Masking by harmonic complexes in budgerigars (*Melopsittacus undulatus*)

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In humans, masking by harmonic complexes is dependent not only on the frequency content of the masker, but also its phase spectrum. Complexes that have highly modulated temporal waveforms due to the selection of their component phases usually provide less masking than those with flatter temporal envelopes. Moreover, harmonic complexes that are created with negative Schroeder phases (component phases monotonically decreasing with increasing harmonic frequency) may provide more masking than those created with positive Schroeder phases (monotonically increasing phase), even though both temporal envelopes are equally flat. To date, there has been little comparative work on the masking effectiveness of harmonic complexes. Using operant conditioning and the method of constant stimuli, masking of pure tones by harmonic complexes was examined in budgerigars at several different masker levels for complexes constructed with two different fundamental frequencies. In contrast to humans, thresholds in budgerigars differed very little for the two Schroeder-phase waveforms. Moreover, when there was a difference in masking by these two waveforms, the positive Schroeder was the more effective masker—the reverse of that described for humans. Control experiments showed that phase selection was relevant to the masking ability of harmonic complexes in budgerigars. Release from masking occurred when the components were in coherent phase, compared with a complex with random phases selected for each component. It is suggested that these psychoacoustic differences may emerge from structural and functional differences between the avian and mammalian peripheral auditory systems involving traveling wave mechanics and spectral tuning characteristics. © *2000 Acoustical Society of America.* [S0001-4966(00)06203-8]

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INTRODUCTION

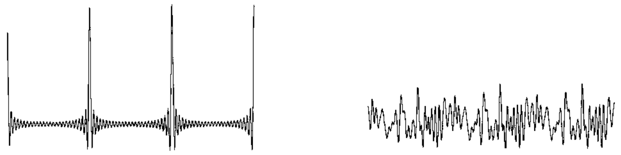
Over the years, masking studies involving the detection of pure tones against a background of broadband noise have been conducted in a number of species of birds (Dooling, 1982, 1991; Fay, 1988). Although there are some exceptions (Dooling, 1982; Dooling and Saunders, 1975; Dyson *et al.*, 1998; Langemann *et al.*, 1998), masking patterns in birds are generally similar to those reported for mammals, with critical ratios increasing about 2–3 dB/octave (Fay, 1988; Klump, 1996; Okanoya and Dooling, 1987). In contrast, there is much less comparative data on the masking of pure tones by complex sounds. Recent studies show that in humans and other mammals, masking by complex sounds is influenced by both the frequency content and the temporal characteristics of the maskers. Harmonic complexes used as maskers offer an intriguing array of results that incorporate aspects of both simultaneous and temporal masking. They lend themselves to manipulation of temporal aspects of stimuli while permitting the long-term spectral information to remain constant. Masking by these complex sounds is strongly affected by the temporal waveform shapes, and interpretations of these effects have focused on specific cochlear functions such as traveling wave mechanics and nonlinear active gain (Kohlrausch and Sander, 1995; Carlyon and Datta, 1997a, 1997b; Summers and Leek, 1998).

Explanations for various masking effects traditionally invoke features of the mammalian auditory system. These features are likely to be important in the avian auditory system as well, supported by mechanisms that may or may not be similar to those found in mammals. In general, the best absolute thresholds for birds fall between about 1 and 5 kHz and approach the levels of sensitivity typically reported for humans and other mammals (Dooling, 1982, 1991). Avian audibility curves are typically more narrowly tuned than those of mammals, with sensitivity falling off at about 15 dB/octave below 1 kHz and about 50 dB/octave above 5 kHz (Dooling, 1980, 1982; Okanoya and Dooling, 1987). While many characteristics of hearing in this frequency region are known to be similar in birds and mammals, the special effects of masking by harmonic complexes have not been studied in birds.

