from $n = 2$ budgerigars and $n = 2$ zebra finches tested on three different comparisons of periods taken from within the same call—beginning/middle (Beg/Mid), beginning/end (Beg/End), and middle/end (Mid/End). b: Experiment 2B results from $n = 6$ budgerigars, $n = 6$ zebra finches, and $n = 2$ human subjects tested on comparisons of middle periods taken from different zebra finch calls. c: Experiment 2C results from budgerigars, zebra finches, and human subjects tested on periods from a single call that were time-reversed (identical in spectrum and period duration, but different in fine structure). Results are provided for both the 0 dB rove and 3 dB rove ($\pm$1.5 dB) conditions ($N = 2$ subjects/bar for 0 dB rove condition; $N = 4$ subjects/bar for 3 dB rove).

a single period extracted from a natural zebra finch call. As a control for whether some kind of onset/offset cues might be used by the birds to make discriminations between time-reversed stimuli, we constructed stimulus period triads by concatenating three periods in which the first and last period in each three-period grouping were ramped up and down in amplitude, eliminating the potential for onset/offset transients, to create a series of pulses (see Figure 4). Such pulses were then reversed without creating transients. We then concatenated these pulses to make a 200-ms stimulus. Target stimuli differed from background stimuli in having some of the pulses in the beginning of the test stimulus reversed. Thus the task was to discriminate between a stimulus in which each pulse was identical from another stimulus of equal duration, envelope, and spectrum, in which some of the pulses in the beginning were reversed.

Method

Each pulse in our synthetic stimulus consisted of three identical zebra finch call periods with the first period ramped up in amplitude linearly, the second kept at constant amplitude, and the third ramped down linearly. The entire synthetic stimulus consisted of 50 of these pulses in succession, for a total stimulus duration of 221 ms. In this task birds were asked to discriminate target stimuli in which a pulse, or group of pulses, were reversed at the beginning of the stimulus. The background consisted of the same synthetic stimulus with no pulses reversed. Figure 4a shows the first 60 ms of a stimulus with the first pulse reversed. Stimuli were presented at a rate of 2/s (cycle length of 500 ms). Target stimuli consisted of stepwise increases in the number of pulses reversed at the beginning of the stimulus. We roved all stimuli in intensity randomly over a range of $\pm$1.5 dB. We defined threshold as the number of reversed pulses required for a 50% detection rate corrected for false alarm rate. We tested 3 zebra finches (1 male, 2 female) in this experiment, all of which had previously been tested in Experiment 2. All subjects received the same set of test stimuli, which we constructed from a single period from the middle of a single natural female zebra finch contact call, and each ran 200 trials (140 targets and 60 sham trials). The duration of this period was 1.450 ms, resulting in a stimulus with a fundamental frequency of 690 Hz.

Results and Discussion

Average thresholds for the 4 zebra finch subjects are given in Figure 4b. Zebra finches required the reversal of an average of

