Detection of modulation in spectral envelopes and linear-rippled noises by budgerigars (*Melopsittacus undulatus*)

Satoshi Amagai and Robert J. Dooling
Department of Psychology, University of Maryland at College Park, College Park, Maryland 20742

Shihab Shamma
Department of Engineering, University of Maryland at College Park, College Park, Maryland 20742

Tracy L. Kidd and Bernard Lohr
Department of Psychology, University of Maryland at College Park, College Park, Maryland 20742

Budgerigars were trained to discriminate complex sounds with two different types of spectral profiles from flat-spectrum, wideband noise. In one case, complex sounds with a sinusoidal ripple in (log) amplitude across (log) frequency bandwidth were generated by combining 201 logarithmically spaced tones covering the frequency region from 500 Hz to 10 kHz. A second type of rippled stimulus was generated by delaying broadband noise and adding it to the original noise in an iterative fashion. In each case, thresholds for modulation depth (i.e., peak-to-valley in dB) were measured at several different ripple frequencies (i.e., cycles/octave for logarithmic profiles) or different repetition pitches (i.e., delay for ripple noises). Budgerigars were similar to humans in detecting ripple at low spatial frequencies, but were considerably more sensitive than humans in detecting ripples in log ripple spectra at high spatial frequencies. Budgerigars were also similar to humans in detecting linear ripple in broadband noise over a wide range of repetition pitches. Taken together, these data show that the avian auditory system is at least as good, if not better, than the human auditory system at detecting spectral ripples in noise despite gross anatomical differences in both the peripheral and central auditory nervous systems. © *1999 Acoustical Society of America.* [S0001-4966(99)03802-3]

INTRODUCTION

A primary goal of hearing research is to understand how complex, naturally occurring sounds such as species-specific vocalizations and speech sounds are processed by the nervous system. Comparative investigations with such sounds can provide an important window on the evolution and adaptation of auditory systems, especially when these sounds can be systematically manipulated. While complex communication signals have become popular stimuli for exploring auditory function in different species, their very complexity renders them a difficult class of sounds to describe and manipulate when used in a systematic exploration of auditory function.

Historically, the alternatives to complex, natural sounds in both physiological and psychophysical experiments have been pure tones and noises. Approaches using these sounds tend to reduce the auditory system to equivalent acoustic engineering systems. This succeeds in addressing the problem of description and logical manipulation of sounds, but such an approach is intrinsically limited by its simplicity, restricting our understanding to an arbitrary and probably unrealistic view of the auditory system. The use of spectrally complex, broadband sounds offers some compromise between simple sounds such as pure tones and noises and more complex, natural sounds such as vocalizations. In particular, spectrally complex sounds with rippled spectral envelopes share some of the characteristics of natural sounds, but may be generated mathematically allowing for precise, quantifiable, and systematic manipulation.

One type of sound having rippled spectral profiles has become useful because of its noted parallel with sine-wave gratings used in studies of vision. These sounds, called log-rippled noises in this paper, are generated by imposing a sinusoidal spectral envelope onto broadband noise in the frequency domain, or by algebraically adding frequency components with amplitudes determined by a sinusoidal envelope. The spectral envelope is sinusoidal when frequency is represented on a logarithmic scale and sinusoidal envelopes are expressed in units of cycles/octave. In vision, this class of stimuli purports to allow for a linear systems analysis of visual function as long as the underlying principle of linearity of summation is not violated (De Valois and De Valois, 1988). Whether a linear systems analysis approach will prove useful for understanding complex signal processing in the auditory system remains to be seen. This approach could provide a powerful tool for comparative explorations of auditory system function at different levels and in different species (Shamma and Versnel, 1995; Shreiner and Calhoun, 1995). In humans, there are strong arguments for studying rippled spectra based on their parallels with the vowel sounds of human speech (Hillier, 1991; Summers and Leek, 1994).

