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Discrimination of auditory gratings in birds

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Abstract

Auditory gratings (also called auditory ripples) are a family of complex, broadband sounds with sinusoidally-modulated logarithmic amplitudes and a drifting spectral envelope. These stimuli have been studied both physiologically in mammals and psychophysically in humans. Auditory gratings share spectro-temporal properties with many natural sounds, including species-specific vocalizations and the formant transitions of human speech (Versnel and Shamma, 1998). We successfully trained zebra finches and budgerigars, using operant conditioning methods, to discriminate between flat-spectrum broadband noise and noises with ripple spectra of different densities that moved up or down in frequency at various rates. Results show that discrimination thresholds (minimum modulation depth) increased as a function of increasing grating periodicity and density across all species. Results also show that discrimination in the two species of birds was better at those grating densities and periodicities that are prominent in their species-specific vocalizations. Budgerigars were generally more sensitive than both zebra finches and humans. Both bird species showed greater sensitivity to descending auditory gratings, which mirrors the main direction in their vocalizations. Humans, on the other hand, showed no directional preference even though speech is somewhat downward directional. Overall, our results are suggestive of both common strategies in the processing of complex sounds between birds and mammals and specialized, species-specific variations on that processing in birds.

Keywords

auditory grating; threshold; budgerigar; zebra finch; human; psychoacoustics

INTRODUCTION

A common assumption that motivates auditory research is that the auditory system of a species has evolved to have processing properties that best serve its survival within its

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ecological niche. The vast majority of natural sounds that an organism hears, including environmental sounds and species-specific vocalizations, are inherently complex. Both humans and birds, for example, produce highly structured acoustic communication signals (speech and birdsong, respectively) that can vary dramatically in frequency content over very short periods of time. Both speech and birdsong consist of a hierarchical arrangement of components, including phonological (sound structure), sequential (sound order), and prosodic (i.e., frequency, amplitude, and timing) elements (Doupe and Kuhl, 1999). In the case of birds, different components of vocalizations can convey information related to individual identification, reproductive status, food availability, and territory ownership, among other things (see Kroodsma and Miller, 1996). This study is broadly inspired by the ethological hypothesis that the auditory system has mechanisms that are especially sensitive to the species' own vocalizations.

Communication signals are often very complex both spectrally and temporally. This renders them difficult to quantify and manipulate in any systematic study of the auditory system. Hearing research, therefore, has historically been limited to investigations of simpler stimuli, such as pure tones and white noise. The use of these simple sounds has the advantage of easily accessing the basic abilities of the auditory system. Such research often proceeds under the assumption that complex sound processing represents the additive contributions of simpler processing components that separately analyze the more fundamental aspects of a sound, such as frequency and modulation rate (Klein et al., 2000).

The presumption that the basic features of a sound are processed independently has not been borne out by recent research, though. Many of the multiple dimensions of a sound stimulus may be processed simultaneously. For example, neuronal responses in auditory cortex can be represented by a spectro-temporal response field (STRF), which is defined by two component axes: a spectral axis that describes the range of frequencies that will affect a given neuron's firing rate and a temporal axis that describes the change in its firing rate over time (Depireux et al., 2001; Klein et al., 2000). Therefore, calculation of the STRF involves finding the spectral and temporal patterns of a sound that reliably result in the maximal stimulation of a given neuron.

Typically, the STRF can be obtained by presenting a parametrically varied series of moving auditory gratings as stimuli (see Methods for details of the auditory gratings). In a manner analogous to the Fourier transform of time-based signals into a sum of individual frequencies and phases, arbitrary sounds can be decomposed into a sum of auditory gratings—providing the bridge from STRF responses to evoking sound stimuli. That is, the representation of a sound in the dimensions of gratings can be used to predict the actual response of a system that is characterized by an STRF. This allows researchers the opportunity to accurately study how the nervous system processes variations within these complex sounds (Depireux et al., 2001), or even behaviorally match the response of the entire auditory system to ecologically relevant sounds (e.g., Chi et al., 1999). Thus, the use of auditory gratings may provide a compromise between simple stimuli, like tones, and more natural sounds, such as vocalizations.

Auditory gratings have been extraordinarily useful in studies of the neuronal responses to dynamic spectral and temporal characteristics of complex sounds (Depireux et al., 2001; Kowalski et al., 1996a; Kowalski et al., 1996b). Neurophysiological studies of domestic ferret (*Mustela putorius*) auditory cortex have described neurons that phase lock their firing rate to the spectral and temporal modulations of moving gratings over a range of densities and periodicities; each neuron appears to have a preferred density/periodicity combination (Depireux et al., 2001).

