DIRECTIONALITY OF AVIAN VOCALIZATIONS: A LABORATORY STUDY[1]

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Abstract. Pure tones of 1, 2, 4, 8, and 10 kHz were broadcast from the body of a dead starling *Sturnus vulgaris,* and sound pressure levels were measured through 360° in three planes. At high frequencies (8 and 10 kHz) there were large troughs in sound pressure levels in the acoustic "shadow" of the bird's body. A physical model based on sound interference phenomena predicts similar patterns of sound pressure levels.

Key words: Acoustics; communication; directionality; laboratory methods; Sturnus vulgaris; *vocalization.*

INTRODUCTION

In a field study on directionality of bird vocalizations, Witkin (1977) showed that high frequency notes (ca. 7 kHz) of the Black-capped Chickadee (*Parus atricapillus*) have different sound pressure levels (SPLs) as measured in front of or behind the bird. Previous reports on directionality primarily involved the echolocation signals of bats (e.g., Schnitzler and Grinnell 1977). The mating calls of some anurans (Gerhardt 1975) and the drumming signals of Ruffed Grouse *Bonasa umbellus* (Archibald 1974) have also been shown to be directional.

Vocal directionality may have ecological significance because it could (1) reduce the likelihood of signal reception by an unwanted receiver, e.g., a predator; (2) maximize transmission distance of a signal by concentrating the energy within a given angle; (3) decrease reverberation (Richards and Wiley 1980); (4) affect the position and orientation of a signaler in a heterogeneous environment; or (5) give cues about the signaler's orientation to a receiver highly familiar with the generated song, i.e., a neighbor or mate.

Witkin's assessment of directionality was limited because he measured only two positions, both in the horizontal plane, and because his estimates of body orientation were accurate only to within ±30°. In this paper we present a model and a laboratory study of acoustic directionality aimed at providing a

more complete and accurate picture of the way sound radiation is affected by the screening effect of a bird's body.

A MODEL

In order to formalize the possible mechanisms underlying directionality of vocalizations, we shall use a theoretical model that is illustrated in Figure 1 (see Roberts et al. 1983). The bird's head or body is assumed to be spherical with radius *R*, opaque to sounds, and containing a sound generating mechanism. The general nature of the radiated sound field may be inferred by noting that as the frequency increases, wavelength becomes smaller; hence the waves radiated from the sound source via different paths to any point in the sound field will have increasingly large differences in path length relative to the wavelength of the sound. Therefore, at higher frequencies interference effects will substantially alter the sound intensity pattern. Such effects will be most noticeable when the points of observation lie behind the sphere (the bird's body). Sound pressure level, $p(r, \theta)$, can be calculated at any point in the space surrounding the sphere by assuming axial symmetry using the following equation, modified from Skudrzyk (1972:400–407) for a plane circular vibrating piston set in the sphere:

$$p(r, \theta) = -\frac{\rho c V e^{-jkr}}{kr} \sum_{m=1}^{m=N} a_m P_m(\cos \theta) e^{(jm\Pi/2)}$$

(1)

Where
$p(r, \theta)$ is the sound pressure at the point defined by
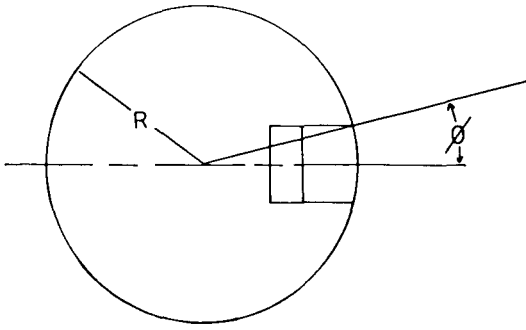
FIGURE 1. Model for sound propagation from a piston set in a sphere. Radius (R) = 1.5 cm, angle θ = 26°.

	Units
r, θ for $kr \gg 1$,	Pa
ρc is the characteristic acoustical impedance of the surrounding medium,	Kg m^{-2} s^{-1}
V is the velocity amplitude of the piston,	m s^{-1}
a_m is the projected surface area of the piston, in the direction θ,	m^2
$P_m(\cos \theta)$ is the Legendre polynomial of order m,	
k is the wave number of the propagating acoustic wave,	m^{-1}
r is the distance from the source to the point of observation,	m
j is $\sqrt{-1}$.	

The predicted SPLs (in the horizontal plane) obtained using equation (1) are shown in Figure 2. In this plane, the radius of the sphere was assumed to be equal to that of the bird's head (1.5 cm). The model is less accurate at predicting SPLs in either of the other two planes because it departs substantially from the actual geometry of the bird.