In human listeners, Smith *et al.* (1986) reported large differences in masking by harmonic complexes that were identical in long-term spectra, but varied in their phase spectra. By selecting phases according to an algorithm developed by Schroeder (1970), the waveform envelope becomes very flat, and the instantaneous frequency within each period sweeps upward or downward, depending on the sign of the phase equation. Two such ''Schroeder-phase'' complexes are shown in Fig. 1(a) and (b). These two harmonic complexes, one the time-reverse of the other, can produce large

(a) Negative Schroeder $\varphi_n=-\pi n(n-1)/N$

(b) Positive Schroeder $\varphi_n=+\pi n(n-1)/N$



(c) Cosine Phase $\varphi_n=0$

(d) Random Phase $\varphi_n=\text{Random}(0{:}2\pi)$

FIG. 1. Temporal waveforms of four harmonic complexes. Three periods (30 ms) are shown for each waveform. Each waveform is constructed of harmonics 2–50 of a fundamental frequency of 100 Hz. All components have equal amplitude. The phase of each component is selected according to the equations shown (φ_n = phase for each component, n; N = total number of components).

differences in masking. The amount of masking for each Schroeder-phase masker is affected by the fundamental frequency of the complex and the frequency location of the signal within the masker bandwidth (Kohlrausch and Sander, 1995). Masking by the positive Schroeder-phase wave may also change dramatically as a function of stimulus level (Carlyon and Datta, 1997b; Summers and Leek, 1998). Summers and Leek (1998) showed that differences in masking by the two Schroeder waveforms were not specific to pure tone signals, in that they also produce a differential amount of interference with speech intelligibility.

While specific cochlear processing mechanisms are thought to underlie the masking of pure tones by harmonic complexes in mammals, possible explanations are much less clear in birds. The masking effects of harmonic complexes in birds are unknown. Moreover, while the inner ears of birds show some general similarities to mammalian inner ears, there are also a host of important differences, including differences in size, morphology, spatial arrangement, and function of cochlear structures (for a review, see Manley, 1990). For these reasons, a comparison of masking by harmonic complexes in mammals and birds might prove useful in trying to understand the relative contributions to masking of various cochlear features and processes. In addition, the manner in which the maskers interact with bird inner ear mechanisms, as revealed by masking differences between Schroeder-phase waveforms, may add to our understanding of important problems in avian hearing such as how the avian auditory system processes complex sounds like species-specific vocalizations.

In this study, we report masking effects of harmonic complexes with phase spectra constructed according to the positive and negative Schroeder algorithms, and some control conditions using cosine-phase [Fig. 1(c)] and random-phase [Fig. 1(d)] maskers. We show for both birds and humans that there is an effect of stimulus phase on masking, as shown by responses to cosine- and random-phase maskers. In contrast to human listeners, however, in whom negative Schroeder complexes are more effective maskers than positive Schroeder complexes, the masking effectiveness of the two Schroeder-phase waveforms in birds is much more similar.

I. METHODS

A. Subjects

Three adult budgerigars (all females) were used as subjects. The birds were kept on a normal day/night cycle correlated with the season and maintained at approximately 90% of their free-feeding weights. For comparison, two humans (laboratory staff members) were also tested in this experiment. All bird and human subjects had hearing within normal limits for their species, as shown by their audiograms.

B. Stimuli

Stimuli consisted of masker harmonic complexes alone and masker-plus-signal, with the pure-tone signal added in-phase to the maskers at appropriate signal-to-masker levels. Stimuli were created digitally, at a sampling rate of 40 kHz, using software from Tucker-Davis Technologies to combine frequencies in the correct phases and amplitudes, followed by an inverse fast Fourier transform (FFT) to create the waveforms. They were created off-line and stored as files for playback during the experiment.

The masking stimuli were positive and negative Schroeder-phase harmonic complexes as shown in Fig. 1(a) and (b), with equal-amplitude components at frequencies that were integral multiples of a fundamental frequency, and starting phases selected according to the Schroeder algorithms as shown in the figure. Maskers included all harmonics of the fundamental frequency from 200 to 5000 Hz. Two fundamental frequencies were used, 50 and 100 Hz. The number of components in the maskers was determined by the fundamental frequency, and was 97 and 49 for the 50- and 100-Hz fundamentals, respectively.

The maskers were 260 ms in duration including 20-ms cosine^2 onset and offset ramps. The tones were 180 ms in duration, including the 20-ms ramps. The signal was temporally centered in the masker, and was always added in-phase with the masker component having the same frequency. Except where noted, the signal frequency was either 2.8 or 2.85 kHz for fundamental frequencies of 100 or 50 Hz, respectively. Signal-to-masker levels were created for testing in 5-dB steps.

