difference between the results from MSF and WTF, even at 10% particle volume fraction.

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Temporal integration in zebra finches (Poephila guttata)

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Three zebra finches were trained with operant techniques to respond to pure tones. Absolute thresholds were obtained for nine durations of a 3-kHz tone and five durations of a 1-kHz tone. The temporal integration functions were described using the negative exponential function proposed by Plomp and Bouman [J. Acoust. Soc. Am. **31**, 749–758 (1959)]. The time constants obtained for zebra finches are about 250 ms, which are similar to those reported for a number of species, including humans and other bird species.

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INTRODUCTION

Despite the large morphological differences between the mammalian and avian cochlea (Smith, 1985; Gleich, 1989), a remarkable functional similarity in the spectral resolving power of birds and mammals is typically reported (Dooling, 1982; Okanoya and Dooling, 1987, in press). Recent psychophysical and physiological investigations of bird hearing are extending this similarity to the temporal domain (Klump and Maier, 1989a, 1990; Buchfellner *et al.*, 1989; Okanoya and Dooling, in press). This study examines the phenomenon of temporal summation in the zebra finch.

I. MATERIALS AND METHODS

A. Subjects

Three adult zebra finches (two females, one male; ages unknown) obtained from a local pet supplier were used. Birds were kept in an aviary at the University of Maryland with a day/night cycle corresponding to the season. Food intake outside of experimental sessions was restricted to 30 min./day during test days. This feeding schedule kept the animals within 85–90% of their free feeding weight.

B. Apparatus

Details of the apparatus and methods have been described elsewhere (Okanoya and Dooling, 1988, in press). Briefly, birds were tested in a small wire cage $(15 \times 15 \times 15)$ cm) suspended in a sound attenuation chamber. A standard pigeon grain hopper was mounted on one side of the cage. A response panel consisting of two sensitive microswitches with attached light emitting diodes (LEDs) was mounted just above the food hopper opening. A wooden perch was placed in front of the food hopper opening. The bird could trip the microswitch by striking the LED with its beak. Puretone signals were generated by a digital-to-analog converter (DAC) (data translation model DT2821) with a sampling rate of 30 kHz. The output of the DAC was fed, in turn, to a programmable attenuator, a 1/3-oct equalizer, a 10-kHz low-pass filter, and finally to a power amplifier that drove a loudspeaker mounted inside the acoustic chamber. Calibration was performed by placing a microphone of a general radio sound level meter (model 1933) in front of the LEDs. This was the location occupied by the bird's head during the experiment.

C. Training and testing procedure

Birds were trained to peck the observation key (the key to initiate a trial) repeatedly when no signal was presented

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and to peck the report key (the key to indicate a response) when a signal was presented (Okanoya and Dooling, 1990). Correct detection of the signal was rewarded by a 4-s presentation of food. To obtain a measure of spontaneous responding, catch trials during which no signal was presented occurred on 25% of the trials in a session. A response on the report key during a catch trial or during the random waiting interval was punished by a timeout period of between 4–16 s. During the timeout period, all lights in the experimental chamber were extinguished.

The method of constant stimuli was used to measure the birds' thresholds for pure tones. Within a single session, six different intensity levels were presented. Psychometric functions based on 20 presentations of each intensity level were constructed from those data. In all, thresholds were obtained for nine durations of a 3-kHz pure tone and six durations of a 1-kHz pure tone between 10 and 640 ms. Rise/fall times were 1.5 ms.

D. Threshold determination

Detection rates for each intensity level were calculated using the false alarm rate following the high-threshold theory of classical psychophysics previously used successfully with birds (Hienz *et al.*, 1977; Sinnott *et al.*, 1980). That is,

$$Pc^* = (Pc - FA)/(1 - FA),$$

where Pc^* is an adjusted correct rate, Pc is a raw correct rate, and FA is a false alarm rate. After adjusting detection rates for each intensity level, a threshold was defined as the stimulus level corresponding to a 50% correct detection point by interpolation with intensity level in decibles plotted on a linear scale. False alarm rates of the birds never exceeded 20%. At least four sessions were run for each of the durations before the final threshold was taken.

Only one duration was tested in a session and the order of durations tested was randomized for all birds. A bird was tested on the same stimulus duration until the threshold variability across sessions was less than 3 dB. Then, the bird was tested in two more sessions and the final threshold estimate for each duration was calculated as the average threshold from these last two sessions.

II. RESULTS

Figure 1 shows the relation between threshold and tone duration for the three birds. Figure 1(a) describes the relation between threshold and duration for 1 kHz and Fig. 1(b) for 3 kHz. In both of these plots, absolute thresholds were converted into relative thresholds using the threshold for the 640-ms tone as a reference. The average absolute threshold for the longest duration was 23.4 dB at 1 kHz and 7.8 dB at 4 kHz. These values are similar to the auditory sensitivity for this species reported by Hashino and Okanoya (1989).

Two estimates of temporal integration time (τ) were obtained based on the equation proposed by Plomp and Bouman (1959):

$$I_{t}/I_{\infty} = I/(1 - e^{-t/\tau}).$$

One estimate of the time constant was obtained for each bird using the thresholds for the 3-kHz pure tone at each of



FIG. 1. (a) Relative thresholds obtained for five durations of the 1-kHz pure tone were plotted for the three zebra finches tested. (b) Relative thresholds for nine durations of the 3-kHz pure tone.

the durations of 20, 40, 80, 160, and 320 using the thresholds for the longest signal (i.e., 640 ms) as an estimate of I_{∞} (Dooling, 1982; Dooling and Searcy, 1985). A similar procedure was followed with the available thresholds for the 1kHz pure tone. The average obtained according this procedure was 252.1 ms at 1 kHz and 227.5 ms at 3 kHz.

A second estimate of the time constant was obtained by solving a simultaneous least-squares equation where both I_{∞} and τ were unknowns (Klump and Maier, 1990). The time constant obtained using the simultaneous least-squares fit procedure resulted in a of 223.3 ms for the 3-kHz pure tone.

Figure 2 compares the present results with three other species of birds tested to date and humans (Dooling and



FIG. 2. The average data for the 3-kHz pure-tone summation function of three zebra finches is compared with budgerigars and field sparrows tested at 2.86 kHz (Dooling and Searcy, 1985; Dooling, 1979) and starlings and humans tested at 2 kHz (Klump and Maier, 1989a; Watson and Gengel, 1969).

Searcy, 1985; Dooling, 1979; Klump and Maier, 1989; Watson and Gengel, 1969) for frequencies between 2 and 3 kHz.

III. DISCUSSION

As is the case for several other avian species, the similarity in the shape of temporal integration function between zebra finches and humans is quite remarkable. This comparison reinforces the idea that the temporal summation process is a fundamental property of vertebrate hearing.

Watson and Gengel (1969) showed that the time constant for humans at low frequencies is longer than at high frequencies. Ehret (1976) observed a similar effect in the house mouse (Mus musculus) and Dooling (1982) reported a similar effect for the budgerigar (Melopsittacus undulatus). In the present experiment, although the time constant obtained for the 1-kHz stimulus was slightly longer than that obtained for the 3-kHz pure tone, this difference was not significant. Klump and Maier (1989) also failed to demonstrate such a tendency in the starling (Sturnus vulgaris). Brown and Maloney (1986) examined the relation between frequency and the time constant of integration in several species of monkeys and also showed no clear trend. Thus we conclude that, although a time constant of roughly 200 ms may be a ubiquitous feature of vertebrate hearing, the frequency dependency of the time constant is somewhat less certain and requires further investigation (Klump and Maier, 1990).

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