Moving auditory gratings also share spectro-temporal properties with many natural sounds, including species-specific vocalizations and the formant transitions of human speech (Versnel and Shamma, 1998). This suggests that moving gratings would make excellent stimuli for psychophysical research involving complex broadband sound perception, especially in species with complex vocalizations such as mammals (particularly humans) and birds. To date, however, psychoacoustic research involving these complex sounds has been performed only in a limited number of mammalian species and not at all in avian species. In humans, moving gratings have been used to measure discrimination thresholds across a variety of spectro-temporal modulations (Chi et al., 1999). More recent work has begun with domestic ferrets (Fritz et al., 2002) and monkeys (*Macaca mulatta*) and humans (Versnel and van Opstal, 2002).

Zebra finches (*Taeniopygia guttata*) are small Australian songbirds that are popular laboratory animals in studies of vocal communication and vocal learning. These birds may be especially interesting test subjects for studies of moving grating perception because they produce complex broadband harmonic songs (see Zann, 1984; Zann, 1996) and they are exceptionally sensitive to the temporal fine structure of their calls. (Lohr and Dooling, 1998) For example, zebra finches are extremely good at detecting mistunings of single harmonics within complex harmonic stimuli (Lohr and Dooling, 1998). Other work has shown that these birds are exceptional at discriminating between complex harmonic waveforms with fundamental periods as short as 1–2 ms (Dooling et al., 2002) and also at detecting small changes in the duration between their song syllables (Nespor and Dooling, 1997). Although only male zebra finches sing their species-specific stereotypical songs (see Figure 1 for an example), there is considerable evidence that the sexes have similar perception over a wide range of stimuli (Dooling et al., 1995; Lohr et al., 2006; but see Ratcliffe and Otter, 1996).

The experiment described herein uses moving auditory gratings of various densities and periodicities to test the sensitivity of the auditory system of zebra finches and, for comparison, budgerigars (*Melopsitticus undulatus*). Budgerigars are small Australian parrots that have a complex, learned vocal repertoire (for review, see Farabaugh and Dooling, 1996; Farabaugh et al., 1992) and much is known about their hearing abilities (e.g., Dooling and Saunders, 1975; Dooling et al., 2000). Previous work in our laboratory has measured modulation depth (i.e., peak-to-trough in dB) thresholds for iterated rippled noise and also for static, non-moving gratings in both budgerigars and humans (Amagai et al., 1999). This work has demonstrated that budgerigars are at least as good as humans at discriminating iterated ripples and outperform humans on tests involving discrimination of static gratings. Similar to zebra finches, most studies show little difference in auditory perception between the sexes (e.g., Dooling et al., 1995; Dooling et al., 2001). Both male and female

budgerigars produce a variety of calls. However, predominantly (though not exclusively) males produce the long, rambling complex song known as warble that seems to be important for social cohesion and mating (Brockway, 1964a; Brockway, 1964b).

Figure 2 shows a spectrogram of one segment from a warble, illustrating the variety of different elements and range of spectrotemporal structures that comprise a song.

These two species make an excellent comparison because, unlike the harmonic vocalizations of zebra finches, budgerigar vocalizations are primarily tonal and frequency-modulated (although they do sometimes produce harmonic vocalizations within warble song) (Ali et al., 1993; Farabaugh et al., 1992). Such differences in the acoustic characteristics of a species' vocalizations may be related to observed perceptual differences in the processing of those vocalizations. For instance, we already know that zebra finches and budgerigars each show superior discrimination of their own species-specific calls (Dooling et al., 1992). Perhaps the present experiment can elucidate potential differences in complex sound processing which may underlie these species-specific perceptual abilities.

In the present experiment, zebra finches and budgerigars were trained using operant conditioning methods to discriminate between flat-spectrum broadband noise and noises composed of dynamic moving auditory gratings. In addition, the natural vocalizations of both species were recorded and analyzed in order to uncover consistent patterns of spectrotemporal changes within them. The modulation patterns present in their vocalizations were then compared with the discrimination results from the psychophysical experiments in order to determine whether special processing of species-specific complex sounds may exist in either, or both, of these species.