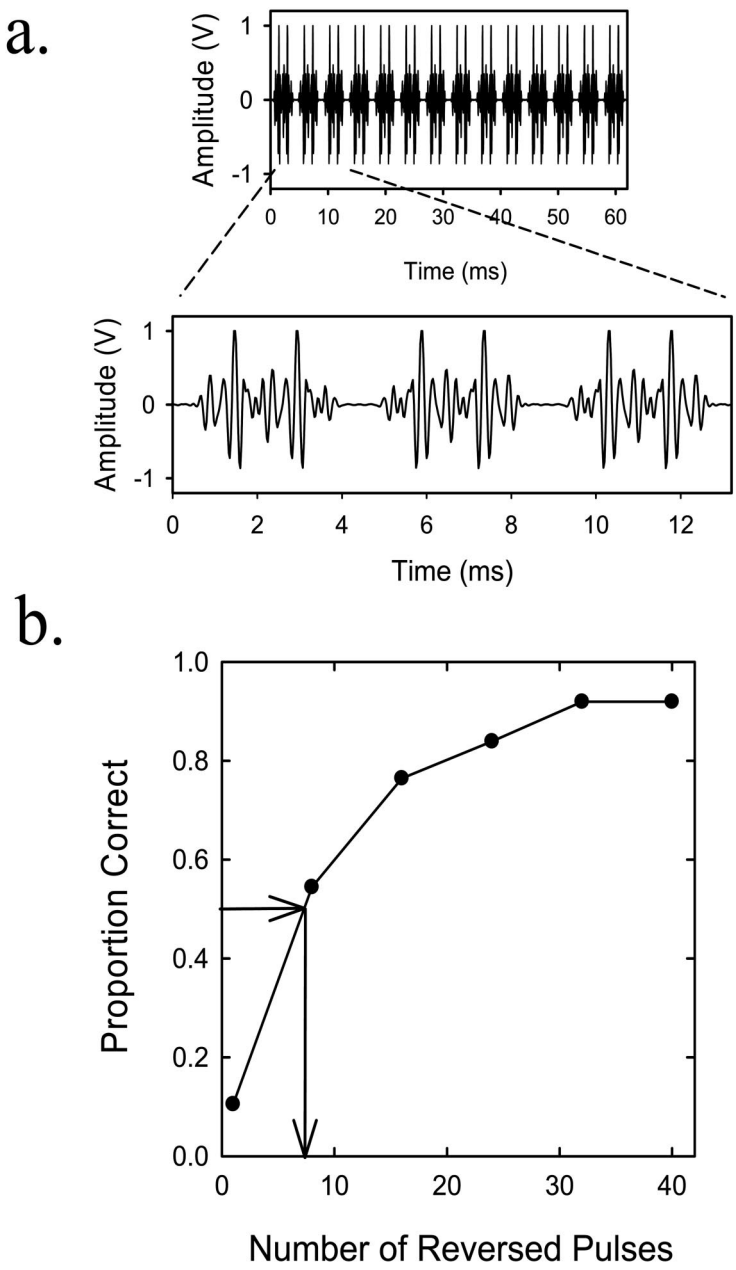

Figure 4. a: Temporal fine structure of synthetic stimulus used in Experiment 3. This stimulus was constructed by concatenating a series of pulses composed of replicated single periods from a natural female zebra finch contact call. Each pulse consisted of three periods with the first period ramped up (linearly), the second period at constant amplitude, and the third period ramped down (linearly). The expanded region shown depicts three such pulses, the first one of which has been reversed. Total stimulus duration consisted of 50 pulses (221 ms). b: Psychometric function showing 50% correct detection threshold for number of reversed pulses at the beginning of target stimuli.

only 7.29 pulses to discriminate the target stimulus from a background stimulus, which amounts to a duration of 31.71 ms. Experiment 3 thus demonstrated that zebra finches were able to make relatively rapid discriminations between stimuli that differed only in the fine temporal structure of individual periods, despite the lack of any potential onset/offset cues that might be related to the beginning and end of those periods.

Experiment 4

Experiment 4 further examined temporal fine structure discrimination abilities using an entirely different type of stimulus manipulation. In this case, adjustments to the fine time scale were expressed as modifications in the relative phase relationship among adjacent frequency bands of a natural vocalization. Such

phase-adjusted stimuli have the advantage of producing a set of sounds with progressively degraded temporal fine structure, creating a series of targets that depart from the background sound in a systematic way both spectrally and temporally. These stimuli have the added advantage of having been used previously to assess the temporal properties of neural responses in higher brain vocal motor centers, in particular HVC, of zebra finches (Theunissen & Doupe, 1998).

Method

We tested 4 zebra finches (2 males, 2 females) and 4 human subjects (2 male, 2 female; ages 18–36) on these stimuli. One high-quality recording of song from each of the two zebra finch males that took part in this experiment were used as stimuli so that we could examine the effects of a BOS. We used single motifs (repeating song units) as our stimuli in this experiment. We presented these motifs at a rate of 0.83/s (cycle length of 1,200 ms) for the longer of the two stimuli (840 ms) and 1.25/s (cycle length of 800 ms) for the shorter of the two stimuli (550 ms). We roved intensity randomly over a range of ± 1.5 dB to minimize the possibility that birds might use subtle amplitude differences as cues, given the different overall amplitude envelopes of the stimuli. We tested birds over 500–700 trials and used the average of the last 200 trials to determine thresholds.