A second class of rippled stimuli may be created by delaying a portion of wideband noise and adding it back to the undelayed original. The resulting stimulus has been

called rippled noise, repetition noise, or cosine noise (Fay *et al.*, 1983; Bilsen *et al.*, 1975; Yost and Hill, 1978). It has spectral peaks at integer multiples of $1/T$, where T is the time of delay. If the delay and add process is combined in a feedback loop, the result is comb-filtered noise (Bilsen and Wieman, 1980; Pick, 1980). These linear-rippled noises produce the perception of pitch corresponding to $1/T$ Hz in human subjects (Bilsen, 1970; Yost *et al.*, 1978). Yost *et al.* (1996) have recently described a variant of these noises created by iterating the delay and add process. Two different digital networks have been outlined for producing iterated rippled noises. In one network, delayed and attenuated noise is added back to the original noise in an iterative process. In the second network, the output of the previous add is delayed and attenuated before the next add. These two networks produce rippled noises with slightly different spectra (Yost, 1996).

The experiments reported herein followed the former procedure for generating iterated rippled noise, and used a large (999) number of iterations to approximate the infinitely iterated comb-filtered noise of Bilsen and Wieman (1980). These stimuli are referred to here as linear-rippled noise, in contrast to the log-rippled noise discussed earlier. The amount of spectral modulation in linear-rippled stimuli is controlled by varying the attenuation of the delayed sound before it is added back to the undelayed original. A series of sounds ranging from spectrally flat to deeply rippled were created by decreasing the amount of attenuation from about 25 to 0 dB. As the attenuation is reduced, the depth of modulation increases, as does the saliency of the repetition pitch. Human subjects are most sensitive to repetition pitches between 100 and 1000 Hz; the sensitivity is independent of overall level above about 20-dB sensation level (Bilsen and Ritsma, 1970; Yost and Hill, 1978).

The details of linear-rippled noise processing are important for theories of vertebrate hearing because models and theories of pitch must be able to account for the pitches and pitch strengths of rippled noises. A variety of sounds can produce the perception of the same pitch in human subjects (Fastl and Stoll, 1979), and it is possible that the neural mechanisms underlying pitch perception share some common properties for these various stimuli. From an ecological standpoint, a case has also been made that complex sounds occurring from multiple reflections in the environment, creating rippled spectra, might be discriminated on the basis of their pitch strength and coloration (Yost *et al.*, 1996).

There is less work on the processing of rippled noises in animals than in humans. As far as we know, log-rippled noises have been used only in studies of ferrets (Shamma *et al.*, 1995; Shamma and Versnel, 1995; Versnel *et al.*, 1995) and cats (Shreiner and Calhoun, 1995) in electrophysiological recordings in the cortex. On the other hand, linear-rippled noises have been used in a number of physiological and psychophysical studies of hearing in a variety of species including cats (Pickles, 1979), guinea pigs (Evans *et al.*, 1992), and chinchillas (Niemiec *et al.*, 1992; Shofner and Yost, 1995; Shofner, 1991). The psychophysical data on repetition-noise perception by goldfish are perhaps the most comprehensive so far published for any nonhuman. As with humans and other animals, these data show that as $1/T$ increases, discrimination of delay differences requires greater spectral modulation depth (Fay *et al.*, 1983). Otherwise said, ''pitch strength'' probably declines for the goldfish at higher values of $1/T$ (Fay, 1988; Fay *et al.*, 1983).

Birds are excellent subjects, in general, for the comparative study of complex sound processing. Furthermore, in spite of many psychophysical and physiological studies over the years using both simple tones and noises as well as natural vocalizations, our understanding is still far from complete. The purpose of the present experiments is to provide baseline data on the perception of these two types of complex sounds with rippled spectra as a foundation for future investigations involving other types of manipulations in rippled spectra, such as phase, shape, pitch strength, or coloration, etc. To this end, thresholds for detecting spectral modulation in log-rippled and linear-rippled sounds were measured in three budgerigars. Budgerigars are small Australian parrots known for their tractability for auditory testing (Okanoya and Dooling, 1987) and superiority in discriminating complex harmonic sounds (Lohr and Dooling, 1998), as well as for their complex learned vocal repertoire and adult vocal plasticity (Farabaugh *et al.*, 1994).

I. METHODS

A. Subjects

The subjects in these experiments were three budgerigars (*Melopsittacus undulatus*, two females and one male). All birds were either bought at a local pet store or hatched at the University of Maryland and housed in individual cages in a vivarium at the University of Maryland. The birds were kept on a normal day/night cycle correlated with the season at approximately 90% of their free-feeding weights. Although the primary focus of the present study was to obtain psychophysical data from budgerigars, four human subjects (students and research assistants) were also tested on the same stimulus conditions. This provided a check on the validity of the test procedures and apparatus, a comparison with existing human data, and a procedural control.

