Proceedings of The Institute of Acoustics

DIRECTIONALITY OF AVIAN VOCALIZATIONS : A LABORATORY STUDY

M Hunter (JR)., University of Maine at Orono, USA
A Kacelnik, Oxford University
J Roberts, M Vuillermoz, Polytechnic of the South Bank,
Borough Road, London

Reporting a field study on directionality of bird vocalizations Witkin (1977) showed that high frequency notes (ca. 7 kHz) of the blackcapped chickadee (*Parus atricapillus*) have different sound pressure levels (SPL) as measured in front or behind the bird. Previous reports on sound beaming 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 ruffled grouse (*Bonasa umbellus*) (Archibald 1974) have also been shown to be directional.

Beaming vocalizations may have ecological significance because it could (1) reduce the likelihood of signal reception by an unwanted receiver, e.g. a predator; (2) maximize a signal's transmission distance by concentrating the energy within a given solid angle; (3) affect the position and orientation of a signaller in a heterogeneous environment; or (4) convey information about the signaller's orientation to a receiver highly familiar with the generated song i.e., a neighbour 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 only accurate to within ±30°. In this paper we present 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.

METHODS

The experiment was done in an anechoic chamber of volume 240 m^3 and background noise level less than 20dB. 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 in place by a thin wire holder in a stance designed to imitate the observed posture of the calling bird.

A 100W loudspeaker was cavity coupled to the tube and both 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 20dB above breakout noise. We shall treat the opening of the tube as a point source of sound 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 analyser with a Bruel and Kjaer type 4220 pistonphone. 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 centre 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°. All planes passed through the base of the beak.

The *horizontal plane* passed between the upper and lower mandibule, leaving the top of the head above and the lower part as well as the rest of the bird's body below. The *saggital plane* was vertical, dividing the body in its left and right sides. The *transverse* plane was also vertical, passing through the ears and thus leaving part of the head with the whole beak in front of the plane and the rest of the head and body behind.

For directivity measurements in the horizontal plane at the level of the head, 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 saggital 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, plugging one nostril, or amputating the beak at its base.

RESULTS

Directionality

Measurements of SPL in the horizontal, saggital and transverse planes are shown in Fig. 1 a, b and c and a summary of data is shown in Table 1.

In the horizontal plane, (Fig. 1a) SPL directly behind the bird was always lower than directly in front. The magnitude of this difference was more pronounced the higher the frequency, ranging from a loss of 2dB at 1kH 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 higher frequencies (above 4 kHz) there were pronounced troughs in intensity bilaterally some angle away from the front. At 8kHz for example, compared to the signal measured to the front, the SPL recorded 130° to either side of the beak was at least 13dB down and that directly behind the animal, some 6dB down.

For the saggital plane (Fig. 1b) the directionality was also strongly dependent on frequency. At 1 kHz the maximum SPL was directly in front of the beak and fell by 2dB in a broad area behind the bird. At 8 and 10 kHz there was a very distinct trough in SPL, a reduction of about 27dB, around 150°, in the acoustic shadow of the bird's body.

The pattern of directionality is much less pronounced in the transverse plane (Fig. 1c) than in either of the others. There was only 1dB drop in SPL at 1 kHz. Maximum SPL was directly above the top of the head and the minimum directly below. At 8 kHz and 10 kHz there was also a difference of 1dB 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 10dB and 6.5dB were recorded at 50° and 300° respectively.

Effect of the Beak and Nostril Radiation

Repetition with the beak tip open at 8 mm, 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 and the measured SPL fell, (see Fig. 2), but the drop in SPL was small. It was observed that the nostrils were good emitters of high frequency sound. This was confirmed by blocking one nostril (the right) and measuring the resulting directivity pattern, Fig. 3.

Fig. 4 shows that there was negligible 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.

PHYSICAL INTERPRETATION

In order to formalise the possible mechanisms underlying the directional effects described above, we shall use a theoretical model that is illustrated in Fig. 5. The bird's head or body are assumed to be spherical with radius R, opaque to sounds, 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 and hence the waves radiated from the sound to any point in the sound field will have increasing path difference relative to the wavelength of the sound. Therefore at higher frequencies, interference phenomena will alter noticeably the sound intensity pattern. Such effects will be most noticeable when the points of observation lie behind the sphere (the bird's body). SPL can be calculated at any point in the space surrounding the sphere by assuming axial symmetry using the following equation, modified from Skudrzyk for a plane circular piston set in the sphere:-

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

Where $p(r,\theta)$ is the sound pressure at the point defined by

r, θ for $kr >> 1$, Pa

ρc is the characteristic acoustical impedance of the surrounding medium, $\mathrm{kg\ m^{-2}\ s^{-1}}$

V is the velocity amplitude of the piston $\mathrm{ms^{-1}}$

a_m is the projected surface area of the piston, in the direction θ, $\mathrm{m^2}$

$P_m (\cos \theta)$ is the Legendre polynomial of order m

k is the wave number of the propagating acoustic wave $\mathrm{m^{-1}}$

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 6.

