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Frequency Shift Discrimination: Can Homing Pigeons Locate Infrasounds by Doppler Shifts?

Douglas B. Quine* and Melvin L. Kreithen*

Section of Neurobiology and Behavior, Division of Biological Sciences, Langmuir Laboratory, Cornell University, Ithaca, New York 14850, USA

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Summary. Homing pigeons can detect small shifts in sound frequency at 1, 2, 5, 10, and 20 Hz. Their thresholds range from a 1% shift at 20 Hz to a 7% shift at 1 Hz. The frequency shifts used were designed to simulate the natural Doppler shifts resulting from changes in flight path. Their ability was sufficiently sensitive to make it feasible that natural Doppler shifts can be detected. Further tests indicated that the birds can perform true frequency discrimination when all subjective amplitude cues are removed. These laboratory tests are further steps in a series designed to find out if homing pigeons use infrasounds as cues for orientation and navigation.

Introduction

It was suggested a decade ago that birds might use infrasounds for navigation, orientation, or weather detection (Griffin 1969). More recently, our group has shown that homing pigeons can indeed detect infrasounds (Yodlowski et al. 1977), and that this detection extends as low as 0.05 Hz (Kreithen and Quine 1979). The pigeons' thresholds between 1 Hz and 10 Hz are 50 dB more sensitive than thresholds reported for human hearing (Yeowart and Evans 1974).

How birds use their capacity to detect infrasounds is still unknown, but we are currently investigating several possibilities. To use infrasounds for navigation, a bird needs to detect, identify, and locate the source of a distant sound. But locating the direction of a low frequency sound source is difficult due to the long wavelengths involved (tens to thousands of meters). It seems unlikely that there are any substantial binaural differences associated with such long wavelength sounds, yet all known sound localization mechanisms rely on interaural differences of phase, intensity, or time.

A possible alternative mechanism of sound localization might be that a flying bird could use the Doppler shifts in frequency induced by its own flight velocity. Doppler shifts of frequency occur whenever there is relative motion between an observer and a sound source. The magnitude of the frequency shifts (percentage shift) does not depend on wavelength, but rather on the relative velocities of the observer and the sound source. To use Doppler shifts, a flying bird would need the ability to detect small changes in sound frequency.

We report here that homing pigeons, *Columba livia*, are sensitive to small shifts in infrasonic frequencies and that their performance in the laboratory is sufficient for the detection and use of Doppler shifts in the natural world.

Methods

10 Cornell homing pigeons, ages 1 to 9 years, with extensive flight experience were tested in a sealed, 40 l pressure chamber. This was the same chamber used in our previous report of the pigeons' audiogram (Kreithen and Quine 1979). Further details about the construction of the chamber may be found in Kreithen and Keeton (1974a) and Quine (1979). Behavioral responses to infrasonic frequency shifts were determined by our standard cardiac conditioning methods. These methods were used in previous tests to measure the pigeons' sensitivity to infrasounds, barometric pressure changes, polarized light, and UV light (Kreithen and Quine 1979; Kreithen and Keeton 1974a, b; Kreithen and Eisner 1978). Infrasonic frequency shifts were presented at random times (10/h). A mild shock was delivered at the end of each frequency shift trial (1 mA 60 Hz constant current sinewave for 0.5 s). The birds responded to the frequency shifts, when detected, by increasing their heart rates before the shock was delivered. A response was counted if the heart rate increased by more than 12 beats/min above the

* Present address: Department of Physiology, 701 Gerard Hall, Halifax Infirmary, Dalhousie University, Halifax, Nova Scotia B3L 2H6, Canada

** Present address: Department of Biology, University of Pittsburgh, and Section of Birds, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania 15260, USA

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maximum heart rate in the 10 s pre-stimulus interval. In these tests, the cardiac responses were proportional to the stimulus magnitude: larger frequency shifts usually produced greater increases in heart rate than did smaller, harder to detect, frequency shifts. Although 12 beats/min was the minimum response required, typical responses ranged from 30–80 beats/min above the usual resting rate of approximately 160 beats/min. Heart rate was recorded from surface electrodes on a beat to beat basis by a tachograph of our own design.

Infrasounds were generated, in the testing chamber, by a system designed to simulate the features of natural Doppler shifts. A continuous reference tone 30 dB above threshold was played in the testing chamber. At random intervals (10/h) the tone was smoothly shifted to a higher frequency, with appropriate wave shaping to avoid switching transients (Quine 1979). The time constant for the frequency shift was approximately 800 ms. This is approximately the time required for a pigeon to turn 90° in flight. The new frequency was presented for 10 s, followed by the mild shock and a return of the tone to the reference frequency.