B. Testing apparatus

The birds were tested in a wire cage ($25 \times 25 \times 25$ cm) placed in a small animal IAC chamber lined with acoustic foam. A response panel consisting of two sensitive microswitches with light-emitting diodes (LEDs) was mounted on the wall of the test cage just above the food hopper. The microswitch was tripped by the bird pecking the LED. The left microswitch was the observation key, and the right microswitch was the report key. Stimuli were delivered from a JBL loudspeaker (model 2105H) mounted 20 cm above the test cage. All experimental events were controlled by an IBM 486 microcomputer operating Tucker-Davis signal-processing modules. Stimulus calibration was performed using a General Radio (model 1982) sound-level meter with octave band filters. Stimulus intensities were measured by placing the microphone in front of the keys of the response panel in the approximate position normally occupied by the bird's head during testing. The intensities of the stimuli were

measured several times during the conduct of these experiments to ensure that the entire system remained calibrated. During testing, the behavior of the bird was monitored by a video camera system.

C. Training and testing procedures

The training and testing procedures have been described in detail previously by Okanoya and Dooling (1987, 1990). The bird was trained by a standard operant auto-shaping program to peck at the left microswitch key (observation key) during a repeating background until a new stimulus was presented alternately with the background sound. If the bird pecked the right microswitch and LED (report key) within 2 s of this alternating pattern, the food hopper was activated for 2 s. The dependent variables in these experiments were percent correct and response latency on trials involving an alternating sound pattern. A failure to peck the report key within 2 s of sound alternation was recorded as a miss, a response latency of 2000 ms recorded, and a new trial sequence initiated. Thirty percent of all trials were ''sham'' trials in which the ''target'' sound was the same as the repeating ''background'' sound. A peck to the report key during a sham trial was recorded as a false alarm and the lights in the test chamber were extinguished while the repeating background continued. The length of this time-out period was normally 5 s, but varied according to the bird's behavior, with longer time-out periods applied with higher false-alarm rates. Sessions with a total false-alarm rate of 16% or higher were discarded. No more than 20% of the sessions for any bird were discarded for this reason.

D. Stimuli

1. Log-rippled spectra

These complex broadband sounds were created using the procedures described by Shamma and his colleagues (Shamma et al., 1995). Briefly, the stimuli were generated by algebraically summing 201 sinusoidal components sampled at 40 kHz that were equally spaced along the logarithmic frequency axis, spanning the frequency range from 0.5 to 10 kHz. The phases of the individual sinusoids were randomized to avoid large-amplitude onset effects. This range was chosen to completely encompass the range of hearing in budgerigars (Dooling and Saunders, 1975). The duration of each stimulus was 100 ms with 10 ms rise/fall times. The spectral envelope of this stimulus complex was then modulated sinusoidally on a logarithmic scale to create a ''ripple'' whose frequency, measured in cycles/octave, was varied from 0.5 to 10 cycles/octave. The phase of the ripple was uniformly set to zero at the low-frequency edge of the complex. A range of sounds with different ripple amplitudes was created for each ripple frequency. The amplitude of the ripple was taken as the ratio of the amplitude of the peak to the trough of the spectral envelope in dB. The resulting waveform was normalized to ±15 bits for playback through the digital-to-analog converter. The overall level of the complex stimulus was measured in the test box and adjusted to 60 dB(A). For each ripple frequency, the repeating background was the sound with 0-dB ripple amplitude. The test stimuli the animal was asked to detect consisted of rippled noises with the same ripple frequency but with varying amount of ripple amplitudes. In each trial, seven test stimuli were used consisting of ripple amplitudes that ranged from either 1–7 or 2–14 dB, depending on the performance of the birds. During testing, the overall level was varied randomly (roved) from stimulus presentation to presentation by ±5 dB to minimize amplitude cues.