We used a bank of overlapping narrowband filters to decompose the original song motifs to create a parametric representation of song using the technique of Theunissen and Doupe (1998; see Figure 5a). The narrowband signals can be described by two parameters, the time-varying amplitude envelope and time-varying phase of the carrier frequency. We constructed a series of progressively altered synthetic songs by choosing an intermediate filter width (62.5 Hz) and systematically adding noise to the instantaneous relative phase relationships across adjacent frequency bands. An intermediate filter width was chosen as an optimal tradeoff between time and frequency resolution, and because identical songs generated with this intermediate filter width elicited good responses from HVC neurons (Theunissen & Doupe, 1998). We specified the amount of noise added to synthetic signals to alter the relative phase between frequency bands to within a given temporal resolution. We changed the value of the temporal resolution in a stepwise fashion by allowing Gaussian deviations from the original relative phase at each time point and varying the width of the Gaussian noise incrementally. The width of the noise was expressed in radians, which were translated into time units by dividing by $(2\pi)62.5$. Alterations in the temporal resolution of the relative phase were made in equal step sizes ranging from 0 ms (identical to the original song, minus an absolute phase adjustment) to 7 ms (relative phase almost completely random).

Results and Discussion

Zebra finches showed a high degree of sensitivity to the alterations in these songs (see Figure 5b). We find it interesting that male zebra finches were not particularly sensitive to BOS, showing similar thresholds to changes in relative phase in their own songs as well as to songs of the other male in the study. Highly sensitive responses were not limited to typical male zebra finch songs, as birds also showed similar thresholds to songs played backward. The threshold for male zebra finches across all treatments was 1.72 ± 0.29 ms (mean $\pm$ 95% CI). Female zebra finches showed similar thresholds when compared with males (2.09 ± 0.69 ms), suggesting that female birds are equally adept at detecting such alterations.

Taken as a whole, birds were better at detecting these alterations than were humans, $t(6) = -3.03$, $p < .05$, $d = 2.14$. Human listeners as a whole also showed similar thresholds across treatments (2.58 ± 0.34 ms), though human subjects had better thresholds for one of the two song types, the song of Male 1 (2.27 ± 0.45 ms) when compared with the song of Male 2 (2.89 ms $\pm$ 0.50 ms); however, this difference was not significant, $t(6) = -1.53$, $p = .18$, $d = 1.08$. Any potential difference in threshold at this level, however, might be due to general acoustic differences between the songs. Song motifs of Male 1, for instance, were longer in duration than those of Male 2, affording more time in which to make a decision.

General Discussion

Studies of the peripheral and central auditory systems of birds have long suggested that birds should have extremely fine temporal processing abilities (Carr & Friedman, 1999; Greenewalt, 1968; Konishi, 1969; Pumphrey, 1961; Schwartzkopff, 1968). Until recently, however, psychophysical tests of general auditory sensitivity have failed to demonstrate any major differences between the hearing abilities of birds and mammals (Dooling et al., 2000). The experiments described here demonstrate that birds are able to discriminate the differences in temporal fine structure that occur in their natural vocal communication signals. Given the rapid modulations in frequency and amplitude that characterize the natural vocal signals of many birds, and the subtle complexities of the short-scale time waveform in some of these signals, it would be surprising if birds were not sensitive to such changes.

The calls and songs of zebra finches—harmonically rich with subtle differences in temporal fine structure—serve as ideal natural signals for testing the abilities of birds to detect fine temporal differences in the waveform of a sound. Our results with such stimuli here reinforce recent results with Schroeder harmonic complexes that varied only in temporal fine structure (Dooling et al., 2001, 2002; Lauer et al., 2006; Leek et al., 2000). The significance of the present results is the demonstration that this kind of temporal fine structure exists in natural calls, and this level of sensitivity in birds enables them to discriminate between calls of different birds; between different segments of the same call; and although an unnatural event, between forward and reversed versions of the same temporal fine structure pattern. This last discrimination task can only involve changes in temporal fine structure, as all other acoustic features are identical.