MATERIALS AND METHOD

Subjects

The subjects in this experiment were three zebra finches (two males and one female) and two budgerigars (one male and one female). All birds were housed in individual cages (approximately 28×28×18 cm) in a vivarium at the University of Maryland. They were maintained at approximately 85–90% of their free-feeding weight and kept on a light/dark cycle correlated with the season. For comparison, three human subjects were also run in the same testing conditions in order to provide a check on the validity of the present procedures and apparatus and also to serve as a comparison with existing human data from another laboratory (Chi et al., 1999).

Stimuli

Moving auditory gratings are broadband stimuli that have a spectral envelope which is sinusoidally-modulated against a logarithmic frequency axis (Figure 3) and can drift up or down in frequency over time (Figure 4) (Depireux et al., 1998). The dynamic pattern of spectral and temporal modulations that characterize these complex synthetic sounds can be precisely quantified and modified across a range of grating densities (the spacing between successive peaks of the sinusoidal envelope) and grating periodicities (the drifting speed of the envelope).

The auditory grating stimuli were created using procedures previously described by Shamma and his colleagues (Depireux et al., 2001; Klein et al., 2000; Kowalski et al., 1996a; Kowalski et al., 1996b). The stimuli used in the present experiment were complex broadband sounds consisting of 500 tones equally spaced on a logarithmic frequency axis across 5 octaves (0.25 to 8 kHz; 100 tones per octave) and had a sinusoidally-shaped (rippled) spectral envelope modulated on a linear amplitude scale. These sounds are dynamic and can be modulated in time by having the sinusoidal profile move either up or down in frequency at a constant periodicity.

An auditory grating can be characterized by five independent parameters: Density (measured in cycles/octave), periodicity (measured in cycles/second [Hz]), amplitude (in percent [%] modulation depth), overall level (or intensity [dB], usually measured as rms), and the initial phase (Φ) of the grating envelope. The stimuli in this experiment consisted of gratings with densities of .5, 2, and 4 cycles/octave and periodicities of 4, 8, 16, and 32 Hz. These specific parameters were chosen because, based on rate-scale plot analyses (see Results section below), they were the most likely densities and periodicities that would encompass all or most of the relevant modulations which may be present in the vocalizations of these species. For each density/periodicity combination, a range of stimuli with differing amplitudes was created (in steps of 5% modulation depth). The amplitude of each sound was taken as the percent deviation of the sinusoidal spectral envelope from a flat-spectrum envelope (0% modulation depth would be equivalent to such a flat spectrum).

All stimuli in this experiment began at zero phase and were presented at intensities roved over a 10 dB range. The average overall sound level across stimulus presentations was 70 dB SPL. All stimuli were 500 ms in duration with an 8 ms rise/fall time (40,000 Hz sampling rate) and band-pass filtered between 50 Hz and 8,500 Hz.

Operant testing apparatus

The birds were tested in a wire cage (23×25×16 cm) mounted in a sound isolation chamber (Industrial Acoustic Company, New York, NY, model IAC-3). A panel consisting of two microswitches, each connected to a light-emitting diode (LED), was mounted on the wall of the cage just above a food hopper. The left microswitch and LED served as the observation key while the right microswitch and LED served as the report key; each microswitch was triggered when a bird pecked its corresponding LED. Sounds were delivered from a loudspeaker (KEF Electronics, Holliston, MA, model 80C) mounted 25 cm above the test cage. Stimulus calibration was performed periodically during the experiment using a Larson Davis (Provo, UT) sound level meter (Model 824). All test sessions were computer-controlled and the birds' behavior was monitored during each test session by a video camera system (Sony Corporation, Park Ridge, NJ, model HVM-322).

Operant training and testing procedures

The training and testing procedures used in this experiment have been described in detail previously by Okanoya and Dooling (1987), but are described briefly. All birds were trained through operant conditioning methods to discriminate between a repeating background sound (a broadband sound that resembles an auditory grating, but with a flat, non-rippled

spectral profile) and a target sound (an auditory grating). The birds were trained to peck the observation key (left LED) during the repeating background until a target stimulus was presented. The time between the first peck of the observation key and the beginning of a target sound (e.g., a trial) was randomized between 2 and 8 s. The bird was then presented with an alternation of the target and background sounds during a 2.5 s response interval (i.e., a total of three target and two background stimuli for a type of “oddball detection” task). If the bird detected a difference between the background and target sounds, it was trained to peck the report key (right LED) within that response interval in order to receive 2-s access to a food reward.