C. Testing apparatus—Birds

The budgerigars were tested in a wire cage ($23\times25\times16$ cm) mounted in a sound-isolation chamber (Industrial Acoustics Company, IAC-3). A response panel consisting of two microswitches with light-emitting diodes (LEDs) was mounted on the wall of the test cage just above the food hopper. The microswitch was tripped when the bird pecked the LED. The left microswitch and LED served as the observation key while the right microswitch and LED served as the report key. The behavior of the animals during test sessions was monitored by a video camera system (Sony HVM-322).

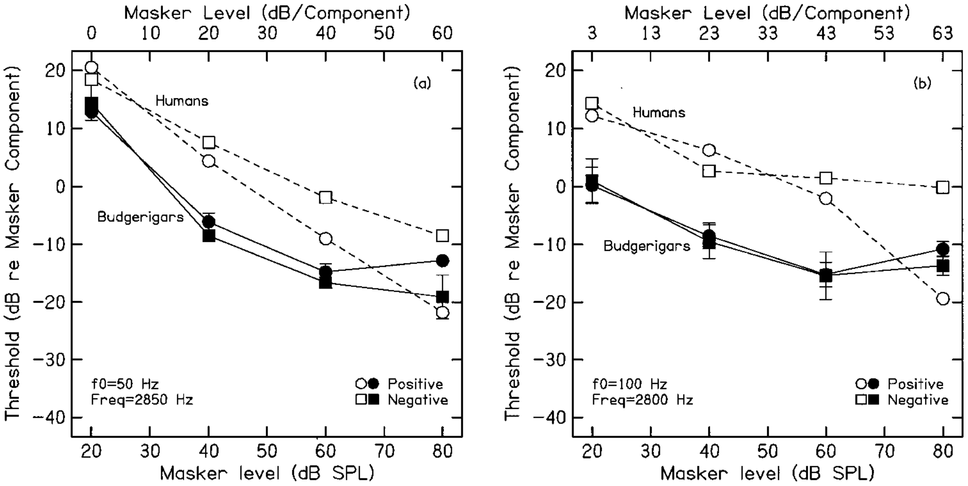


FIG. 2. Mean thresholds are plotted as signal level in dB relative to each component of the masker as a function of overall masker level at the bottom of the figures, and for the level per component of the masker along the top. Average data are shown for budgerigars in solid symbols, and for two human listeners by open symbols. Error bars indicate standard deviations for the three birds. Larger numbers on the ordinate (toward the top of the graphs) indicate more masking and smaller numbers denote less masking. Left panel (a) shows data for a fundamental frequency of 50 Hz, and a signal frequency of 2.85 kHz; right panel (b) shows data for a fundamental frequency of 100 Hz, signal frequency of 2.8 kHz.

Test sessions were controlled by an IBM 486 computer. The digital stimuli were output to a KEF loudspeaker (model 80C) via Tucker-Davis modules at a sampling rate of 40 kHz and presented at masker levels of 20, 40, 60, or 80 dB SPL. Stimulus calibration was performed using a General Radio sound level meter (model 1982). Stimulus intensities were measured with a 1/2-in microphone attached to the sound level meter via a 3-m extension cable. The microphone was placed in front of the response keys in the approximate position occupied by the bird's head during testing. Masker intensities were measured several times during these experiments to ensure that stimulus levels remained constant and the entire system was calibrated.

D. Training and testing procedures—Birds

Birds were trained by standard operant auto-shaping procedures (Dooling and Okanoya, 1995) to peck at the left microswitch key (observation key) during a repeating background until a new stimulus was presented alternately with the background sound. The time between pecking the observation key and the initiation of alternating sounds was random, with a range of 2–7 s. 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 variable was percent correct 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, and a new trial sequence was 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 the 2 s 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 an individual bird's behavior, with longer time-out periods imposed if birds began developing higher false alarm rates. Sessions with a total false alarm rate of 16% or higher were discarded. In all, 14% of the test sessions were discarded, which is typical for these procedures (Dooling and Okanoya, 1995)

For each experimental condition, signal levels in 5-dB steps were presented using the method of constant stimuli (Dooling and Okanoya, 1995). Signal levels within a condition were selected to bracket the presumed threshold, and psychometric functions were developed. At the conclusion of testing, thresholds were defined as the level of the tone detected 50% of the time, adjusted by the false-alarm rate, which corresponded to d' of about 1.5–1.8.