2. Linear-rippled stimuli

The second type of rippled stimuli tested were those with a linear-rippled spectra. Figure 1 shows the spectrum of a log-rippled noise and a linear-rippled noise used in these experiments. These sounds were generated by starting with a wideband noise, delaying it, attenuating it, and repeatedly adding this delayed noise to the undelayed noise. In practice, frozen segments of rippled noise with 999 iterations were created with a Tucker-Davis Technologies array processor (AP2) at a sampling rate of 40 kHz. This network used to create these noises has been referred to as iterated rippled noise in an add-original network (Yost, 1996). The overall level of these complex sounds was adjusted so that the wideband noise and rippled noise had equal root-mean-squared (rms) voltages. All sounds were then randomized in amplitude by ±5 dB during stimulus presentation. Thus, the birds could not use a loudness cue during the presentation of rippled noise. The six delays (T) used to generate rippled noises ranged from 8 down to 0.25 ms to create repetition pitches (as perceived by humans) ranging from 125 to 4000 Hz in octave steps.
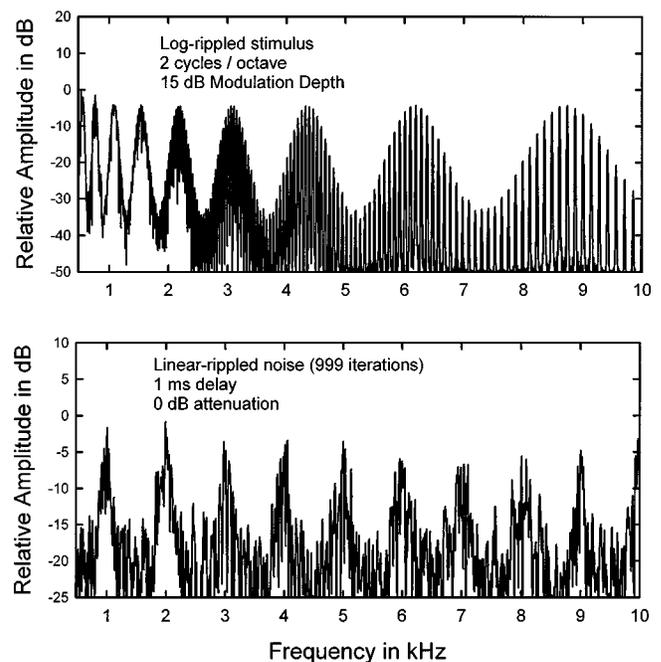

FIG. 1. (Top) Power spectrum of a log-rippled stimulus used in these experiments. This stimulus has a ripple frequency of 2 cycles/octave and a peak-to-valley modulation depth of 15 dB. (Bottom) Power spectrum of a linear-rippled stimulus used in these experiments. This stimulus was constructed using 999 iterations, a delay of 1 ms, and no attenuation (i.e., gain or ''g'' is equal to 1).
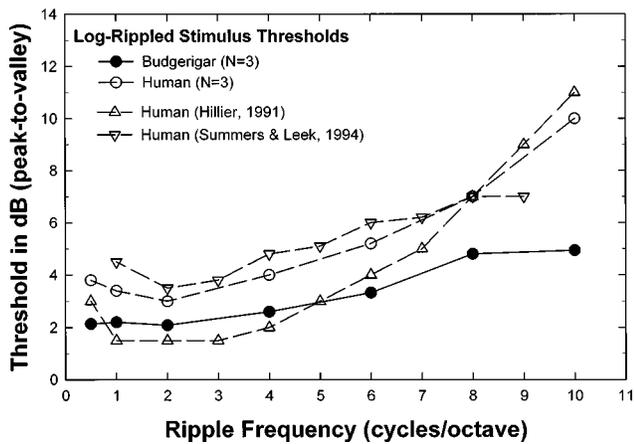
FIG. 2. Detection thresholds for log-rippled noise. The ripple amplitude threshold for detection defined as 50% chance of detection is plotted in peak-to-valley ripple amplitude in dB as a function of the ripple envelope frequency (cycles/octave). Solid circles are data from budgerigars ($n=3$) and open circles are data from human subjects ($n=3$) tested with the same stimuli and procedures. Other open symbols are previously published data from Hillier (1991) and Summers and Leek (1994).
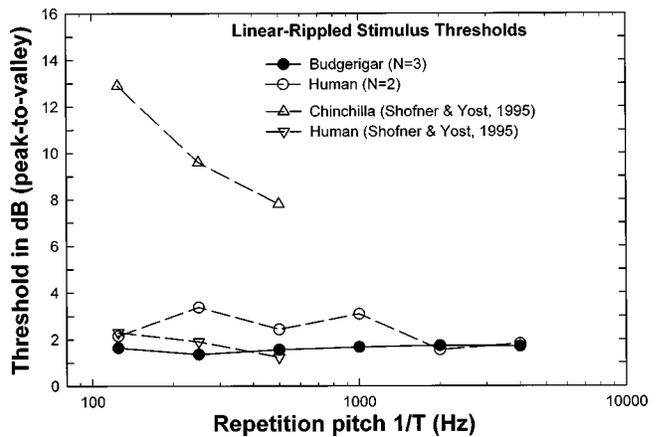