Temporal fine structure may be quite salient to these birds, because as a general rule, birds were easily able to detect differences between target and background sounds in our stimuli. Stimuli made from periods taken from the beginning and middle of a call differed by only 14 Hz in fundamental frequency, whereas stimuli made from middle and end periods, the next closest in duration, differed by 27 Hz. The former is at the limit of what budgerigars and songbirds can detect in terms of frequency difference limens for tones (Dent, Dooling, & Pierce, 2000; Dooling & Saunders, 1975; Sinnott, Sachs, & Hienz, 1980). A contrast between stimuli made from the periods of different calls in Experiment 2B resulted in equally high discrimination thresholds (see Figure 3b). As with sounds made from different periods of the same call, birds (and human subjects) were able to distinguish among such stimuli at near 100% accuracy, because the stimuli also differed in period duration/fundamental frequency as well as in their overall spectral structure.

The use of time-reversed stimuli precluded differences in either spectral structure or period duration/fundamental frequency from

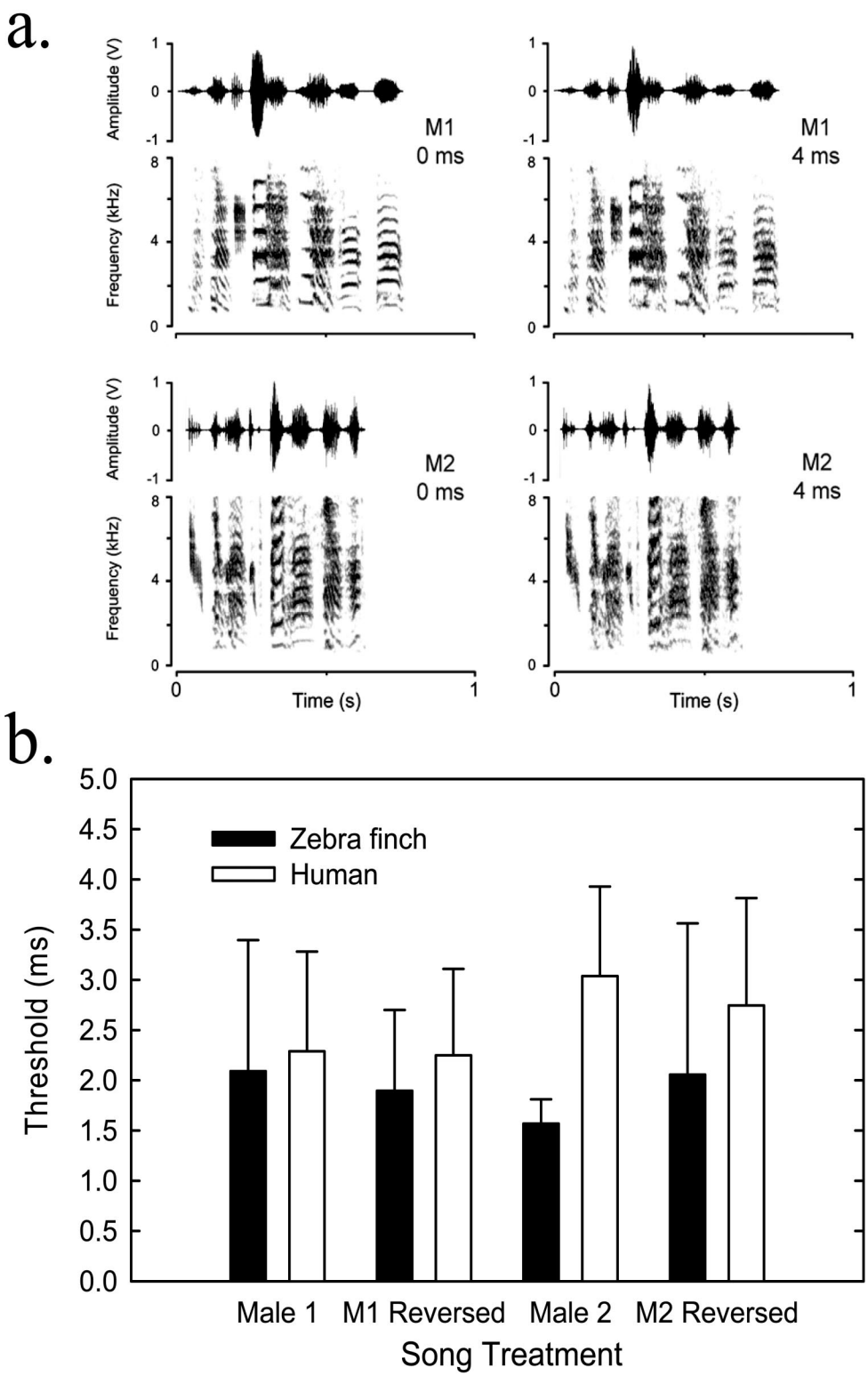

Figure 5. a: Synthetic song stimuli for Experiment 4. M1 = song of Male 1, M2 = song of Male 2. Synthetic stimuli were created by systematically adding noise to the instantaneous relative phase relationships across adjacent frequency bands. The left spectrograms show songs with 0 ms relative phase precision in song reassembly (identical to the original stimulus). The right spectrograms show songs with 4 ms relative phase precision. b: Thresholds for detecting the relative phase precision in progressively degraded song segments using a background stimulus with 0 ms phase precision (mean ± 95% confidence limits). Each bar represents the response of $N = 4$ subjects (2 male, 2 female for both zebra finches and humans).