E. Testing apparatus and procedures—Humans

The human subjects were seated in a sound-treated booth, facing a touch-screen terminal. The same stimulus files used for the birds were played through Tucker-Davis modules to one TDH-49 earphone. Stimulus levels were calibrated with the earphone in a 6-cc coupler using a sound level meter.

A standard/two alternative forced choice procedure (S/2AFC) was used to generate abbreviated psychometric functions for each threshold (Macmillan and Creelman, 1991). Correct answer feedback was provided after each trial. Stimuli were tested in 40-trial blocks. For each experimental condition (phase selection and masker level), three to five signal levels were tested. Linear interpolation was used to estimate a threshold level that would produce about 85% correct performance ($d'=1.5$).

II. RESULTS

A. Effects of masker level

Masking by the positive and negative Schroeder-phase maskers as a function of masker level for two fundamental frequencies is shown in Fig. 2. The human data are consistent with previous studies of Schroeder-phase masking in humans (Summers and Leek, 1998; Kohlrausch and Sander, 1995). Human listeners showed larger masking differences as the masker level increased, and the positive Schroeder-phase stimuli were the less effective maskers. At the highest masker levels, the difference in masking for the two phase selections was 15–20 dB. At both fundamental frequencies, however, the birds showed only small masking differences between the two Schroeder-phase maskers. The amount of masking difference increased slightly with increasing level at both fundamental frequencies, as seen with the humans, with masking differences of 5 to 8 dB at the highest masker level for a fundamental of 50 Hz (left panel), and 3–4 dB for complexes with 100-Hz fundamental frequency. A major difference between the birds and the humans, however, is that the negative Schroeder-phase masker was the less effective masker for the birds.

A two-way analysis of variance (ANOVA) with repeated measures was carried out for the budgerigar data, separately for the two fundamental frequencies. For the 50-Hz fundamental, there was a significant effect of stimulus level ($F_{3,6}=201.90$, $p<0.001$), but no effect of phase selection ($p>0.05$). The interaction between level and phase was also not significant ($p>0.05$). However, a Bonferroni *t*-test indicated that the phase difference at a masker level of 80 dB was significant ($t=3.49$, $p=0.01$). Differences due to phase selection were not significant at any other masker levels. Similar results emerge from the ANOVA for a fundamental frequency of 100 Hz. There was a significant effect of masker level ($F_{3,6}=43.95$, $p<0.001$), with no other significant main effects or interactions. Here again, however, the negative Schroeder masker provided significantly less masking than the positive masker at a stimulus level of 80 dB ($t=2.36$, $p<0.05$).

Within species, in both birds and humans, the overall differences in thresholds between the two fundamental frequencies shown in the two panels of Fig. 2 were minor. However, the masking patterns for the two fundamental frequencies within a species differed somewhat. In budgerigars, larger masking differences between positive and negative Schroeder waves occurred with the lower fundamental frequency [Fig. 2(a)] than the higher one [Fig. 2(b)]. This suggests that some characteristics of the 50-Hz fundamental frequency stimuli might have affected the amount of masking by the positive and negative Schroeder maskers. The maskers generated with the lower fundamental frequency contained more components and a longer period than maskers with a fundamental of 100 Hz, and there was also a different spectral spacing of the components. Either of these aspects of the maskers might have contributed to the Schroeder masking differences observed. This masking difference is especially obvious at the highest masking level, where the greater masking for the positive Schroeder is clearly seen for the 50-Hz fundamental.

Humans also showed some differences in the patterns of masking at the two fundamental frequencies. For a fundamental frequency of 100 Hz, masking by the negative Schroeder phase waveforms did not change as the masker level increased over a 40-dB range (from 40 to 80 dB SPL). This masker became less effective at higher masker levels when the fundamental was 50 Hz. For both fundamental frequencies, however, the positive Schroeder masker became systematically less effective over the range of masker levels from 40 to 80 dB. In all, a drop in relative masking of nearly 25 dB occurred over that masker range for both fundamental frequencies. In contrast, over the same range of masker levels, the amount of masking for budgerigars for both maskers changed by only about 10 dB.

Overall, the budgerigars were more resistant to masking than humans, with most of their thresholds falling below (i.e., less masking) those of the human listeners. Such differences in masking may be related to critical ratios in the frequency region of the signal used here. Critical ratios of budgerigars near 2.8 kHz are smaller than those reported for humans (Dooling and Saunders, 1975; Dooling, 1980, 1982; Farabaugh *et al.*, 1998; Saunders *et al.*, 1979).

