Temporal integration of acoustic signals by the budgerigar (*Melopsittacus undulatus*)

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Avoidance conditioning and a modified method of limits psychophysical procedure were used to study temporal integration of tone and noise signals in the budgerigar (*Melopsittacus undulatus*). Integration of both tone and noise signals can be described by a negative exponential function with a time constant of about 200 ms. At very short durations there were differences in the integration of tone and noise signals. These data are similar to those reported for a number of other vertebrates, including man. Thresholds for two complex natural vocalizations of the budgerigar are similar to those of pure tones of equivalent duration.

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INTRODUCTION

Comparative data on auditory temporal summation of pure tones are available for a number of vertebrates including monkey (Clack, 1966), mouse (Ehret, 1976), chinchilla (Henderson, 1969), goldfish (Offutt, 1967; Popper, 1972; Fay and Coombs, 1983), bottlenosed dolphin (Johnson, 1968), and man (Watson and Gengel, 1969). Preliminary studies of temporal summation in the budgerigar have established that this species probably integrates acoustic energy for signal durations of 32 to 1000 ms in a manner similar to that found for most other vertebrates. The maximum integration time for pure tones is about 200 ms (Dooling, 1979, 1980). This is somewhat surprising in view of the considerable differences between these two vertebrate classes in both peripheral and central auditory systems (Boord, 1969; Tanaka and Smith, 1978).

Because of the acoustic complexity of avian vocalizations and their importance in communication, there has always been considerable interest in all aspects of temporal processing by the avian auditory system. Many bird vocalizations contain rapid frequency transitions or other very short notes that birds can clearly learn to imitate with a high degree of precision (Marler and Peters, 1982). It has often been suspected that the avian ear is unusually sensitive to such short sounds (Pumphrey, 1961; Greenewalt, 1968; Konishi, 1969). For these reasons, the present study extends earlier observations of temporal summation to include noise signals and tones of shorter duration. It is of interest to know: (1) whether there are differences in the integration of tone and noise signals, (2) whether short (< 32 ms) and long acoustic signals are integrated in a similar manner, and (3) whether thresholds for more complex acoustic signals such as natural vocalizations are at variance with what is known from the temporal integration of more simple acoustic signals. There is some evidence for enhanced detection of calls in noise by the lovebird (*Agapornis roseicollis*) (Busnel and Mebes, 1976).

I. MATERIALS AND METHODS

A. Subjects

The subjects were six commercially available budgerigars or parakeets (three males, three females), ranging in age from 4–24 months old.

B. Apparatus

The birds were tested in a double-walled, sound-shielded chamber (IAC-1200). Sound was delivered by a TDH-49 earphone mounted 15 cm in front of the bird's head. Tone and noise stimuli of varying durations were shaped by an electronic switch (Coulbourn Instruments S84-04). The duration of test stimuli was taken as the time between successive on and off pulses to the electronic switch. Rise/fall times were 4 and 1 ms for the tone and noise signals, respectively. For tonal signals, a bandpass filter (Genrad model 1952) was inserted between the electronic switch and the power amplifier. The high and low cutoffs of this filter were set to 20% above and below the test tone frequency. The audiometric circuits consisting of logic and analog modules (Coulbourn Instruments) has been described previously (Dooling, 1979).

C. Training and testing

The apparatus for avoidance conditioning as well as the training and testing procedure has previously been described in detail (Dooling and Saunders, 1975a; Dooling, 1979). The bird was gently restrained in a tubular holder and trained to bite a response bar positioned 3 cm in front of its beak. The training stimulus was a 2.8-kHz pure tone burst of 512 ms presented at a level of 70 dB SPL. A trial interval lasted 5 s, during which four tone bursts were presented. Failure to respond during the trial interval resulted in the delivery of a loud buzzer and the application of a mild electric shock to the bird's legs until a correct response occurred. Once the birds learned to avoid shock on 90% of the trials, a modified method of limits procedure was used to obtain threshold estimates.

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During threshold testing, intertrial intervals were randomized between 15–60 s so that approximately 50–60 trials could be run in a daily test session. A modified method of limits procedure was applied as follows. A threshold run began with the stimulus intensity set at 70 dB SPL. Following each correct response, the intensity of the probe was lowered 10 dB and another trial was run. After a miss, the intensity of the stimulus was raised 5 dB and a final trial was run. Threshold was taken as the sound pressure level halfway between the last correct and incorrect responses. A sham trial was identical in every respect to a normal trial with the exception that the attenuator controlling the intensity of the stimulus was set to a nominal − 128 dB and negative reinforcement was omitted. The final measure of false alarm rate was taken as the percentage of sham trials on which a response occurred.