A hit rate was calculated based on the proportion of correct responses during those trials that involved the target sound. A failure to peck the report key during presentation of the target sound was recorded as a “miss”, and a new trial sequence was then initiated. Thirty percent of all trials were sham trials in which the target sound was the same as the repeating background sound. Pecking the report key during a sham trial was recorded as a “false alarm”, and the chamber lights were extinguished (a “blackout”). The length of this blackout period was normally 5 s, but varied according to an individual bird’s behavior (longer blackouts were imposed if a bird’s false alarm rate increased). Pecking the report key when no target sound was present (e.g., after the response interval of a trial) also resulted in a blackout period.

For each experimental condition, stimuli were presented across a range of grating amplitudes presented in steps of 5% modulation depth (percent change from the flat spectrum repeating background) using the Method of Constant Stimuli (Dooling, 1995). Thresholds for grating detection were defined as the modulation depth of the spectral envelope that was detected 50% of the time, after being corrected for false alarm rate according to the high threshold theory [$Pc^* = (Pc - FA) / (1 - FA)$] (Dooling, 1995).

The birds were tested in two daily sessions of about 100 trials each until their threshold values stabilized. Testing then continued for at least another 100 trials; final thresholds estimates are based on a minimum of 200 trials. Sessions with a false alarm rate higher than 20% were discarded (about 5% of all sessions).

Vocalization analysis

Consistent patterns of spectro-temporal changes present in the species-specific vocalizations of these birds were assessed through the construction of rate-scale plots. The creation of these plots has been described previously by Chi et al. (1999) using human speech. Briefly, the spectrogram of any arbitrary time-varying sound pattern can be represented by its separate grating density/periodicity components at any point in time; rate-scale plots display the total modulation content of the sound pattern at that point for each density/periodicity combination regardless of its spectral distribution. The individual plots derived from a spectrogram can then be averaged into one grand plot, which displays the modulation content across the entire signal.

Samples of representative zebra finch songs and budgerigar warble were used to generate an average rate-scale plot for each species’ vocalizations. Each rate-scale plot is the average of

ten individual birds' vocalizations. Each sample for an individual consisted of up to 60 seconds of song or warble. These vocalizations, as opposed to the much shorter calls of each species, were chosen because they are each of sufficient length to require relatively few samples for the generation of a rate-scale plot (several seconds of continuous vocalization is all that is necessary for a representative plot; one zebra finch song can last several seconds and budgerigar warble can continue for several minutes). Another reason for choosing song and warble instead of calls is that both types of vocalization contain harmonic elements; zebra finch song is primarily harmonic while budgerigar warble is both tonal and harmonic. This shared acoustic structure may make comparisons between rate-scale plots more meaningful.

Statistical analyses

All inferential statistics were calculated using SPSS (version 15, SPSS Inc., Chicago, IL). In general, the ANOVA results reported here used a mixed model of repeated measures for within-subject factors and standard between-subject factors for the appropriate contrasts. Suitable corrections (e.g., Bonferroni) were calculated for post-hoc comparisons. For brevity, the results section will simply label the inferential test as "ANOVA" or "paired t-test". Our lab's experience suggests that even the relatively small number of subjects in this study provides sufficient statistical power, since individual variability tends to be extremely low in these highly trained animals. The data in Results below illustrate this point, with generally very low variance across birds of the same species and therefore relatively little predicted increase in statistical power with more subjects.

RESULTS

Vocalization analysis

The average rate-scale plots generated for typical zebra finch song and budgerigar warble are shown in Figure 5 and Figure 6, respectively. Each plot graphs spectral density (cycles/octave) along the ordinate and spectro-temporal periodicity (Hz) along the abscissa. The upward-moving frequency modulations present in a vocalization are shown in the left panel of each species' plot while the downward-moving modulations are shown in the right panel. Colors indicate the relative amount of modulation present at a given density and periodicity (red indicates more modulation, blue indicates less or none).

Both zebra finches and budgerigars have much stronger downward-moving modulations in their vocalizations than upward-moving modulations, especially at spectral densities below 5 cycles/octave and periodicities below 16 Hz. Zebra finch song, however, also contains strong downward-moving modulations at approximately 2 cycles/octave; there is very little upward-moving content at that spectral density. Budgerigar warble contains no significant downward-moving or upward-moving modulations at 2 cycles/octave.