FIG. 3. Detection thresholds for linear-rippled noise. Threshold for ripple detection (50% chance of detection) is plotted as a function of the repetition pitch $1/T$, where T is the delay of the added waveform. The amplitude of the ripple is expressed as a peak-to-valley of the resulting waveform as calculated from the attenuation of the added waveform. Solid circles are data from budgerigars ($n=3$), and open circles are data from humans subjects ($n=2$) tested with the same stimuli and procedures. Other open symbols are from previously published human and chinchilla data (Shofner and Yost, 1995).

In this experiment, the repeating background was always a frozen noise sample with zero iterations of delayed addition. Target rippled noises had varying amounts of attenuation ranging from 25 to 0 dB. Spectral modulation depth (P/V in dB) was calculated as described by Shofner and Yost (1995) as:

$$\frac{P}{V}(\text{dB}) = 10 \log\left(\frac{(1+g)^2}{(1-g)^2}\right),$$

where "g," the gain or attenuation of the delayed noise, is greater than 0. The level of these stimuli presented during testing was monitored by placing a condenser microphone from a General Radio sound-level meter (model 1982) in the free-field in the approximate position of an animal's head and measuring the A-weighted sound pressure level.

To permit comparison, both log- and linear-rippled noises are plotted on the same linear abscissa in Fig. 1. Note that these spectra differ not only in their envelope frequency but also in their shape. The spectral envelope for the log-rippled stimulus is sinusoidal (on a log axis), while the spectrum resulting from 999 iterations of iterated rippled noise is nearly a line spectrum. Spectral modulation depth for the log-rippled stimuli is specified directly in the creation of these stimuli (peak-to-valley in dB). For linear-rippled stimuli, spectral modulation depth is also calculated as a peak-to-valley ratio in dB as described by the formula above.

II. RESULTS

The average modulation-depth thresholds for log-rippled sounds are shown in Fig. 2 for three budgerigars, along with similar data from several human studies. Budgerigars showed thresholds of modulation detection that were in the range of 2–3 dB at low ripple frequencies rising to about 4 dB as ripple-envelope frequency increased above about 4 cycles/octave. For comparison, data from our human subjects and from two previous investigations on human subjects (Hillier, 1991; Summers and Leek, 1994) are plotted on the

same axes. The human thresholds ranged from a 3–4 dB peak-to-valley modulation depth at low ripple envelope frequencies to about 10 dB peak-to-valley depth as the ripple frequency exceeded 10 cycles per octave. The results for our humans, tested with the same procedures used for testing our birds, are very similar to previous human data in both the amplitude of the threshold values and the shape of the threshold curves as a function of envelope frequency. In the direct comparison of our bird and human data, budgerigars consistently outperformed our human subjects throughout the range of ripple frequencies, especially at high ripple frequencies. The point of testing humans on the same stimuli using the same procedures used for testing the birds is to ensure the validity of the present procedures and provide a hedge against the existence of any stimulus artifacts that might contaminate the bird thresholds.

The average results for three budgerigars tested on linear-ripple noise are shown in Fig. 3. Both budgerigars and humans show a reasonably flat pattern of thresholds of between 2 to 4 dB peak-to-valley modulation depth over a range of repetition pitch from 125 to 4000 Hz. For comparison, human and chinchilla data from a previous study (Shofner and Yost, 1995) are also plotted. The present values for humans are very similar to those reported by Shofner and Yost (1995) over the same range. The results for birds, however, while agreeing well with the human data, stand in marked contrast to data from the chinchilla, which shows much higher thresholds in the range of 8 to 12 dB.