METHODS

The experiment was carried out in a 240 m³ anechoic chamber with a background noise level less than 20 dB re 2 × 10^{-5} Pa. The carcass of a starling Sturnus vulgaris was mounted on top of a stainless steel loudspeaker tube (4.75-mm bore, 500 mm long) and held by a thin wire holder in a posture designed to imitate that of a singing bird.

A 100-W loudspeaker was attached to the tube and both were encased in plasticine with the speaker immersed in a bucket of sand so that at all frequencies of interest the sound emitted from the open end of the tube was at least 20 dB above any noise that escaped from other parts of the apparatus. We shall treat the opening of the tube as a point source of sound
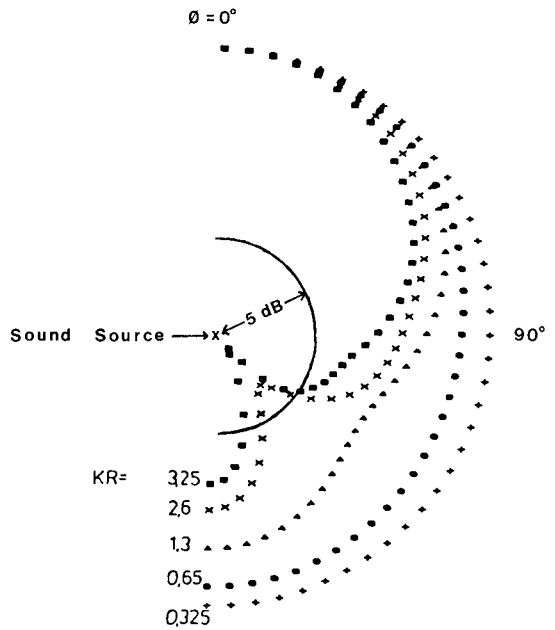

FIGURE 2. Predicted directionality of sounds propagated by the model illustrated in Figure 1. KR is the ratio of sphere circumference to wavelength of the radiated sound. A large sphere radiating a high-pitched sound would have a high KR value.

since at all frequencies of interest the tube diameter was less than one sixth of a wavelength. The system was mounted on a Bruel and Kjaer Type 3922 turntable so that the set-up could be rotated through 360°.

Sound pressure levels in dB re 2 × 10^{-5} Pa were measured using a Bruel and Kjaer Type 2120 frequency analyzer. Pure tones of 1, 2, 4, 8, and 10 kHz with intensities adjusted to give a SPL of 65 dB re 2 × 10^{-5} Pa at 1 m directly in front of the open beak were generated by a Bruel and Kjaer Type 1024 sine-random oscillator and power amplifier (Quad 50E). The microphone was positioned perpendicular to the steel signal tube, at the level of the opening and 1 m from the center of rotation (the opening of the tube). The beak was kept open with a tip separation of 24 mm except when specified differently in the text.

By suitably positioning the bird's body, measurements were obtained in each of three planes through a rotation of 360° (Fig. 3). All planes passed through the base of the beak. The horizontal plane passed between the upper head and lower mandible, leaving the top of the head above and the rest of the bird's body below. The sagittal plane was vertical, dividing the body into its left and right sides. The transverse plane was also vertical, passing through the ears, leaving part of the head with the whole beak in front of the plane and the rest of the head and body behind.
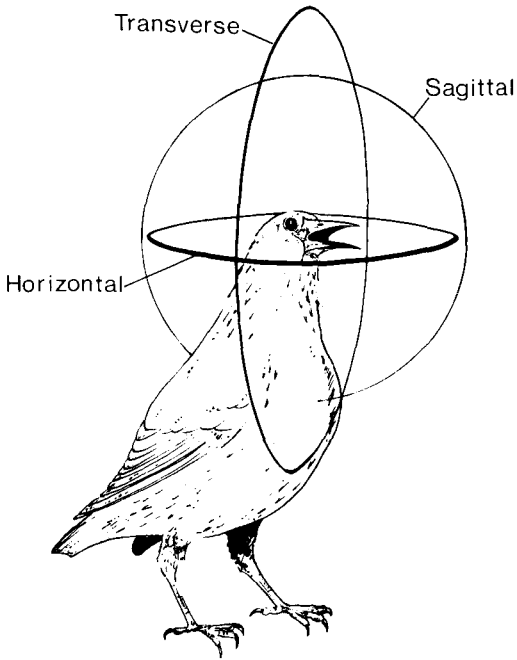
FIGURE 3. Horizontal, sagittal, and transverse planes around a starling.

For directivity measurements in the horizontal and transverse planes, the bird was mounted vertically upon the tube which entered the body at the base of the neck and ended at the back of the mouth. For directivity measurements in the sagittal plane the bird was mounted so that the vertical tube entered through the side of the neck and ended at the back of the mouth.

Some measurements were also taken after altering the width of the beak opening, plug-ging one nostril, or amputating the beak at its base.