For comparison purposes, a rate-scale plot of human speech (English) is shown in Figure 7 (from Chi et al., 1999). Most of the modulation content in speech is downward-moving, a pattern strikingly similar to that seen in both zebra finches and budgerigars. The temporal modulations in speech are also similar to those seen in birds (with most of the content falling

between 4 and 8 Hz); the range of spectral densities represented in speech, however, are broader (with modulations present beyond 4 cycles/octave) than either of the two avian species.

Threshold testing

In all three species, modulation depth thresholds increased as a function of increasing grating density and increasing periodicity. The precise pattern of increase differed depending on multiple parameters, though, including the particular density/periodicity combination, the species, and the grating direction. It is predicted that there should be significant effects of the stimulus parameters on thresholds, if hearing capabilities follow vocalization acoustic constraints; the perceptual sensitivity should broadly match the analysis of the vocalizations. Thus, given the overall differences in the different species' vocalizations as mentioned above, we predict an overall species difference in thresholds plus possible interaction of species and specific stimulus parameters. A four-way ANOVA showed significant main effects for periodicity ($F[3,15] = 62.41$, $p < 0.001$) and density ($F[2,10] = 49.98$, $p < 0.001$). A non-significant trend for both species ($F[2,10] = 4.14$, $p = 0.087$) and direction ($F[1,5] = 5.64$, $p = 0.064$) was revealed; post-hoc tests showed that the human subjects' variability appeared to be relatively higher than the birds' and that the power of these analyses could be improved by additional human subjects, supporting the further use of these factors for additional analyses. There were also significant interactions between periodicity and density ($F[6,30] = 4.75$, $p < 0.01$), periodicity, density, and species ($F[12,30] = 4.58$, $p < 0.001$), periodicity, direction, and species ($F[6,15] = 4.53$, $p < 0.01$), and periodicity, density, and direction ($F[6,30] = 2.94$, $p < 0.05$). No other main effects or interactions were significant ($p > 0.05$).

Since the differences in modulation content described in the rate-scale plot for each species appear to be most clearly observed across periodicities at a particular density, the remaining analyses focus on testing differences at each density. Figure 8 graphically depicts the threshold results and Figure 9 shows the threshold differences that are detailed below.

5 cycles/octave—Modulation depth thresholds at .5 cycles/octave increased as a function of increasing grating periodicity across all three species. Both humans and budgerigars had lower thresholds than zebra finches for upward-moving gratings, but all three species performed similarly on discrimination of downward-moving gratings. Overall, thresholds for downward-moving gratings were generally lower across periodicities at this density for both bird species, but not humans (see below). A three-way ANOVA showed significant main effects for periodicity ($F[3,15] = 52.83$, $p < 0.001$) and direction ($F(1,5) = 75.74$, $p < 0.001$). The interactions between periodicity and species ($F[6,15] = 5.82$, $p < 0.01$) and between direction and species ($F[2,5] = 17.15$, $p < 0.01$) were also significant. No other interactions were significant ($p > 0.05$).

Paired-samples t-tests were used to analyze differences between the two directions for each periodicity at this density for each species. Zebra finches were found to have better discrimination of (i.e., lower thresholds for) downward-moving, rather than upward-moving, gratings at both 8 Hz ($t[2] = 4.34$, $p < 0.05$) and 16 Hz ($t[2] = 32.49$, $p = 0.001$) at this

density; there were no significant differences between the two directions at 4 Hz ($p = 0.55$) or at 32 Hz ($p = 0.30$). Budgerigars also have lower thresholds for downward-moving gratings at both 8 Hz ($t[2] = 19.15$, $p < 0.05$) and 16 Hz ($t[2] = 29.31$, $p < 0.05$), but not at 4 Hz ($p > 0.32$) or 32 Hz ($p > 0.35$). No significant differences were found between the two directions for any of the human thresholds.

2 cycles/octave—Modulation depth thresholds at 2 cycles/octave generally increased as a function of increasing grating periodicity for all three species. Threshold curves differed, however, depending on the species and the grating direction. The curves for both birds were very similar for upward-moving sounds whereas the human curve was different from both bird species; “threshold curves were different for all three species across the downward-moving periodicities, though. Both budgerigars and zebra finches had very low thresholds for 16 Hz upward-moving gratings. Budgerigars also had a low threshold for the downward-moving sounds at the same periodicity. The zebra finches’ lowest threshold was for the 8 Hz downward-moving periodicity. A three-way ANOVA showed significant main effects for periodicity ($F[3,15] = 23.63$, $p < 0.001$) and direction ($F(1,5) = 13.36$, $p < 0.05$). There were also significant interactions between periodicity and direction ($F[3,15] = 4.52$, $p < 0.05$) and between periodicity, direction and species ($F[6,15] = 6.18$, $p < 0.01$). No other interactions were significant ($p > 0.05$).

