DISTANCE PERCEPTION BY ECHOLOCATION: THE NATURE OF ECHO SIGNAL-PROCESSING IN THE BAT

by

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Bats orient themselves in the environment by emitting ultrasonic cries and detecting echoes of these cries that are reflected from near-by objects. [4]) One of the many intriguing questions about echolocation, this active sonar sense used by bats, is whether it can serve for the perception of depth or differences in the distance to targets. Bats must often face situations which involve multiple targets; for example, a cluster of several flying insects or an insect flying near branches. It would be of obvious value to the bat in detecting and identifying objects if its sonar could distinguish among such multiple targets. Depth perception is of theoretical interest to us because we might be able to determine something about how the bat processes echoes if we knew how well it could perceive distance or range. Many of the theories about echolocation and the kinds of information extracted from echoes by bats have been proposed in the form of hypothetical mechanisms for the determination of distance. [1,3,9-18]) The experiments to be described here are attempts to measure the acuity of the bat in discriminating differences in distance. Their results identify echo travel time as an important auditory cue for target range and suggest how this cue might be processed in the bat's auditory nervous system.

DISTANCE DISCRIMINATION

The experiments were conducted on blinded specimens of *Eptesicus fuscus* (Vespertilionidae), a small North American insectivorous bat, and *Phyllostomus hastatus* (Phyllostomidae), a large, carnivorous and frugivorous neotropical bat.

Both of these species emit short-duration, frequency-modulated cries. *Eptesicus* is representative of FM bats with cries that have a broad bandwidth due to an extensive frequency sweep, with relatively little energy in harmonics. *Phyllostomus* represents those FM bats with a restricted frequency sweep in their cries but still a broad bandwidth due to the presence of strong harmonics.

The bats were trained with food as reward to fly from an elevated platform to one of two nearby landing platforms carrying triangular targets. Figure 1 shows the arrangement of these platforms and the bat's response. The landing platforms were 40° apart and were at different distances from the bat on the starting platform. One platform and target was fixed at 30, 60, or 120 cm, and the experiment was begun with the other placed 10 cm closer. The closer platform and target was alternated pseudorandomly from the left to the right, and the experiment followed the procedure for simultaneous discrimination without correction of error trials. The bat's performed on a 10 cm range difference for 50 trials, and then the closer target was moved back so that the range difference was 9 cm. Fifty trials were conducted and the

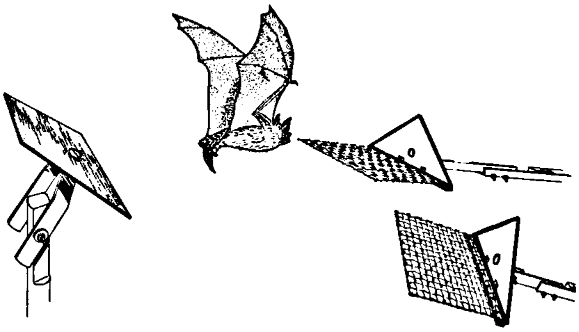

Fig. 1. The distance discrimination apparatus and the bat's response.

range difference was again reduced. In this manner the bat performed for 50 trials on range differences extending from 10 cm down to zero in small steps. Range discrimination was measured at absolute ranges of 30, 60, and 120 cm.

The "empirical" curves in figs. 2 and 3 are graphs of the average percentage of correct responses made by three bats of each species discriminating at an absolute range of 60 cm. The curves are not significantly different from those obtained at 30 and 120 cm for each species. The range difference discriminated 75 % correctly is a satisfactory, if arbitrary, summary of the data. For *Eptesicus* these 75 % "thresholds' averaged 12 to 13 mm at 30, 60, and 120 cm. *Phyllostomus* averaged 11 to 12 mm at 30 and 60 cm and 10 mm at 120 cm. The acuity of distance discrimination as represented by the entire discrimination curve or by the 75 % "threshold" is essentially independent of absolute distance at least to 120 cm.