During final threshold testing, a bird was tested at a single stimulus duration until stable threshold values were obtained over a number of days. The final threshold estimate for each bird at each stimulus duration is based on the mean of the last five threshold determinations. Responses to sham trials presented at the end of each threshold run were recorded as a measure of false responding. The order of stimulus durations tested was randomized and a different random sequence was used for each bird.

D. Stimulus conditions

All thresholds were measured against a background of continuous broadband white noise maintained at a spectrum level of − 10 dB. The tone durations tested were 8, 12, 16, 20, 24, 28, 32, 64, 128, 256, 512, and 768 ms. The noise durations tested were 1, 2, 4, 8, 16, 32, 64, 128, 256, 512, and 768 ms. Sound pressure levels of continuous tone and noise signals were measured directly with a General Radio 1933 sound level meter using a slow meter response. During calibration, a microphone was placed in the position normally occupied by the bird's head during testing. The sound pressure levels of the short calls used in this study were measured with the meter response of the sound level meter at the peak detection setting.

As a test of whether more complex acoustic signals are integrated in a manner similar to that described for simple pure tones and noises, threshold was measured for two exemplars of a species specific contact call vocalization of the budgerigar (Brockway, 1964). The calls were elicited from two of the subjects. The calls were 140 and 155 ms in duration with peak spectral energy of both calls concentrated in the frequency region of best hearing for the budgerigar (2.5–3.0 kHz). Both calls contained a considerable amount of amplitude modulation. For the first trial in the descending method of limits, the calls were presented at a peak sound pressure level of 70 dB SPL as measured with the sound level meter. Digital representations of these calls were stored in the memory of a PDP 11/10 computer and converted to analog form through a 10 bit A/D convertor (AR-11) at a rate of 20 kHz. The output of the AR-11 was low-pass filtered at 10 kHz and led to the amplifier circuits of the same audiometric circuits used for presenting the tone and noise stimuli. Spectrograms and time waveforms of these two calls are shown in Fig. 1.

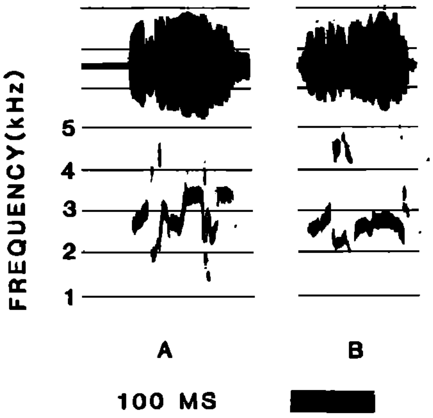

FIG. 1. Sonograms and time waveforms of two budgerigar contact calls used as test stimuli. Frequency markers are from 1 to 8 kHz. Time marker is 100 ms.

II. RESULTS

Figure 2 (top) shows the relation between masked threshold and the duration of both tonal and noise signals. For both tone and noise signals, threshold improves as the duration of the signal increases. It is also clear that very short signals are integrated differently than longer signals as has been found in previous studies of humans (Blodgett *et al.*, 1958; Garner, 1947; Garner and Miller, 1947). Data such as these are traditionally characterized in several ways. For the pure tone signals between 8 and 32 ms, there is about a 4.5 dB decrease in threshold with each doubling of duration. Tone durations greater than 32 ms show approximately a 2.0 dB decrease with each doubling in duration. For noise signals

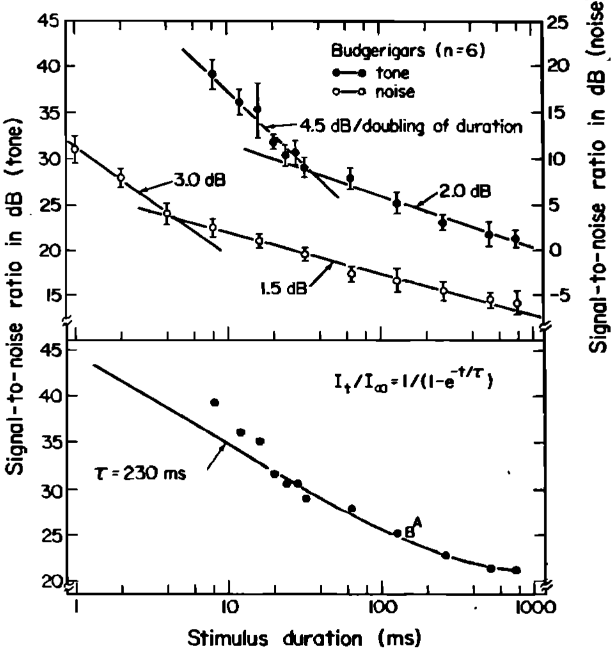

FIG. 2. Top: masked threshold as a function of duration for a 2.86-kHz pure tone (closed circle) and a noise (open circle) stimulus. Noise thresholds are referred to the right ordinate and tone thresholds to the left ordinate. Solid lines are fit to the data by eye and corresponding slopes are shown. Bottom: a negative exponential function with a time constant of 230 ms is fit to the data for the 2.86-kHz pure tone signals. Thresholds for two contact calls of the budgerigar are also shown as "A" and "B."

greater than about 4 ms, threshold improves about 1.5 dB with each doubling of duration. These findings are similar to previous results on humans (Green, 1960).