Comparisons between grating directions were calculated for this density. Paired-samples *t*-tests uncovered no significant differences between the upward-moving and downward-moving directions in either budgerigars or humans at this grating density. Zebra finches, however, do have significantly lower thresholds for downward-moving gratings at both 4 Hz ($t[2] = 6.12$, $p < 0.05$) and 8 Hz ($t[2] = 7.21$, $p < 0.05$), but not at 16 or 32 Hz ($p > 0.20$).

4 cycles/octave—Modulation depth thresholds at 4 cycles/octave increased as a function of increasing grating periodicity for all three species, but the threshold curves differed depending on the species. Budgerigars and humans showed similar curves for the upward-moving gratings; zebra finches had a very high threshold at 8 Hz for this direction. Budgerigars, on the other hand, had very low thresholds for at 16 Hz for the downward-moving sounds. A three-way ANOVA showed a significant main effect for periodicity ($F[3,15] = 44.76$, $p < 0.001$) and a significant interaction between periodicity and species ($F(1,5) = 9.56$, $p < 0.001$). No other main effects or interactions were significant ($p > 0.05$).

Again, comparisons between upward-moving and downward-moving gratings were calculated for each species. Paired-samples *t*-tests uncovered no significant differences between the two grating directions in either zebra finches or humans at this density. Budgerigars did have significantly lower thresholds for downward-moving gratings at 16 Hz ($t[2] = 21.88$, $p < 0.05$), though.

As a final check, the present human data and previous data from Chi et al. (1999) were compared. By inspection, the two data sets agree in modulation depth thresholds and also in the shape of the threshold curves.

DISCUSSION

This experiment shows that both birds and humans appear able to discriminate gratings better at lower density/periodicity combinations than at higher density/periodicity combinations, at least within the density and periodicity ranges tested here (.5 to 4 cycles/octave; 4 to 32 Hz). These findings agree with the results of the rate-scale analyses, which showed that the spectral modulations present in all three species' vocalizations contained the strongest modulation content at densities below 4 cycles/octave. These analyses also showed that the temporal modulation content present in the vocalizations of all three species was greatest between 4 and 8–16 Hz and grew weaker as the periodicity increased to 32 Hz.

The differences seen in each species between upward-moving and downward-moving discrimination thresholds may reflect similar differences in their vocalizations. Zebra finches appear to have significantly better sensitivity to some periodicities of downward-moving gratings (vs. upward-moving gratings) at both .5 and 2 cycles/octave (see Figure 9). These birds also show similar directional differences in the modulation content present in their vocalizations at both of these densities. Specifically, zebra finch song contains much stronger downward-moving modulations between 4 Hz and 16 Hz at .5 and 2 cycles/octave (Figure 5), which corresponds to those grating densities and periodicities that zebra finches can discriminate the easiest.

A neurophysiological study showed that the auditory forebrain of zebra finches contains cells that are exquisitely sensitive to the temporal and spectral information contained within their own species-specific vocalizations (Theunissen and Doupe, 1998). Other studies of auditory neurons in the zebra finch have shown that STRFs can be calculated from neuronal responses to ensembles of conspecific songs (Theunissen et al., 2000). The distribution of these STRFs across the auditory forebrain varies according to multiple parameters such as the breadth of spectral resolution and the presence of fast changes in the temporal structure of songs (Sen et al., 2001). This latter type of STRF may be especially important since zebra finch songs often contain frequency sweeps with fast temporal modulations (see Figure 3). This suggests that these neurons play a specific role in the detection and discrimination of frequency sweeps in these songs (Sen et al., 2001).

Budgerigars show very similar thresholds for both upward-moving and downward-moving gratings across most periodicities. A significant sensitivity to some downward-moving gratings, but not to upward-moving gratings, exists primarily at .5 cycles/octave (Figure 8). This density is also the one that includes most of the modulation content, particularly downward-moving content, that is present in warble song (Figure 6). Budgerigars also show exceptionally low thresholds for both directions of 16 Hz sounds at most densities. This was unexpected, since the rate-scale analysis uncovered no significant modulation content for high periodicities at any density, and implies that these birds may be processing something other than their vocalizations at those periodicities.