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. 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.

DISCUSSION

A number of changes take place in the patterns of bird song as the sound travels away from the source. In the first place, the power spectrum of all vocalizations shifts to the lower frequencies due to the greater attenuation of high frequency components. Also, degradation of the temporal structure of the signals is to be expected from reflections, atmospheric turbulence, etc. It has been suggested (Morton, 1975, Richards & Wiley, 1980) that receivers might be able to make use of some of these changes if they were familiar with the original, undegraded signals. From comparison of the received with the undegraded signal receivers might infer how far away the signaller is.

Our results add further complexity 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 signaller. Because directionality of high and low frequency components differ at any given distance from the signaller the relative intensity of the different frequency components will depend upon signaller 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 signal. Conversely, the directivity pattern implies that if the receiver knows the distance from the signaller as may be the case when a neighbouring bird regularly sings from the same post, it can infer the orientation of the signaller from the difference between the received and the undegraded signals.

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

Acoustic signals differ in their suitability to convey information about orientation because clues about orientation depend on relative attenuation of different frequency components. Thus signals containing a broad range in frequencies will carry more orientational clues than those consisting of a narrow band. In the latter, changes of orientation will only produce changes in intensity and thus would be indistinguishable from signals emitted at different intensity levels. It follows that broad band signals should be favoured when the signaller might benefit from giving information about its orientation, 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 inform other flock members of the predator's direction by facing the predator and delivering a broad band signal. Alternatively, the bird could use a narrow band signal to alarm other flock members without giving clues as to the predator's location. Directional alarm calls (broad banded) might be favoured when concerted action against the predator is required (as in mobbing), while the opposite is probably favoured when the alarm is associated with seeking refuge from an attacking predator. In the latter case the signaller might benefit by the possession of information unavailable to other flock members (as in the discussion of "manipulation" by (Charnov and Krebs, 1975). 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 showed 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 may complement 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 (1973) and Krebs (1981) have suggested that it may be important for a resident male to inform intruders and neighbours that it is responding directly to them, and that birds do this by matching song types. By using a song with orientational clues a resident might inform a receiver that it is 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.

REFERENCES

ARCHIBALD, H.L.	AUK 91 (1974): 517-521
BREMOND, J.C.	Cited in A study of Birdsong, ed. Armstrong A. New York: Dover, 1973
CHERNOV, E.L. and KREBS, J.R.	Am. Naturalist 109 (1975): 107-112
GERHARDT, N.C.	J. Comp. Physiol. 102 (1975): 1-12
KREBS, J.R., ASHCROFT, R. & Van ORSDOL, K.	Animal Behaviour (29) (1981): 918-923
MARLER, P.	Nature 176 (1955): 6-8
MORTON, E.S.	Am. Naturalist, 108 (1975): 17-34
RICHARDS, D.C. & WILEY, R.H.	Am. Naturalist, 115 (1980): 381-399
SCHNITZLER H.V. & GRINNELL, A.D.	J. Comp. Physiol. 116 (1977): 51-61

SKUDRZYK, E. Foundations of Acoustics, New York: Springer-Verlag, 1971: Section 26

WITKIN, S.R. The Condor, 79 (1977): 490-493

TABLE 1

Frequency kHz	SPL, dB Max- Min	Angle of Minimum (^{o})
HORIZONTAL		
1	2	180
2	2	180
4	6.5/7	240/130
8	16.5/12.5	230/130
10	20/17	207/150
SAGGITAL		
1	2	180
2	3.5	95
4	7/6	175/115
8	26.5	155
10	27.5	147½
TRANSVERSE		
1	1	180
2	1	105
4	2⅓/1⅓	65/280
8	4/4	50/285
10	10/6½	52½/300

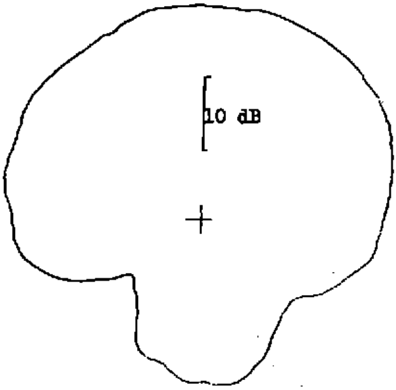


FIG. 1(a) HORIZONTAL (8kHz)