RESULTS

DIRECTIONALITY

Measurements of SPL in the horizontal, sagittal, and transverse planes are shown in Figure 4 and a summary of data is shown in Table 1.

In the horizontal plane (Fig. 4A), SPL directly behind the bird was always lower than directly in front. The magnitude of this difference was more pronounced at higher frequencies; it ranged from a loss of 2 dB at 1 kHz to 17 dB at 10 kHz. This relationship between directionality and frequency coincides with Witkin's (1977) field observations. However, the maximum difference in SPL observed was not always along the main axis. At frequencies above 4 kHz, there were pronounced troughs in intensity bilaterally some angle away from the front. At 8 kHz, for example, the SPL recorded 130° to either side of the beak was at least 13 dB lower than the signal in front while directly behind the animal, it was only 6 dB lower.

There is good qualitative agreement in the horizontal plane between the predicted directionality and that found experimentally. We take this to imply that the physical assumptions embodied in equation (1) are appropriate for explaining the mechanisms underlying the observed directivity patterns.

For the sagittal plane (Fig. 4B), the directionality was also strongly dependent on frequency. At 1 kHz the maximum SPL was directly in front of the beak and fell by 2 dB in a broad area behind the bird. At 8 and 10 kHz
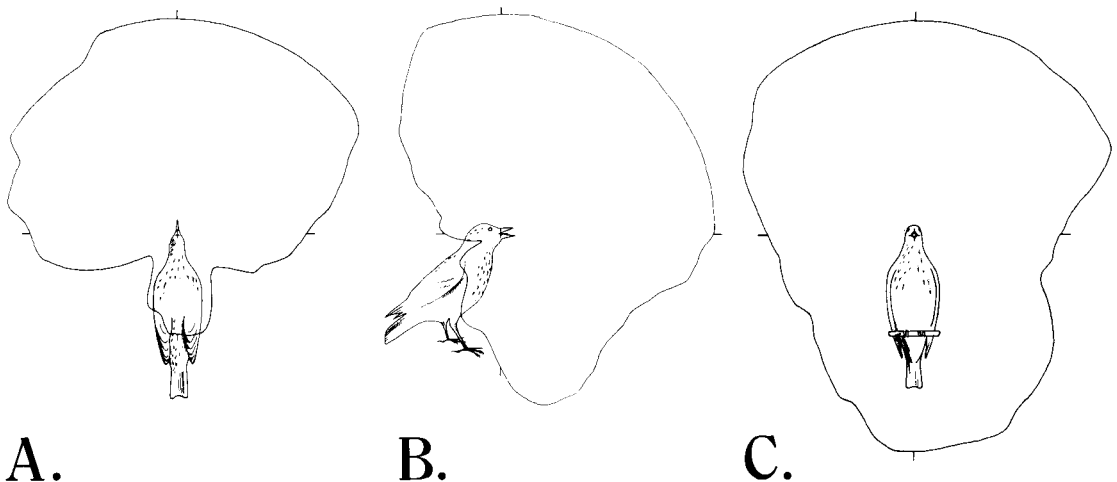

A.   **B.**   **C.**

FIGURE 4. Vocal directionality patterns in the horizontal (A), sagittal (B), and transverse (C) planes. The distance from the bird's mouth to the 0° point represents a normalized reference value with all other values expressed as a linear proportion. Thus the pattern portrays the relative distance at which an 8 kHz vocalization could be heard (at any given SPL) in different directions from the bird.

TABLE 1. The sound pressure levels (SPL) of five frequencies were measured in three planes and their strength expressed as the relative distance at which their SPL equals the SPL directly in front of the beak (angle = 0°). In Column 2, the angles at which the minima occurred are listed, and the relative distance at which the minima occurred are in Column 3. For example, a 1-kHz signal measured in the horizontal plane is weakest directly behind the bird's head (angle = 180°) and has the same SPL at 79 cm as the signal would have at 100 cm in front of the bird. In Column 4 the differences between the SPL at the minima and the SPL in front of the beak are given in dB.

Frequency (kHz) and planes	Angles of minima	Relative distances	SPL (dB)
Horizontal			
1	180	0.79	2
2	180	0.79	2
4	240/130	0.47/0.45	6.5/7
8	230/130	0.15/0.24	16.5/12.5
10	207/150	0.10/0.14	20/17
Sagittal			
1	180	0.79	2
2	95	0.67	3.5
4	175/115	0.45/0.50	7/6
8	155	0.05	26.5
10	147.5	0.04	27.5
Transverse			
1	180	0.89	1
2	105	0.89	1
4	65/280	0.75/0.84	2.5/1.5
8	50/285	0.63/0.63	4/4
10	52.5/300	0.32/0.47	10/6.5

there was a very distinct trough in SPL, a reduction of about 27 dB, around 150°, in the acoustic shadow of the bird's body.