III. DISCUSSION AND CONCLUSIONS

These experiments show that despite having remarkably different peripheral and central auditory systems (Manley, 1990; Manley et al., 1993), budgerigars are roughly similar to humans in the ability to detect amplitude modulation in both log- and linear-spaced spectral rippled stimuli. These

results raise a number of questions, including a set of methodological issues involved in the conduct of comparative studies with complex sounds. On the methodological issues, studying the detection, discrimination, or perception of complex sounds in animals always carries the concern that procedural differences between animal and human tests weaken the comparison of sensory capabilities. To this end, the agreement of our human data (obtained with the same repeating-background procedure used to test the birds) with data from humans tested on both log- and linear-ripples in other laboratories can be taken as evidence that no stimulus or procedural artifacts affect thresholds in our tests. In addition, the amplitude of the stimulus was randomly varied over a range of 10 dB on a stimulus presentation-by-presentation basis, so that any slight overall amplitude changes that might have occurred through spectral manipulations could not be used by the birds to detect the presence of rippled spectral envelopes in these sounds.

Potentially more problematic is the use of frozen noise samples in the test using linear-rippled noises. The use of frozen stimulus samples raises the possibility that a particular sample might have some unique features that aid detection. The evidence against this possibility is that it would likely lead to spuriously low thresholds or psychometric functions with an unusual shape, neither of which occurred in these experiments. As an additional check against this kind of problem influencing our results, once our birds and humans reached threshold levels of performance on a set of stimuli at a particular ripple frequency or delay, they were transferred to several entirely new sets of rippled stimuli and their thresholds were measured again. In all cases, birds and humans gave similar threshold values on the new stimulus sets. As a final control, an additional budgerigar was tested using multiple background and target exemplars presented at random during testing. Thus, the bird was tested with random presentations of 10 different frozen background stimuli and 5 different frozen targets at each ripple depth. The thresholds for this bird were very similar to those for the three budgerigars in the main experiment.

Another interesting issue raised by the present results concerns the mechanisms underlying modulation detection for the two different kinds of ripple stimuli. The theoretical basis for studying the detection and perception of noise spectra with log-spaced ripple patterns is, first and foremost, the logarithmic representation of frequency along the cochlear partition that underlies a number of related phenomena including critical bands, critical ratios, frequency difference limens, etc. (Hillier, 1991; Moore, 1997). The construction of log-spaced rippled noises parallels the increasing filter widths in the auditory system at higher frequencies. At low ripple envelope frequencies, the width of the ripple peaks and troughs span more than a single critical-band filter, allowing for comparisons across critical-band filters (channels). As the ripple envelope frequencies increase, however, the differences in stimulation in any two adjacent auditory system filters or channels diminish and eventually disappear as the ripple frequency exceeds the critical bandwidth. This is the likely reason that thresholds for detection of sounds with log-rippled spectra become worse at higher ripple fre-

quencies in humans. The fact that budgerigars are better than humans at detecting modulation at high-ripple frequencies is consistent with other psychophysical data showing exceptionally narrow filter bandwidths for the budgerigar around 3 kHz as measured by critical ratios, critical bands, and psychophysical tuning curves (Dooling and Saunders, 1975; Saunders et al., 1979; Okanoya and Dooling, 1987).

Log-rippled spectra lend themselves particularly well to explorations of spectral or place-code models of auditory processing. Linear-rippled noises, by contrast, lend themselves more to an analysis of time domain processing by the auditory system. Linear-rippled stimuli have been studied more frequently than log-rippled stimuli, and the prevailing interpretation of the processing of linear-rippled noises is that the auditory system is performing a time-domain waveform analysis something like an autocorrelation (Fay et al., 1983; Shofner, 1991; Shofner and Yost, 1994, 1995; Yost et al., 1996). The similarity between budgerigars and humans in the detection of modulation in linear-rippled noises is consistent with a wealth of other comparative data on birds (including budgerigars and zebra finches) that show they are at least as good as humans on a variety of temporal detection and discrimination tasks including duration discrimination, gap detection, temporal integration, and modulation transfer functions (Dooling, 1979; Dooling and Searcy, 1979, 1981; Dooling, Zoloth, and Baylis, 1978; Fay, 1988; Klump and Maier, 1989; Okanoya and Dooling, 1990). It is interesting in this regard that the chinchilla, the only other mammal besides humans tested on linear ripples, is so poor at detecting linear-rippled spectra (Shofner and Yost, 1995).

The promise of using linear-spaced and log-spaced ripples as probes of auditory system function and complex sound perception is that they may offer a solution to the dilemma of whether to use simple, artificial signals or complex, natural sounds to understand the function, adaptation, and evolution of the vertebrate auditory system. Comparative studies have shown there are numerous species, spanning different vertebrate classes, including fish, frogs, birds, and mammals, that preferentially use complex, multiple-harmonic, periodic sounds as communication signals. In these species, there is strong evidence at the behavioral and physiological levels that the auditory system extracts periodicity cues from these harmonic patterns and transmits the information by arrays of phase-locked activity to the central auditory system (Langner, 1992; Simmons and Buxbaum, 1996).