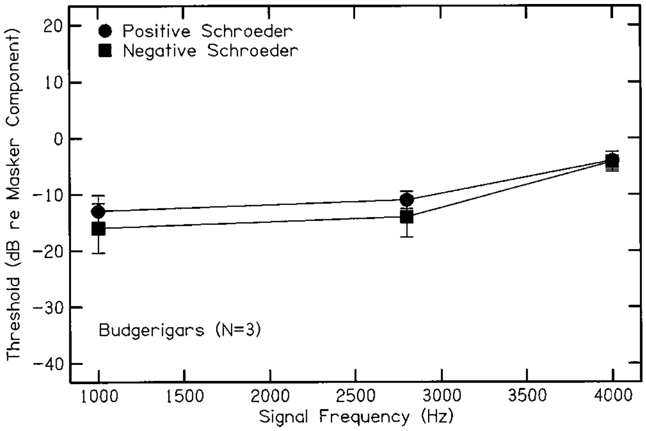


FIG. 3. Mean thresholds as a function of signal level in dB relative to each component of the masker as a function of signal frequency. Maskers had a fundamental frequency of 100 Hz, and were tested at an overall level of 80 dB SPL.

B. Effects of signal frequencies

Because budgerigars are known to have their smallest critical ratios around 2.8 kHz and larger critical ratios at 1.0 and 4.0 kHz, one test of whether the reduced effectiveness of Schroeder maskers for budgerigars compared with humans is related to the unusual shape of the critical ratio function is to test the birds on different signal frequencies. Figure 3 shows the masking for three signal frequencies provided by positive- and negative-phase maskers with a fundamental frequency of 100 Hz, tested at an overall masker level of 80 dB SPL. For signal frequencies of 1.0 and 2.8 kHz, two of the notable masking effects observed earlier are also shown here: small differences between masked thresholds, and those differences are in the reverse order of those shown in humans, with the negative Schroeder masker being less effective for birds. At 4.0 kHz, however, there was an increase in masking and no differences between the positive and negative Schroeder masked thresholds. Recall that critical ratios for these birds around 2.8 kHz are about 2 dB less than they are at 1.0 or 4.0 kHz. Thus the increase in masking by harmonic complexes from 2.8 to 4.0 kHz is consistent with earlier critical ratio results, but the similarity in masked threshold at 1.0 and 2.8 kHz is not. The critical ratios were measured with a continuous broadband noise as the masker, whereas the energy in the maskers used here is discretely distributed, occurring only at whole number multiples of the fundamental. Perhaps the failure to conform completely with critical ratio results is due to the difference in energy spacing within continuous random noise and harmonic complexes used as maskers.

C. Cosine maskers versus random maskers

It might be supposed that, given the results for the two Schroeder maskers, budgerigars are simply less sensitive than humans to phase changes in harmonic maskers. Figure 4