A least-squares linear best fit of a plot of signal level in dB versus log duration showed that for tone signals between 32 and 768 ms, the average slope of the power function describing the integration of acoustic energy is -0.607. For noise signals between 4 and 768 ms, the average slope of the power function is very similar at -0.530. These slopes are not significantly different by a t test for related samples ($t = 0.87$, $df = 5$, $p > 0.05$).

Plomp and Bouman (1959) suggest an alternative model for describing these data (Fig. 2, bottom). Using this model, the time constant τ is calculated from thresholds at each tone duration. The average time constant of integration is 230 ms for tonal signals. At durations shorter than about 32 ms, thresholds are slightly elevated above that predicted by a negative exponential function. These results are similar to those previously reported for the budgerigar (Dooling, 1979) and the human (Watson and Gengel, 1969).

Masked thresholds for pure tones in the range of 100–150 ms show a signal-to-noise ratio of about 23–25 dB. The thresholds for the two "contact" calls show a signal-to-noise ratio of 26.5 and 25.5 dB. Thus there is close agreement between the signal-to-noise ratios of simple pure tones and the masked thresholds of more acoustically complex vocalizations.

III. DISCUSSION

For signals longer than about 32 ms, a negative exponential function proposed by Plomp and Bouman (1959) provides an adequate description of temporal integration of both noise and a 2.86-kHz tone for the budgerigar. The data for integration of pure tones agrees well with previous results of both humans (Watson and Gengel, 1969; Zwislocki, 1960) and budgerigars (Dooling, 1979).

Both of these sets of data can also be fairly well characterized by power functions. Plotted in this way, there is good agreement between the present results and those from a number of other vertebrates, including the human (Green, 1960), mouse (Ehret, 1976), and goldfish (Fay and Coombs, 1983). Like the mouse, the slopes of the power functions describing integration of noise and tone signals by the budgerigar are very similar. These results are in contrast to those for the goldfish (Fay and Coombs, 1983) and man (Garner, 1947), showing somewhat shallower slopes for noise signals compared to tonal signals.

The similarity in temporal summation of both noise and tonal signals for the budgerigar suggests that events within the critical band around 2.86 kHz may be determining the slope of the temporal integration function for noise signals. Further support for this suggestion is evident when comparing the integration of short tonal signals (< 32 ms). Previous results for the human suggest that short acoustic signals (< 20 ms) show a somewhat steeper slope because of the spread of energy over the frequency domain (Garner, 1947; Garner and Miller, 1947). This effect is also apparent in the budgerigar data, but with the slope change occurring at 32 ms rather than 20 ms. Perhaps this difference is due to the smaller critical band of budgerigars at 2.86 kHz. The change in slope for noise signals cannot be explained by a similar reasoning. Rather, it may be that the critical bandwidth of the auditory system widens at very short durations.

The present data fit well with results from other studies of hearing in this species. Masked thresholds for the longest tone durations approached a signal-to-noise ratio of 20 dB. This is close to the critical ratio measured for the budgerigar at 2.86 kHz of 18.8 dB (Dooling and Saunders, 1975a). The threshold for the longest noise durations approach signal-to-noise ratios of about -5.5 dB. Viewing the detection of a broadband noise masked by a second, uncorrelated noise as an intensity discrimination task, the budgerigar intensity difference limen is about 1 dB. This value corresponds well with intensity difference limens as calculated from amplitude modulation thresholds of broadband noise (Dooling and Searcy, 1981) and agree very well with recent data from the goldfish (Fay and Coombs, 1983).

Finally, the contact call was chosen for comparison because it is a loud vocalization given by separated budgerigars to maintain contact with the flock. Given its function, it is reasonable to speculate that budgerigars might show unusually sensitive thresholds for detection of this call against a background of noise. For this reason, it is interesting to compare the thresholds for pure tone signals and contact calls even though a direct comparison between the two is a complicated matter. The pure tone signal has all of its energy concentrated within a single critical bandwidth (Dooling and Saunders, 1975a) with no variation in amplitude over time. By contrast, the two contact calls are far more complex. It is clear from Fig. 1 that the peak energy extends over several critical bandwidths of the budgerigar auditory system and the amplitude is not uniform over time, sometimes even dropping to zero. In spite of these differences the budgerigar shows similar thresholds for both tones and calls.