Infrasonic tones were generated by our standard system of loudspeakers, modified to act as a bellows pump between two sealed air volumes. Because the loudspeakers were used in a sealed pressure system and further because the cones of the speakers were coated with silicone sealing grease, the speakers were not limited to their free air response, but instead could produce low distortion sinewaves as low as 0.01 Hz. The loudspeakers were powered by a 60 W D.C. amplifier driven by a sinewave generator with external control of amplitude and frequency (Exact model 119M).

Mechanical low-pass filters (6 dB attenuation per octave above 2 Hz) were used on the pressure and vacuum lines that provided 5 l/min of fresh air for respiration while excluding ambient infrasounds. A similar low-pass filter was used between the dual loudspeaker system and the testing chamber to further insure against high frequency artifacts. Sound pressure levels were monitored within the chamber either by a B & K condenser microphone, or by a calibrated low frequency pressure transducer made by linking a barometer bellows to a strain gauge displacement transducer. As in all previous pressure and infrasound experiments, white noise was added to the chamber. The noise spectrum was approximately 60 dB SPL in octave bands from 250 Hz to 2,000 Hz (see exact spectrum in Kreithen and Keeton 1974a).

To check for artifacts, 10% of the trials were randomly selected as blank trials in which everything was turned on normally – except for the frequency shift itself. This also indicated the background level of spontaneous cardiac responses (always less than 20%) against which threshold response levels could be compared.

Results

Thresholds for frequency shifts were obtained for 1, 2, 5, 10, and 20 Hz. The results of these tests are shown in Fig. 1. The thresholds ranged from 1% at 20 Hz to 7% at 1 Hz. In these tests, the pigeons could detect the differences between 1.00 Hz and 1.07 Hz, and between 2.00 Hz and 2.08 Hz even though none of those signals were audible to us.

Thresholds for frequency shifts were determined by reducing and (then) increasing the magnitudes of the frequency shifts while observing the corresponding variations in the percentage of positive cardiac responses. Thresholds for frequency shifts were arbitrarily defined as the shift values estimated to produce a 50% probability of a cardiac response. Fig. 2 shows

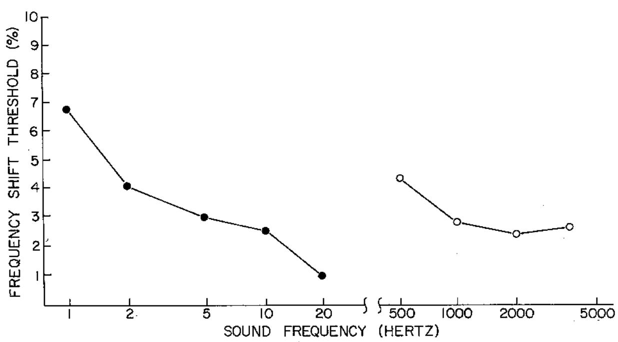

Fig. 1. Thresholds for frequency shifts. Low frequency data (solid circles) are from this study. Each point is the average of thresholds from 5 birds. Audible frequency data (open circles) are from Delius and Tarpy (1974) and Price et al. (1967)

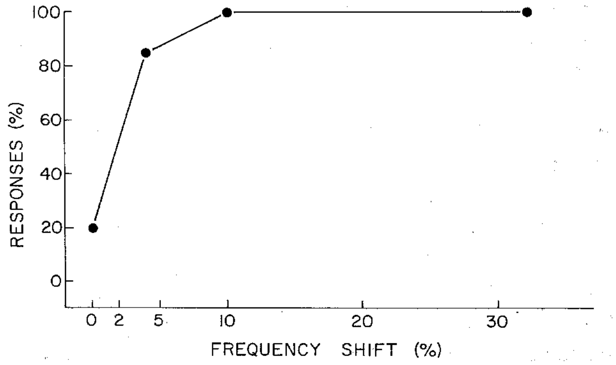

Fig. 2. Sensitivity of pigeon No. 9625 to frequency shifts about a 10 Hz center frequency. The 50% threshold value is estimated from these data to be 3%. Similar sensitivity curves formed the basis of the thresholds reported in Fig. 1

the results of a threshold test performed at 10 Hz on pigeon No. 9625.