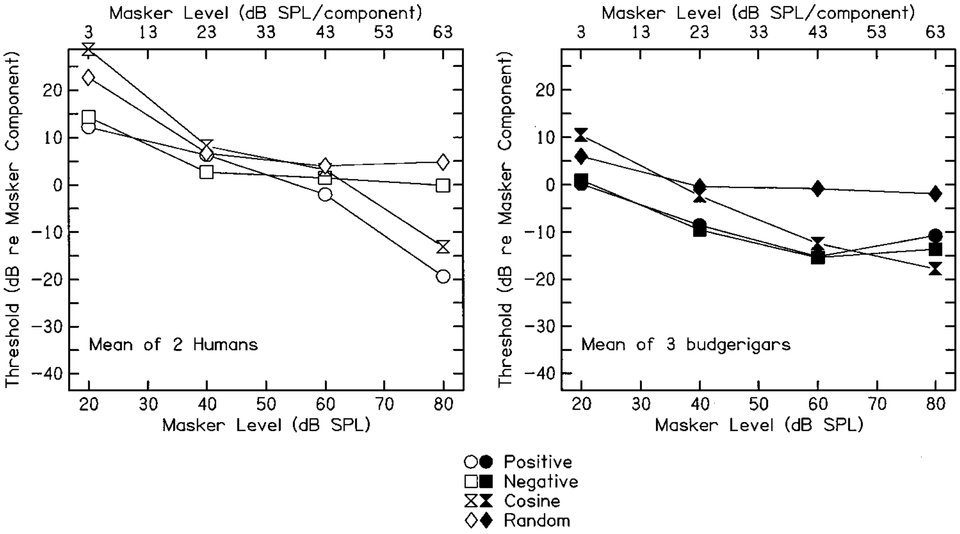


FIG. 4. Thresholds for two Schroeder-phase maskers, the cosine-phase masker, and means of two random-phase maskers as a function of overall masker level. Human data are shown in the left panel; budgerigars are shown in the right panel. The Schroeder-phase data are replotted from Fig. 2.

shows that this is not the case. This figure shows masked thresholds for harmonic maskers constructed with all components in cosine phase or with component phases selected randomly. Results from the Schroeder maskers are replotted from Fig. 2. Masking data for humans are shown in the left panel and for the budgerigars in the right panel. In this experiment, the masker fundamental frequency was 100 Hz, and the signal frequency was 2.8 kHz. For the random phase selections, two different maskers with separate phase draws were used, and the results were averaged.

For both humans and budgerigars, masking by random-phase harmonic complexes changes very little as masker level increases from 40 to 80 dB SPL. However, for both species, there is a release from masking by the cosine-phase stimuli over this range, with masking dropping by 15–20 dB for both birds and humans. Cosine- and random-phase complexes, therefore, produce distinctive patterns of masking that are similar in budgerigars and in humans. The species differences emerge with the Schroeder-phase maskers. In birds, both Schroeder-phase maskers produce a release from masking relative to the random-phase maskers across the entire range of masker levels. In humans, however, it is only the positive Schroeder phase that shows the same release from masking evidenced by the cosine-phase masker. The negative Schroeder phase masker has nearly the same effectiveness as the random-phase masker over the range of masker levels. In aggregate, these results suggest that processing mechanisms involved in masking by harmonic complexes are fundamentally different between humans and birds.

III. DISCUSSION

Masking by harmonic complexes in humans is thought to be influenced by a number of processes in the peripheral auditory system. Schroeder-phase harmonic maskers are particularly intriguing in that they have identical long-term spectra and waveform envelopes, while having temporal fine structure that is reversed. Explanations of the masking differences between the two Schroeder waves observed in human listeners have primarily addressed traveling wave mechanics and within-processing-channel differences in internal crest factors. It is likely, therefore, that the species differences in masking by harmonic complexes observed here might also be related to species differences in the same anatomical and/or physiological factors. The major findings that must be explained here are: (1) birds generally show less overall masking from harmonic complexes than do humans; (2) although clear differences in masking effectiveness of harmonic complexes occur with different phase selections (e.g., cosine-phase maskers relative to random-phase maskers), large differences between the positive and negative Schroeder-phase maskers were not observed in the budgerigars in any of the conditions tested here, in contrast to results from human listeners; and (3) when differences between masking by Schroeder-phase complexes in birds occur, the positive Schroeder waveform is the more effective masker—the reverse of the asymmetry observed in humans.

Turning first to the finding of less masking in the birds than in the human listeners, recall that the frequency analyzing channels at the signal frequency (2.8 kHz) in budgerigars are narrower than those found in humans (Dooling and Saunders, 1975; Dooling and Searcy, 1979, 1985; Saunders *et al.*, 1978a, 1978b, 1979). Less masker power within the relevant critical bands near the signal frequency would result in lower thresholds for the birds than for humans. The bandwidth of the analyzing channel surrounding the signal frequency also determines how many harmonic components will interact to produce a within-channel output waveform. To the extent that the individual components are more nearly resolved by the relatively narrow analyzing channels, the influence of the temporal waveform shape on masking will be reduced.