The pattern of directionality was much less pronounced in the transverse plane (Fig. 4C) than in either of the others. There was only a 1 dB drop in SPL at 1 kHz with the maximum SPL directly above the head and the minimum directly below. At 8 kHz and 10 kHz there was also a difference of 1 dB between readings above and below the head. However, at these frequencies there were two troughs in intensity bilaterally below the top of the head. At 10 kHz reductions of 10 dB and 6.5 dB were recorded at 50° and 300° respectively.

EFFECT OF THE BEAK AND NOSTRIL RADIATION

Repetition with the beak tip open at 8 mm, open at 2.5 mm, and closed showed the same directivity patterns with only minor variations. Not surprisingly the emitted sound power decreased as the beak closed but the drop in SPL was small. It was observed that the nostrils were good emitters of high frequency (8 kHz and 10 kHz) sound. This was confirmed by blocking the right nostril and measuring the resulting directivity pattern. There was negli-

gible change in sound output power or directivity pattern after the beak had been amputated near its base. This negative result supports the view that the so-called megaphone effect is of little significance (Witkin 1977).

DISCUSSION

A number of changes take place in the structure of bird song as the sound travels away from the source. Firstly, the power spectra of vocalizations shift to lower frequencies due to the greater attenuation of high frequency components. Also, degradation of the signal's structure is to be expected from reflections, reverberations, atmospheric turbulence, etc. It has been suggested (Wiley and Richards 1982) that receivers might be able to use these changes to determine distance to the signaler. Morton (1982) felt that determining distance to the receiver would require familiarity with the undegraded signal. Further, Morton's (1982) "ranging hypothesis" indicates that signalers try to disturb their receivers by disguising their distance from them, and/or signalers attempt to threaten receivers by informing them of their proximity. (For empirical work, see Richards 1981 and McGregor et al. 1983.)

Our results add a further dimension to these ideas. We have shown that a complex but predictable set of changes can be expected for acoustic signals radiating in different directions from the signaler. Because directionality of high and low frequency components differ, at any given distance from the signaler the relative intensity of the different frequency components will depend upon signaler orientation. This implies that to use the shift in power spectrum to estimate signal-receiver distance, the receiver must take into account the orientation of the signaler. Conversely, the directivity pattern implies that if the receiver knows the distance from the signaler, as may be the case when a neighboring bird regularly sings from the same perch, it can infer the orientation of the signaler from the difference between the received and undegraded signals.

Power spectrum shifts due to orientation and due to distance may be different and recognizable, and the distance and orientation could each be assessed without knowing the other, but this would probably be a very complicated comparison.

Acoustic signals differ in their suitability to give cues about orientation of the sender, because cues about orientation depend on relative attenuation of different frequency components. Thus signals containing a broad range of frequencies will carry more orientational clues than narrow band signals. In the latter, changes of orientation will produce changes

only in intensity and thus could be indistinguishable from signals emitted at different intensity levels. It follows that broad-band signals should be favored when the signaler might benefit from having its orientation known, while narrow-band signals would be advantageous when revealing one's orientation might be harmful. For example, if a bird in a flock observed a predator it might be able to provide cues to other flock members as to the predator's direction by facing the predator and delivering a broad-band signal. Directional alarm calls might also be favored when concerted action against the predator is required, as in mobbing. Alternatively, the bird could use a narrow-band signal during a predator attack without giving cues as to its location. This may be favored in a situation such as that discussed by Charnov and Krebs (1975), who described how a signaler might manipulate the behavior of other flock members to minimize its chance of being captured.

Marler (1955) observed that alarm calls used while mobbing a sitting raptor were normally short, broad-banded *clicks*, while alarm calls associated with attacking hawks were narrow-band, high pitch whistles with ill-defined onset and ending. Discussing the reception of alarm calls by the predators themselves, Marler stated that high-frequency signals with vague contours are more difficult to locate by binaural phase comparisons. Our hypothesis about orientational clues refer to reception by flock members rather than by potential predators and complements Marler's hypothesis in understanding the difference in band width between mobbing and escaping calls.

Directionality may also be important as a design feature in territorial songs. Bremond (cited in Armstrong 1973) and Krebs et al. (1981) have suggested that it may be important for a resident male to threaten intruders and neighbors by responding to them directly, and that birds do this by matching song types. By using a song with orientational clues, a resident might threaten a receiver more effectively by singing in its direction, for example, to acknowledge detection of a silent intruder.

The biological implications of directivity patterns as discussed here are admittedly very speculative. Until further field work is done to test the directionality of real animal sounds and the association between acoustic structure and function of vocalizations, our suggestions will forcedly remain in need of further testing.

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