Additional experiments were performed to clarify the mechanism used to detect frequency shifts. Shifts may be detected directly, or indirectly by using subjective loudness cues. Loudness cues can occur when the shift is to a new frequency with a substantially different hearing threshold. Similar changes in subjective brightness occur when testing color vision. In both vision and hearing, the appropriate testing procedure is to try to mask a frequency (or color) shift with a variety of concurrent amplitude, or brightness, changes. In subjects relying on amplitude cues there will be an intensity match, where frequency discrimination is no longer possible. If, however, the subjects are able to discriminate among frequency changes regardless of amplitude differences, then this constitutes evidence for true frequency discrimination. Such was the case in our tests.

We presented a standard frequency shift from 1.7 Hz to 2.0 Hz accompanied by a wide variety of concurrent amplitude shifts covering a 15 dB range. 3 pigeons were tested for a total of 1,470 trials. Fig-

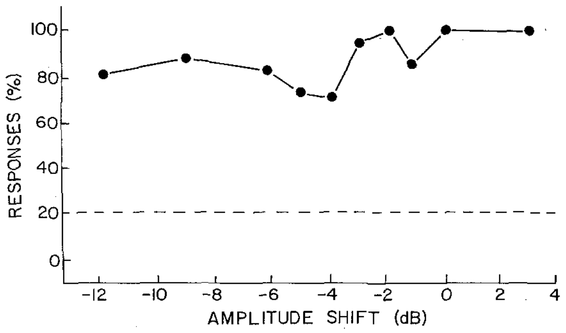

Fig. 3. Responses of pigeon No. 9625 to a frequency shift accompanied by a variety of concurrent amplitude shifts. In all trials, the frequency was shifted from 1.7 Hz to 2.0 Hz. The value of the amplitude shift is indicated on the x axis. Spontaneous response rates always fell below the dashed line. See text for further explanation

ure 3 shows the results of the testing of pigeon No. 9625. The bird was clearly able to detect the frequency shift regardless of amplitude shifts, real or subjective. The estimated intensity match should occur at approximately -3 dB, since the pigeon's threshold is 3 dB more sensitive at 2 Hz than at 1.7 Hz, and therefore we presented the stimuli in 1 dB steps in this critical range.[1]

All three birds tested responded to the frequency shifts regardless of amplitude variations. Thus it appears likely that pigeons can detect frequency shifts directly without the aid of amplitude cues. In nature, infrasonic Doppler shifts are always accompanied by subjective amplitude changes which might make detection easier.

Discussion

Homing pigeons often fly at a flight speed of 20 m/s. This can produce as much as 12% Doppler shifts, depending on changes of flight path. Since the results of our tests show that the pigeons' ability to detect frequency shifts between 1 Hz and 20 Hz is much less than 12% (i.e. from 1% at 20 Hz to 7% at 1 Hz), it therefore seems plausible that the detection and use of Doppler shifts is within the sensory capabilities of the birds.

Doppler shift localization can work at any frequency, but it would be especially useful at low frequencies where other mechanisms may fail.

Since atmospheric infrasounds can travel thousands of km from their sources and since the sounds carry information about geographic location, weather patterns, wind paths, and ocean waves, it has been tempting to speculate about the use of this information by migrating and homing birds. There are many things we don't know about what the birds actually use. There is, for example, the formidable task of recognizing true infrasonic signals imbedded in the complex array of wind noises (pseudosounds) and the sounds generated by the birds' own flight movements. But central to any signal processing mechanism is an ability to discriminate among different frequencies, and this study clearly indicates that pigeons have excellent frequency resolution.

We have learned much about the infrasound sensitivity abilities of the homing pigeon. In the laboratory, the pigeons respond to 0.05 Hz signals, and they detect signals designed to mimic natural Doppler shifts. We also have evidence that they can detect man-made infrasounds outdoors (Quine 1979).

We must emphasize that we do not yet know if birds actually use infrasonic cues for navigation. We do know that their ability to detect and to distinguish frequencies in the infrasonic range is remarkable; it may help them in some ways to obtain useful information about distant storms, winds, or landmarks. These possibilities, like infrasonic navigation, remain to be tested in the field.

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[1] Hienz et al. (1979) report that the pigeon's ability to detect amplitude changes is about 3 dB between 500 Hz and 4,000 Hz; our own preliminary tests at 2 Hz and 5 Hz confirm and extend this ability to low frequencies. Therefore, 1 dB steps should have been adequate to locate any subjective intensity matches