Within-channel waveform shapes also may be altered by cochlear processes other than the bandwidths of analyzing channels, and these other processes may contribute to the equal effectiveness of positive and negative Schroeder-phase harmonic complexes for the birds. Smith *et al.* (1986), and later, Kohlrausch and Sander (1995), argued that, in humans, because of an interaction between the phase spectrum of the Schroeder-phase maskers and the phase characteristic of the basilar membrane, the positive-phase masker becomes trans-formed internally (i.e., on the basilar membrane) into a highly modulated waveform, with relatively long intervals of low-amplitude activity—much as is seen externally in a cosine-phase wave. The interaction between the basilar membrane and the negative Schroeder masker, however, does not create such peaks in the internal waveform. Instead, it produces an envelope that is more like its external waveform shape, or like a random-phase wave. Thus the (internally) modulated positive-phase masker would be a poorer masker than the (internally) flat-envelope negative Schroeder masker, as the signal could be detected within the low-amplitude portions of the positive Schroeder waveform. Additional reductions in masking by the positive Schroeder masker might also be due to active gain mechanisms in the mammalian cochlea, which differentially amplify low- and high-amplitude portions of a sound. Carlyon and Datta (1997a) and Summers and Leek (1998) have reported changes in the effectiveness of the positive-phase masker with increasing level that are consistent with the activity of the nonlinear gain mechanism in the cochlea. The contribution of the active gain mechanism was further demonstrated by Summers and Leek by showing a loss of the differential masking effect in human listeners with sensorineural hearing impairment—a condition usually involving damage to active cochlear processing (Patuzzi *et al.*, 1989).

An explanation of the Schroeder masking results in birds that relies on the dynamics of cochlear processing and active nonlinear mechanisms is somewhat problematic. This is because of the small size of the avian basilar papilla, our lack of knowledge regarding the phase characteristics of the avian inner ear, and uncertainty about the existence and characteristics of nonlinear processing in birds. The length of the budgerigar basilar papilla is only about 3 mm—an order of magnitude smaller than the human basilar membrane (Manley *et al.*, 1993). Moreover, the stiffness gradient of the chicken basilar papilla is much steeper than its counterpart in the human cochlea (von Bekesy, 1960). Though there is undoubtedly a traveling wave on the bird basilar papilla, its time course is likely to be much shorter from base to apex than that observed in humans. These, and possibly other structural and functional differences, suggest that the phase characteristics of the inner ears of the two species differ considerably. There is no evidence for the kind of hair cell motility in birds that is responsible for the active gain processes, and therefore nonlinearity, in mammals (Manley, 1995). Other nonlinear gain mechanisms may exist in the avian inner ear, possibly related to the function of the tectorial membrane (Manley, 1995).

Perhaps the most intriguing finding from this study is the reversal in birds of the Schroeder masking effect observed in humans. In the budgerigars, the positive Schroeder-phase maskers were more effective, while in humans, the negative-phase complexes produced the greater amounts of masking. We would expect that species differences in inner ear tuning or neural firing patterns may contribute to these masking differences. Gleich (1994) reported that tuning curves and excitation patterns in birds are generally more symmetrical and change less with increasing stimulus levels than those of mammals. At very high levels, the tuning curves broaden slightly and the excitation patterns begin to show a slightly shallower lower-frequency side than high-frequency side (Gleich, 1994). In contrast, mammalian tuning curves at frequencies above 1 kHz broaden significantly with level, with the low-frequency tail becoming more shallow. Excitation patterns on the mammalian basilar membrane become increasingly asymmetrical with level, as the high-frequency side of the excitation becomes ever more shallow and the low-frequency side remains fairly steep, in contrast to patterns exhibited in birds.

On the basis of tone-on-tone masking studies, budgerigars appear to share with other birds a tuning curve shape that is more symmetrical than that typically found in mammals (Saunders *et al.*, 1979; Dooling and Searcy, 1985). In fact, if budgerigars follow the typical avian patterns of tuning, only at the highest levels might the slightly increased asymmetry contribute to a difference in masking between the negative and positive Schroeder maskers. Thus to the extent that tuning asymmetries observed in mammals are involved in masking differences found there, we might expect less masking differences between Schroeder-phase complexes in birds. Moreover, because the tuning curve asymmetry is opposite to the asymmetry observed in mammals, the direction of any masking difference would be the reverse of that seen in humans. This, of course, is exactly the pattern observed in the budgerigars as masker level increases (see Fig. 2).