In the spectral domain, there are also countless examples from a variety of vertebrates including humans in which spectral features or the change in spectral features are the important components of species-specific communication signals. One particularly relevant example is the discrimination and categorization of vowel sounds. Studies have shown adult humans, prelinguistic humans, and other mammals whose auditory systems are structurally and functionally similar to those of humans, are generally quite sensitive to the acoustic features that define vowel phonetic categories and can form phonetically appropriate acoustic categories (see, for example, Burdick and Miller, 1975; Kuhl, 1986, 1991; Sinnott, 1989). It is somewhat surprising that several

species of birds, whose peripheral and central auditory systems are structurally very different from mammalian auditory systems, can also discriminate among vowels (Hienz *et al.*, 1981) and perceive vowel categories in a phonetically appropriate way without extensive training, even in the face of talker variation (see, for example, Dooling and Brown, 1990).

Parallels in the perception of complex sounds, including speech sounds, by birds and humans present somewhat of a conundrum. On the one hand, such parallels are consistent with general similarities in psychoacoustic thresholds between birds and mammals in their respective ranges of best hearing (Fay, 1988). This fits with the wealth of evidence that some birds can mimic human speech sounds, which argues that they must hear the sounds of speech as humans do. On the other hand, there are consistent differences in the hearing of birds and mammals. In the lower frequency range critical for human speech, pure-tone thresholds, masked thresholds, and frequency- and intensity-difference limens in humans are generally much superior to birds (Fay, 1988). From these psychoacoustic data, then, one might not predict strong similarities between birds and humans in the perception of speech sounds. It is interesting, then, that the present results show considerable similarity between humans and budgerigars in the detection of modulation in log-rippled noises.

In considering the perception of vowel sounds particularly, the preservation of spectral contrast in the internal representation of spectral shapes is undoubtedly important for locating formant peaks underlying vowel identity. For humans, previous work has shown that the perceived similarities among vowels is mainly determined by the amount of spectral similarity and contrast present at ripple frequencies up to about 2–3 cycles/octave (van Veen and Houtgast, 1985). These results are consistent with an analysis of English vowels spoken by male, female, and child talkers (Peterson and Barney, 1952) that suggests that frequency resolution at ripple frequencies above 4 cycles/octave is probably unnecessary for accurate vowel identification (Summers and Leek, 1994). Budgerigars, like humans, show best detection performance at ripple frequencies below 4 cycles/octave—a capability that may underlie the similarities between budgerigars and humans in vowel speech-sound categories (Dooling and Brown, 1990; Dooling, 1992). Future probes of avian hearing using log-rippled stimuli might explore sensitivity to other aspects of these complex sounds that are known to be represented at the single-unit level in the mammalian primary auditory cortex, such as ripple frequency, ripple phase, and ripple shape (Shamma *et al.*, 1995; Shamma and Versnel, 1995; Versnel *et al.*, 1995).

Finally, there has long been the suggestion that the avian auditory system may be specialized for processing certain kinds of complex sounds. The two classes of complex sounds used in the present experiments may shed new light on this issue. In the case of log-rippled stimuli, it would be interesting to know whether the superior performance of budgerigars at higher ripple frequencies is related to the rapid frequency-modulation characteristic of the vocalizations of budgerigars and many other birds. In the case of

linear-spaced ripples, these sounds offer a way of probing the limits of a kind of temporal processing, and birds may turn out to be exceptional in detecting or discriminating certain aspects of these sounds as well. For example, thresholds for detecting the mistuned harmonic in budgerigars and zebra finches are up to an order of magnitude smaller than human thresholds (Lohr and Dooling, 1998). This task almost certainly involves sensitivity to the temporal fine structure of harmonic waveforms. A recent study on single-unit responses in the zebra finch auditory forebrain to complex harmonic stimuli shows greater sensitivity to temporal rather than to spectral cues (Theunissen and Doupe, 1998). Further, this study provides evidence that this extremely precise preservation of temporal cues in the auditory forebrain is necessary for a full response to complex, learned, species-specific vocalizations.

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