Humans show no differences in sensitivity between upward-moving and downward-moving gratings at any density/periodicity combination. This is surprising in light of the fact that speech appears to contain stronger downward-moving modulations at spectral densities

between .5 and 4 cycles/octave. This suggests that humans may be processing these dynamic, complex sounds in ways that do not relate directly to their vocalizations.

The finding that both humans and budgerigars may show perceptual abilities for some auditory grating sounds which do not relate to the modulation content of their vocalizations presents two additional points for consideration. First, the modulation depth thresholds for budgerigars tend to be lower than either zebra finches or humans at higher periodicities, particularly for downward-moving sounds. It is not clear why this species should show such a distinct threshold pattern, although this finding may relate to differences in the acoustic structure of these species' vocalizations. For example, both the formant structure of speech and the harmonic structure of zebra finch song are more spectrally complex than the primarily tonal vocalizations of budgerigars. Perhaps less spectrally-dense vocalizations require lower perceptual thresholds and, therefore, greater processing capacities across a greater range of periodicities and densities than more spectrally-dense vocalizations.

Second, humans have little or no directional differences in their ability to perceive auditory grating sounds even though there are large differences in the directional content of speech. Again, there is no clear reason why this should be the case; it is possible that humans are using their vocalizations differently than either avian species in this study and, therefore, do not need to discriminate between directions. For example, female zebra finches choose which males to mate with based on the quality of those males' songs (Zann, 1996) and male warble song has been shown to stimulate ovulation in female budgerigars (Brockway, 1965). One might expect to find better discrimination of and lower thresholds for certain components present in an individual's species-specific vocalizations (e.g., downward frequency sweeps) if the reproductive success of an individual is partially dependent on its ability to accurately perceive those components.

These results are the first to describe auditory grating perception in multiple species tested under the same conditions and using the same methodology. Different species are commonly tested behaviorally in different laboratories using a variety of procedures. For example, prior studies of auditory grating perception have utilized a 2- Alternative, 2-Interval Forced Choice task to study humans (Chi et al., 1999), a conditioned avoidance task to study domestic ferrets (Fritz et al., 2002), and a hold-release task to study macaques (Versnel and van Opstal, 2002). Such methodological differences between animal and human tests often weaken potential comparisons of perceptual capabilities. Here, every animal was subjected to the same acoustic conditions, stimuli, and behavioral task, all of which adds a level of reliability to comparisons between species. Additionally, the agreement between the present human data and data from humans in another laboratory can be considered evidence that no stimulus or procedural artifacts influenced the present results.

This experiment also shows that, despite having remarkably different audible frequency ranges and peripheral hearing structures (Echteler et al., 1989; Gleich et al., 1994; Manley, 1990; Manley et al., 1993), these three species have exceedingly similar modulation depth thresholds and similar threshold functions. All three species show an increasing sensitivity with decreasing grating density and periodicity. This pattern may reflect a more general perceptual capacity between birds and mammals and may underscore a common constraint

imposed by the auditory system of these animals on the perception of sounds with complex spectro-temporal properties. These results are in line with other research describing common strategies in the processing of complex acoustic signals between human and nonhuman animals, including similarities in the discrimination of speech and speech-like sounds in birds (e.g., Dent et al., 1997; Dooling, 1992; Dooling et al., 1995) and also auditory discrimination and left hemisphere specializations in monkeys and cats (for references, see Fitch et al., 1997).

More interesting is the finding that the discrimination of upward-moving vs. downward-moving gratings is different for each species and that these differences, in birds at least, may relate to similar differences in those species' vocalizations. There is a growing body of evidence supporting the view that animals may possess perceptual specializations for recognizing their own species-specific vocal signals and for processing them more efficiently than they do the vocal signals of other animals. This capacity is present in a wide variety of vertebrate species (Brenowitz, 1991; Gerhart, 1986; Ghazanfar and Hauser, 2001), most notably in humans listening to speech (Liberman, 1982). Previous research has shown that both budgerigars and zebra finches may process their own species' vocalizations differently than they process the vocalizations of other species (Brown et al., 1988; Dooling et al., 1992; Dooling et al., 1987; Okanoya and Dooling, 1991). The present finding provides additional evidence that the auditory system of these two birds may be specialized for processing complex, species-specific sounds.