While considering the possible contributions of tuning curve shapes to these masking differences, however, it must be remembered that the long-term spectra of the Schroeder complexes are identical, with differences only in the direction of the within-period glides in their instantaneous spectra. Upward-sweeping instantaneous frequencies found in the negative-Schroeder harmonic complex would change the dynamic aspects of neural firing relative to that produced by instantaneous frequencies sweeping downward, as in the positive Schroeder-phase waveform. Differences in Schroeder-phase masking may in part result from the glide-like aspects of the maskers interacting with temporal characteristics of neural firing. For example, Carney *et al.* (1999) reported that, in cats, impulse responses of auditory nerve fibers show an initial upward or downward frequency glide, depending on the best frequency of the neuron in question. Frequency-modulated impulse responses in basilar membrane motion at high frequencies have also been reported (de Boer and Nuttal, 1997; Recio *et al.*, 1998), and several recent auditory models of tuning characteristics in mammals incorporate an upward- or downward-sweeping impulse response (e.g., Irino and Patterson, 1997). These glides in the impulse responses may reflect the phase characteristic of the basilar membrane, and may relate to the Schroeder masking differences observed in humans. It is not clear whether such frequency glides might be found in neural impulse responses in birds, or whether such glides might be reversed relative to those found in mammals, perhaps in conformity with the symmetry characteristics of avian tuning curves.

There are two other minor factors that deserve mention in considering the contrasting findings here from humans and from budgerigars. First, there is a possible contribution from different transducers in the experimental setups. Birds performed this listening task in a sound field, and were free to move around (although in practice, because they were busy pecking the observing key, their heads moved very little in this sound field). Humans listened to these complex sounds over earphones. Informal testing of humans in the same free field as the birds confirmed the human pattern of Schroeder masking effects (i.e., negative producing more masking than positive), but the masking differences were slightly smaller than under earphones. Depending on the size of the room and the amount of reverberation, some phase alterations might occur in some sound fields between the loudspeaker and the ear. However, the masking differences for humans listening in the bird's testing box were still much larger than observed in the birds. The results of this sound field testing make it unlikely that these transducer differences were responsible in any major way for the differences in performance observed between species. Further confirmation that these masking differences are not due to random movements of the birds within the listening boxes may be found in the reliability of response patterns in replications of experimental conditions by the birds, suggesting that the stimuli were controlling responses in a systematic manner.

Finally, the effect of the bird middle ear system on these data is not clear. The middle ears of birds are connected through an interaural pathway in their highly trabeculated skull. It is now known that this interaural pathway can influence the nature of the acoustic stimulus perceived by the binaural auditory system (Coles *et al.*, 1980; Larsen *et al.*, 1997; Lewis, 1983; Rosowski and Saunders, 1980) and probably affects certain binaural phenomena such as sound localization (Park and Dooling, 1991) and binaural masking release (Dent *et al.*, 1997). It is not known whether the interaural pathway differentially distorts the positive and negative Schroeder maskers in ways that affect their masking effectiveness.

IV. CONCLUSIONS

The shape of the temporal waveform has a significant impact on the ability of harmonic complexes to mask pure tones in both humans and budgerigars. In both species, highly peaked waveforms with all components in cosine phase generally produce less masking than random-phase maskers, and the masking differences between the two maskers increase monotonically with stimulus level, again in both species. Significant species differences emerge, however, with other selections of harmonic component phases.

As previously reported in humans, masking by positive and negative Schroeder-phase complexes produce differences in signal threshold that increase as masker level increases from low to moderate levels. The negative Schroeder waveform is usually the more effective masker. These results hold for fundamental frequencies of 50 and 100 Hz.

In budgerigars, however, the two Schroeder phase maskers produced nearly identical thresholds until the highest masker level was reached. When small differences in masking were observed, the direction of masking effectiveness was reversed relative to that found in humans, with the positive Schroeder masker showing the greater masking effects. In addition, in most cases the budgerigars showed less masking than did humans. These differences in masking performance between species are likely due to differences in structure and function of the two auditory peripheries. They may relate to differences in traveling wave characteristics and to different manifestations of active cochlear processing in avian and mammalian ears. A known difference between species relating to shapes and widths of neural tuning curves may emerge as a significant contributor to these observed masking differences.

The differences in masking between budgerigars and humans observed here encourage the use of these types of harmonic complex stimuli in studies relating auditory perception to species-specific structures and processing mechanisms. Stimulus manipulations of both long-term and instantaneous frequencies, as well as control of dynamic aspects of sounds such as temporal envelopes and fine structure, open a broad vista of challenges to comparative explorations of auditory function.

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