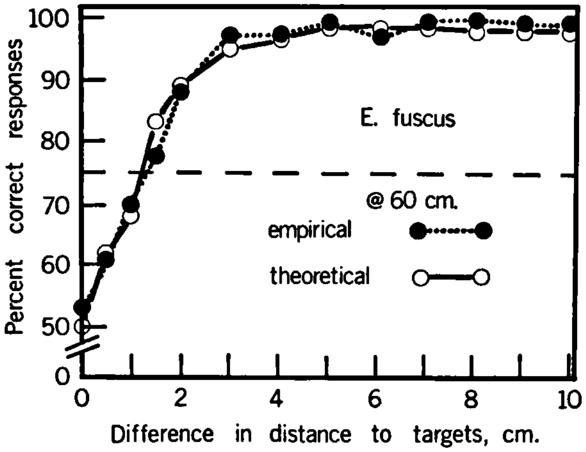

Fig. 2. Actual and predicted range discrimination behavior of *Eptesicus.*

ARRIVAL TIME DISCRIMINATION

For each millimeter of distance to a target, the arrival time of an echo is delayed by 5.8 μsec. The echo is reduced in intensity by atmospheric attenuation, which varies with frequency, and by the smaller apparent size of the target. In the experiment on arrival time discrimination by the bat an electronic echo-producing system isolated the difference in echo arrival time from the other changes in the echo. The cries used by the bat while examining the targets during the discrimination were picked up by two Bruel and Kjaer 1/4-inch condenser microphones placed 10 cm from the bat's mouth, amplified, and returned to the bat as sounds from electrostatic loudspeakers on the left and the right landing platforms. With the triangular targets removed and the electronics functioning properly, every time the bat emitted a cry it received a reproduction of that cry much as though it were an echo from a target. The arrival times of these artificial echoes could be varied with delay lines included in the electronic system. The bats were trained to fly to whichever platform was associated with the earlier echo. The time intervals associated with range differences of 10 cm, 9 cm, 8 cm, etc. were set on the delay lines, and the distance discrimination experiment at 30 cm was repeated using differences in echo travel time as stimuli rather than differences in distance.

Both *Eptesicus* and *Phyllostomus* discriminated differences in echo arrival time of 60 to 70 μsec 75% correctly out of a total of 1.7 msec (the echo time delay associated with 30 cm). This time difference "threshold" corresponds to a difference in distance of 10 to 12 mm. The time discrimination curves were not significantly different from the distance discrimination curves for either species. Since *Eptesicus* and *Phyllostomus* appear to discriminate distance and arrival time in an interchangeable manner, it seems reasonable to conclude that both species discriminate distance from the arrival time of echoes.

ECHO INFORMATION-PROCESSING

The autocorrelation properties of the transmitted waveform ultimately limit the capacity of a sonar system to resolve small differences in range. If the bat's sonar is ideal, that is, if it uses all the information in each echo related to arrival time and destroys all other information, then the bat's acuity in discriminating distance can be predicted from the autocorrelation functions of its echolocation cries.[2,20] Current theories on the functioning of the cochlea assume that sounds of frequencies as high as those used by bats (roughly 25 to 150 kHz) are mechanically and neurally processed by the Organ of Corti, and that phase information is lost before it becomes input to the higher auditory centers of the brain, since to preserve it would require impossibly high rates of information transfer in the auditory nerve. Without phase information the envelopes of the autocorrelation functions of the bat's cries govern distance determination if the bat's sonar is ideal and the echo signal-to-noise ratio is high relative to unity.

The cries of both *Eptesicus* and *Phyllostomus* were recorded during the distance discrimination experiments. Representative cries were autocorrelated with a Princeton Applied Research Corp. Model 101 correlation computer, and the performance of an ideal sonar system using these waveforms in discriminating distance was predicted from the envelopes of the autocorrelation functions. The predictions included compensation for the unavoidable, slight head movements of the bats in the experiments. The "theoretical" curves in figs. 2 and 3 are graphs of the predicted performance of the two ideal bat sonar systems. There are no striking or statistically significant differences between the predicted performance and the actual behavior of either *Eptesicus* or *Phyllostomus*. The accuracy of the predictions suggests that these bats use the correlation properties of returning echoes to extract information about differences in target range or echo arrival time. It is simpler to suppose that the bat crosscorrelates the echoes from the left with the echoes from the right to determine which is first to arrive. The possibility cannot be eliminated, however, that the bat crosscorrelates the outgoing cry with the returning echo, separately determining the distance to each target before responding to the closer one.