Finally, there is the possibility that the present study does not describe an adequate test of the relationship between grating perception and the modulation content present in a species' vocalizations. Most of the vocalizations produced by an animal are well above that animal's discrimination threshold and, therefore, perceptual tests employing such thresholds as the parameter of interest may overlook other more salient characteristics of a vocalization that the animal may be preferentially attending to. Future research might keep this caveat in mind and concentrate on tests using gratings that are very easy to discriminate from a flat spectrum (50–90% modulation depth) to examine perceptual differences between other grating parameters. For example, a categorization (i.e., SAME-DIFFERENT) task can be used to determine the largest difference in spectral density between two auditory grating sounds that an animal perceives as similar.

Overall, the present results are suggestive of common strategies in the processing of complex sounds employed by both birds and mammals and of a species-specific sensitivity to, and preferential discrimination of, certain spectral features of those complex sounds, in birds at least, which are similar to features present in that species' vocalizations. Because these sounds can be mathematically manipulated in precise ways, they may provide new and exciting opportunities to explore species-specific perception in the future.

Abbreviations

STRF	spectro-temporal response field
LED	light-emitting diode

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Figure 1. Representative spectrogram of a selection from a budgerigar warble

One segment from a multiple-minute warble is shown here, demonstrating the typically complex structure and mix of broad-band, harmonic and frequency-modulated tonal elements.

Figure 2. Representative spectrogram of a selection from a budgerigar warble
One segment from a multiple-minute warble is shown here, demonstrating the typically complex structure and mix of broad-band, harmonic and frequency-modulated tonal elements.

Figure 3. A spectrographic representation of the acoustic grating stimulus

A spectrogram of an acoustic grating is shown here (red indicates spectral peaks, blue indicates valleys). Graphic representations of the stimulus time waveform are also shown on the right. The top right figure displays the measurement of modulation depth and the bottom right figure displays measurement of acoustic density.

Figure 4. Temporal properties of the acoustic grating stimulus

This graph shows how the spectral envelope of an acoustic grating moves at a constant rate over time. Here, an acoustic grating with a density of .4 cycles/octave, and 100% modulation depth, drifts downward in frequency at a periodicity of 4 Hz.

Figure 5. Average rate-scale plot of zebra finch song

This is an average of ten zebra finch songs from unrelated males. The strongest modulation content in this vocalization is downward-moving (right panel) and exists primarily at those densities below 4 cycles/octave and at periodicities between 4 Hz and 16 Hz. The directional differences are greatest at densities between 1 cycle/octave and 2 cycles/octave and periodicities between 4 Hz and 16 Hz.

Figure 6. Average rate-scale plot of budgerigar warble song

The figure shows an average of ten warble songs (20 to 60 seconds long each) from different individuals. The strongest modulation content in this vocalization is downward-moving (right panel) and exists primarily at those densities below 2 cycles/octave and at periodicities below 16 Hz. The directional differences are greatest at densities at and below 1 cycle/octave and periodicities at and below 8 Hz.

Figure 7. Rate-scale plot of human speech (English)

The strongest modulation content in this vocalization is downward-moving and exists across a wide range of densities (the strongest modulations occur at approximately 2 cycles/octave) and at periodicities below 16 Hz. The directional differences are greatest at periodicities between 4 Hz and 8 Hz. (From Chi et al. 1999).

Figure 8. Discrimination thresholds at different densities

Modulation depth thresholds increase as a function of increasing acoustic grating periodicity at .5 cycles/octave in the top panel. In contrast in the middle panel with 2 cycles/octave density, budgerigars have low thresholds for 16 Hz acoustic gratings at both directions; zebra finches also appear to have a low threshold for 16 Hz upward-moving acoustic gratings. The lowest threshold for zebra finches at this density is for 8 Hz downward-moving acoustic gratings. In the lower panel representing the 4 cycles/octave density,

budgerigars show a low threshold for 16 Hz downward-moving acoustic gratings. Zebra finches have a rather high threshold for 8 Hz upward-moving acoustic gratings.

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Figure 9. Threshold differences between acoustic grating directions at different densities
 Upward-moving acoustic grating thresholds are symbolized with (▲) whereas downward-moving acoustic grating thresholds are symbolized with (▼). Both zebra finches and budgerigars have lower thresholds for downward-moving acoustic gratings at both 8 Hz and 16 Hz at the .5 cycles/octaves. Zebra finches have lower thresholds for downward-moving acoustic gratings at both 4 Hz and 8 Hz at 2 cycles/octave. Budgerigars have a lower threshold for downward-moving acoustic gratings with 16 Hz at 4 cycles/octave. No such

differences exist in humans. Asterisks (*) represent significantly different threshold values ($p < 0.05$).