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Blodgett, H. C., Jeffress, L. A., and Taylor, R. W. (1958). "Relation of masked threshold to signal-duration for various interaural phase combinations," Am. J. Psychol. 71, 283–290.

Boord, R. L. (1969). "The anatomy of the avian auditory system," Ann. NY Acad. Sci. 167, 186–198.

Brockway, B. F. (1964). "Ethological studies of the budgerigar (*Melopsittacus undulatus*)," Behaviour 23, 193–222.

Busnel, R. G., and Mebes, H. D. (1976). "Hearing and communication in birds: The cocktail-party-effect in intraspecific communication of *Agapornis Roseicollis* (*AVES, Psittacidae*)," Life Sci. 17, 1567–1570.

Clack, T. D. (1966). "Effect of signal duration on the auditory sensitivity of humans and monkeys (*Macaca mulatta*)," J. Acoust. Soc. Am. 40, 1140–1146.

Dooling, R. J. (1979). "Temporal summation of pure tones in birds," J. Acoust. Soc. Am. 65, 1058–1060.

Dooling, R. J. (1980). "Behavior and psychophysics of hearing in birds," in *Comparative Studies of Hearing in Vertebrates*, edited by A. N. Popper and R. R. Fay (Springer-Verlag, New York), pp. 261–288.

Dooling, R. J., and Saunders, J. C. (1975a). "Hearing in the parakeet (*Melopsittacus undulatus*): Absolute thresholds, critical ratios, frequency difference limens, and vocalizations," J. Comp. Physiol. Psychol. 88, 1–20.

Dooling, R. J., and Saunders, J. C. (1975b). "Auditory intensity discrimination in the parakeet (*Melopsittacus undulatus*)," J. Acoust. Soc. Am. **58**, 1308–1310.

Dooling, R. J., and Searcy, M.H. (**1981**). "Amplitude modulation thresholds for the parakeet (*Melopsittacus undulatus*)," J. Comp. Physiol. **143**, 383–388.

Ehret, G. (**1976**). "Temporal auditory summation for pure tones and white noise in the house mouse (*Mus musculus*)," J. Acoust. Soc. Am. **59**, 1421–1427.

Fay, R. R., and Coombs, S. (**1983**). "Neural mechanisms in sound detection and temporal summation," Hear. Res. **10**, 69–92.

Garner, W. R. (**1947**). "The effect of frequency spectrum on temporal integration of energy in the ear," J. Acoust. Soc. Am. **19**, 808–815.

Garner, W. R., and Miller, G. A. (**1947**). "The masked threshold of pure tones as a function of duration," J. Exp. Psychol. **37**, 293–303.

Green, D. M. (**1960**). "Auditory detection of a noise signal," J. Acoust. Soc. Am. **32**, 121–131.

Greenewalt, C. H. (**1968**). *Birdsong: Acoustics and Physiology* (Smithsonian Inst., Washington, DC).

Henderson, D. (**1969**). "Temporal summation of acoustic signals by the chinchilla," J. Acoust. Soc. Am. **46**, 474–475.

Johnson, C. S. (**1968**). "Relation between absolute thresholds and duration-of-tone pulses in the the bottlenosed porpoise,"J. Acoust. Soc. Am. **43**, 757–763.

Konishi, M. (**1969**). "Time resolution by single auditory neurons in birds," Nature (London) **222**, 566–567.

Marler, P., and Peters, S. (**1982**). "Subsong and plastic song: Their role in the vocal learning process," in *Acoustic Communication in Birds, Vol. 2*, edited by D. Kroodsma and E. Miller (Academic, New York), pp. 25–50.

Offutt, G. C. (**1967**). "Integration of the energy in repeated tone pulses by man and the goldfish," J. Acoust. Soc. Am. **41**, 13–19.

Plomp, R., and Bouman, M. A. (**1959**). "The relation between hearing threshold and duration for tone pulses," J. Acoust. Soc. Am. **31**, 749–758.

Popper, A. N. (**1972**). "Auditory threshold in the goldfish (*Carassius auratus*) as a function of signal duration," J. Acoust. Soc. Am. **52**, 596–602.

Pumphrey, R. J. (**1961**). "Sensory organs: hearing," in *Biology and Comparative Anatomy of Birds*, edited by A. J. Marshall (Academic, New York), pp. 69–86.

Tanaka, K., and Smith, C. A. (**1978**). "Structure of the chicken's inner ear: SEM and TEM study," Am. J. Anat. **153**, 251–272.

Watson, C. S., and Gengel, R. W. (**1969**). "Signal duration and signal frequency in relation to auditory sensitivity," J. Acoust. Soc. Am. **46**, 989–997.

Zwislocki, J. (**1960**). "Theory of temporal auditory summation," J. Acoust. Soc. Am. **32**, 1046–1060.