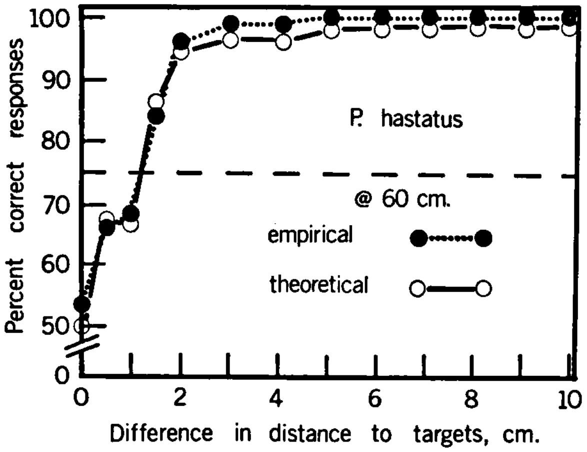

Fig. 3. Actual and predicted range discrimination behavior of *Phyllostomus*.

Further experiments are under way to differentiate between these two possible models.

INTERFERENCE FROM NOISE

The processing of echoes by correlation is relatively unaffected by jamming noise as long as the signal-to-noise ratio is above the region of about 1 to 5. If the bat does use correlation in extracting information from echoes, that fact might account for their ability to echolocate successfully in intense noise.[6,7] *Phyllostomus* used cries of 5 to 10 dynes/cm^2 average peak pressure (at 10 cm), and *Eptesicus* used cries of 60 to over 100 dynes/cm^2. The *Phyllostomus* echoes from targets at 30 cm were about 0.05 to 0.1 dynes/cm^2. *Eptesicus* echoes were 0.7 to 1.0 dynes/cm^2. The signal-to-noise ratios for even the weakest echoes of *Phyllostomus* in the distance discrimination experiments were in excess of 30 to 100; limitations in equipment for measuring very low level ultrasonic ambient noise prohibited an exact measurement. To obtain discrimination data from *Phyllostomus* at lower signal-to-noise ratios, ultrasonic noise was used. Not enough noise could be generated to conduct this experiment on *Eptesicus*. The noise, generated by an electrostatic loudspeaker, was fairly uniform in spectrum, being ± 3 to 4 dB from 25 kHz to about 130 kHz. Two noise intensities were used, one that gave *Phyllostomus* an echo signal-to-noise ratio of 2.5 to 4.0 for a target at 60 cm and one that gave a signal-to-noise ratio of 0.6 to 1.5. The intensities were chosen after measuring the way in which *Phyllostomus* adapted the intensity and duration of its cries to the noise. The distance discrimination experiment at 60 cm absolute range was repeated for both noise intensities. In the experiments without noise, when the signal-to-noise ratio was more than 30 to 100, *Phyllostomus* discriminated 10 to 12 mm 75 % correctly. When the signal-to-noise ratio was between 2.5 and 4.0, the bats discriminated 11 to 20 mm. When the signal-to-noise ratio was between 0.6 and 1.5, the bats were reluctant to respond and discriminated 30 to 32 mm. Distance discrimination by *Phyllostomus* was only slightly affected by noise until the signal-to-noise ratio had declined to the region of 1 or less. It appears that this bat is resistant to the effects of interfering noise in a situation where it may be using correlation processing.

CONCLUSIONS

The species used here are fairly good representatives of bats using FM cries. *Eptesicus* uses intense cries, a characteristic of insectivorous bats in general. *Phyllostomus* uses rather weak cries under ordinary conditions, although it can generate louder cries (more than 20 dynes/cm^2) as an adaptation to intense, high-frequency noise. Both species perceive differences in the distance to targets from differences in the arrival time of echoes returned by these targets. They behave as though they extract time information from the correlation properties of echoes. The predictions of the bats' discrimination performance, which were very successful, were based on the assumption that the envelopes of the autocorrelation functions of the cries represented the true distance discrimination performance of each bat's sonar system. This appears to be the case, and therefore *Eptesicus* and *Phyllostomus* can probably discriminate range differences of 2 to 5 mm (12 to 30 μsec) when head movements do not interfere.

Eptesicus and *Phyllostomus* may crosscorrelate returning echoes either with each other or with the outgoing cries. It is not yet certain which of these two versions of correlation processing they use. If the bat crosscorrelates the outgoing cry with the echo, it possesses a "pulse compression" sonar, including a memory for the outgoing waveform. Echo detection with a neural "template" or with a matrix of specialized cells in the inferior colliculus might be the neurophysiological mechanism underlying such processing.[5,8,12,19]) The behavior of the bats in these experiments strongly indicates that correlation processing must take place in some manner. It remains to be seen whether these conclusions are restricted to FM bats or whether they will also apply to bats such as *Rhinolophus* with long-duration cries of relatively constant frequency.

ABBREVIATED REFERENCES

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