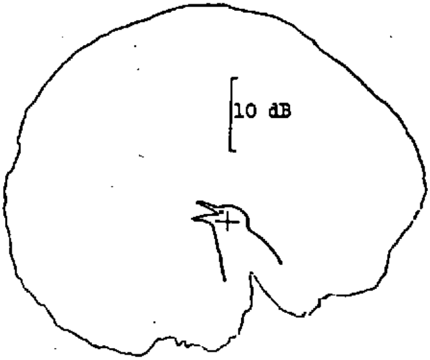


FIG. 1(b) SAGGITAL (8kHz)

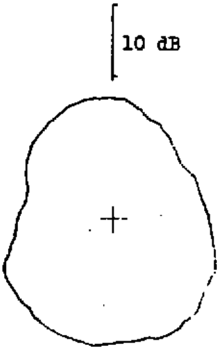


FIG. 1(c) TRANSVERSE (8kHz)

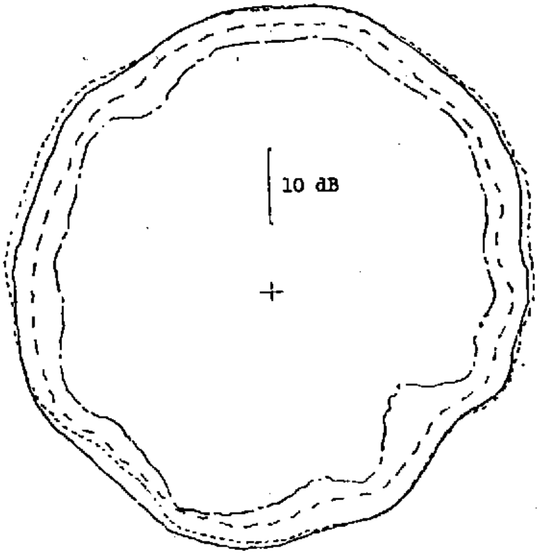
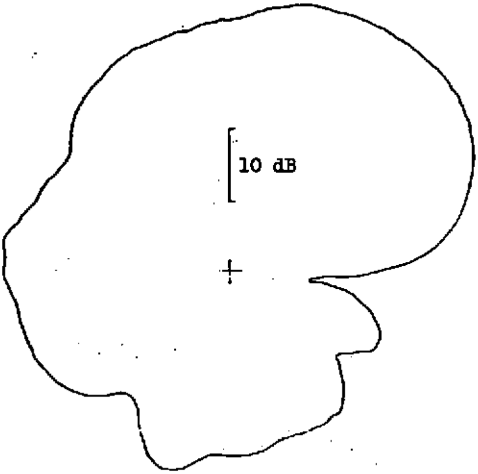


FIG. 2 BEAK OPENING

HORIZONTAL (4kHz)



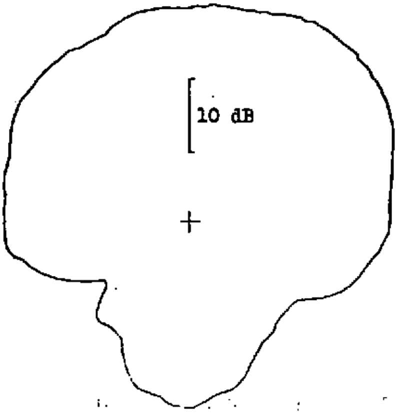


FIG. 4 BEAK AMPUTATED HORIZONTAL (8kHz)

FIG. 3 ONE NOSTRIL BLOCKED - BEAK CLOSED HORIZONTAL (8kHz)

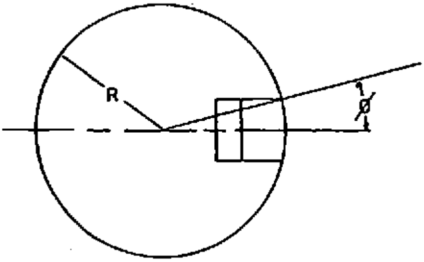


FIG. 5 PISTON SET IN RIGID SPHERE

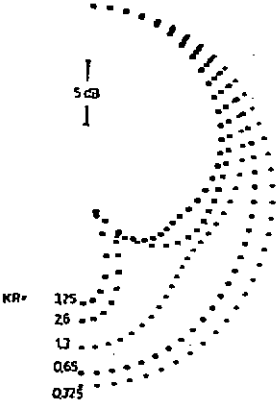


FIG. 6 PREDICTED DIRECTIVITY WITH kR ($\emptyset = 26^{\circ}$) (AFTER MORENO)