influencing discrimination abilities, as stimuli played forward and backward have identical spectral structure and period duration. Both zebra finches and budgerigars were adept at detecting reversed versions of the background sound, but human subjects performed poorly (see Figure 3c). It is interesting to note that roving the amplitude of stimuli decreased performance in zebra finches and budgerigars somewhat, but still not to the level of humans. This suggests that birds could be on the edge of their perceptual limits in detecting time-reversed natural periods with durations as short as 1.225 ms. This again parallels studies with time-reversed Schroeder harmonic complexes showing zebra finches and budgerigars discriminating between stimuli with period durations as brief as 1–2 ms, whereas human subjects required at least 3–4 ms (Dooling et al., 2002).

Experiment 3 examined how much stimulus reversal was required to discriminate forward versus reversed stimuli. To evaluate this integration time for detecting a time-reversed stimulus, and as an additional check on the effects of slower, overall changes in amplitude, we designed a stimulus composed of ramped pulses consisting of three-period groupings (see Figure 4). The stimuli used in these tests were 200 ms long. Although the differences between the stimuli occurred only within a period, there were obviously many periods within a stimulus. The birds were able to detect target sounds in which slightly more than seven pulses at the beginning of the stimulus had been reversed, resulting in a total integration time of 31.71 ms. Because each three-period grouping contained a ramped period at either end, and a constant amplitude period in the middle, birds on average required a total of 10.57 ms of reversed periods at full amplitude to detect target sounds against a background sound with no pulses reversed. Birds therefore required a relatively brief time period in which to recognize that the temporal fine structure of otherwise identical stimuli had been altered.

Another way in which natural sounds may be modified and tested on a fine time scale is through the decomposition of the narrowband components of such sounds into their constituent amplitude and instantaneous phase signals and the consequent alteration in the relationship of these components to one another. The amplitude of each signal reflects the overlying envelope structure of each frequency band, and the instantaneous phase describes the temporal fine structure. This general technique has been applied commonly in studies of human speech perception (Flanagan, 1980; Smith, Delgutte, & Oxenham, 2002). Song stimuli were decomposed into their constituent amplitude and phase portions using the analytical signal (Cohen, 1995), following the techniques of Theunissen and Doupe (1998). Rather than female contact calls, our model stimuli in this case were the harmonic songs of male zebra finches, as we wished to make a direct comparison with previous neurophysiological recordings using these vocalizations. Our behavioral results for zebra finches on the phase-adjusted stimuli of Experiment 4 accord well with results from a prior study investigating responses of HVC neurons to zebra finch song stimuli generated in an identical manner. Theunissen and Doupe (1998) showed that the selectivity of HVC units dropped off in a linear manner when temporal resolution of the instantaneous relative phase across frequency bands was increased beyond 2.0 ms for BOS. Birds and humans in our study were very sensitive to such modifications (though birds more so), giving thresholds very similar to those obtained from neural recordings in HVC. Unlike electrophysiological recordings in HVC, however, the behavioral thresholds for discriminating changes in zebra finch song did not show selectivity for an individual's own song, nor for the song played forward versus backward. These results suggest that precise temporal information present in the relative phase of any complex sound is preserved in both high-level general auditory areas as well as in areas specialized for detecting particular songs. The similarity in sensitivity of the time-frequency scale between the auditory periphery and higher auditory areas in the central nervous system may reflect a coevolution in the perceptual and motor structures of the songbird.

In general, human subjects performed more poorly on fine scale temporal auditory tasks when compared to birds. This result was particularly true for time-reversed stimuli. In human speech perception, envelope characteristics take precedence over fine structure for the intelligibility of speech, and fine structure cues predominate for sound localization and pitch perception (Smith et al., 2002). Birds may be only marginally more sensitive than humans to larger scale changes in the stimulus envelope, such as the across-channel cues in comodulation masking release, a mechanism of signal detection potentially important in natural habitats (Dooling et al., 2000; Klump & Langemann, 1995). Without discounting the potential importance of envelope cues for birds, their enhanced sensitivity to relatively brief acoustic time scales suggests that the temporal fine structure of birdsongs and calls may be meaningful in terms of its potential for transmitting information in biologically important contexts. Enhanced sensitivity to temporal fine structure, for instance, may play a role in the detection of within-channel cues in comodulation masking release (Klump & Langemann, 1995; Schooneveldt & Moore, 1987). Our data suggest that among birds, temporal resolving ability for call-like stimuli does not differ dramatically between species, though further comparative studies are needed to determine the range of sensitivity to temporal fine structure across phylogenetic groups within birds.

In these experiments we have shown that birds can discriminate subtle temporal changes within the context of differences typically found in their natural vocal communication signals. Our results support more recent studies of peripheral auditory sensitivity in birds that have begun to demonstrate their enhanced temporal acuity, beyond the abilities reported for humans and many other mammals. Other recent tests have shown the remarkable sensitivity of birds to certain types of spectral changes in complex, harmonic sounds. For instance, zebra finches are capable of detecting 2–5-dB alterations in the relative amplitudes of single components in harmonic sounds (Cynx, Williams, & Nottebohm, 1990; Lohr & Dooling, 1998). Such enhanced spectral abilities may in part reflect underlying sensitivity to small changes in the temporal components of these signals. Indeed, estimates of auditory channel bandwidth in birds (reviewed in Dooling et al., 2000; Fay, 1988) suggest that bird filter bandwidths are no narrower than those of humans.

Past studies of bird vocalizations have focused predominantly on the spectral characteristics of these sounds but less on the overall temporal features, with fewer still on variations in the temporal fine structure (Lavenex, 1999). Given the types of natural signals that some birds produce in the wild, and recent findings on the fine degree of motor control of such signals in vocal production (Brainard & Doupe, 2001; Fee, Shraiman, Pesaran, & Mitra, 1998; Tchernichovski, Mitra, Lints, & Nottebohm, 2001; Yu & Margoliash, 1996), the perception of the fine-scale temporal characteris-

tics of complex sounds may be more relevant to the problems of acoustic communication than previously thought. Sensitivity to the fine-scale temporal structure of natural vocal signals is well known in insects, anuran amphibians, and even some mammals that produce and rely on rapid changes in the waveform (Gerhardt & Huber, 2002; Moss & Simmons, 1996). We have provided evidence here that birds can resolve temporal differences as brief as 1–2 ms using naturally produced waveform periods and that they are therefore capable of discriminating changes on the level of single periods of complex natural vocal signals such as zebra finch calls.

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