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DIRECTIONAL HEARING IN THE JAPANESE QUAIL (*COTURNIX COTURNIX JAPONICA*)

II. COCHLEAR PHYSIOLOGY

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SUMMARY

The directional sensitivity of cochlear microphonics (CM) was studied in the quail by rotating a free-field sound source (pure tones, 160–10 kHz) through 360° in the horizontal plane, under anechoic conditions. Sound diffraction by the head was monitored simultaneously by a microphone at the entrance to the ipsilateral (recorded) ear canal. Pressure-field fluctuations measured by the microphone were non-directional ($\leqslant$ 4 dB) up to 4 kHz; the maximum head shadow was 8 dB at 6·3 kHz. In comparison, the CM sensitivity underwent directional fluctuations ranging up to 25 dB for certain low, mid and high frequency bandwidths. There was noticeable variation between quail for frequencies producing maximum directional effects, although consistently poor directionality was seen near 820 Hz and to a lesser extent near 3·5 kHz. Well-defined CM directivity patterns reflected the presence of nulls (insensitive regions) at critical positions around the head and the number of nulls increased with frequency. Five major types of directivity patterns were defined using polar co-ordinates: cardioid, super-cardioid, figure-of-eight, tripartite and multilobed. Such patterns were largely unrelated to head shadow effects. Blocking the ear canal *contralateral* to the recorded ear was shown to effectively abolish CM directionality, largely by eliminating regions of insensitivity to sound.

It is inferred that the quail ear functions as an asymmetrical pressure gradient receiver, the pressure gradient function being mediated by the inter-aural cavity. It is proposed that the central auditory system codes directional information by a ***null detecting method*** and computes an unambiguous (i.e. intensity independent) directional cue. This spatial cue is achieved by the difference between the directional sensitivities of the two ears, defined as the *Directional Index* (DI). The spatial distribution of DI values (difference pattern) demonstrated ranges and peaks which closely reflected the extent and position of nulls determined from monaural directivity functions. Large directional cues (up to 25 dB) extended throughout most of the audible spectrum of the quail and the sharpness of difference patterns increased with

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frequency. Primary 'best' directions, estimated from peaks in difference patterns, tended to move towards the front of the head at higher frequencies; rearward secondary peaks also occurred. From the properties of directional cues it is suggested that the ability of birds to localize sound need not necessarily depend on frequency; however, spatial acuity may be both frequency and direction dependent, and include the possibility of front-to-rear errors. The directional properties of bird vocalizations may need to be reassessed on the basis of the proposed mechanism for directional hearing.

INTRODUCTION

Mechanisms for directional hearing based on interaural time and intensity have been thought to operate in all vertebrates but are based almost exclusively on data collected in mammals (Erulkar, 1972). It is believed that directional cues can be derived from a consideration of ear separation (time and phase differences) and the shadow effect of the head (interaural attenuation). Serious problems arise when these concepts are applied to non-mammalian vertebrates whose acoustic communication systems use airborne sound pressures whose wavelengths exceed the separation of the two ears. The problems associated with understanding the mechanisms of directional hearing in birds for example, were recognized by Schwartzkopff (1950, 1952, 1962), who provided behavioural evidence indicating the inability of small song birds to use time cues during sound localization. A similar conclusion was reached by Konishi (1973*a*, *b*) when studying the extremely accurate sound locating abilities of the barn owl. Studies such as these have supported the idea that birds may rely solely on binaural intensity cues during sound localization.

For practically all birds, the separation between the tympanic membranes never exceeds the wavelength of even the highest audible frequencies. In fact, at the most sensitive frequencies, interaural separation is usually a small fraction of the wavelength. Under these circumstances a considerable part of the acoustic spectrum available to most avian species may yield little interaural shadow or phase delay.

The existence of well-developed air spaces directly connecting the middle ears in birds has long been recognized (Wada, 1923; Stellbogen, 1930; Schwartzkopff, 1963; Payne, 1971), but the functional significance of this connexion has remained obscure (Schwartzkopff, 1963; Payne, 1971). It is now clear that this interaural cavity plays a critical role in the directional hearing of birds by establishing the necessary biophysical conditions for a pressure gradient system (Hill *et al.* 1980). In the present study the directional sensitivity of the cochlea in the quail was measured by recording the cochlea microphonic (CM). The results provide direct physiological evidence for the operation of a pressure gradient system.

METHODS

Data were collected from nine Japanese Quail (*Coturnix coturnix japonica*) of both sexes, weighing 180–240 g. The quail were anaesthetized with Sagatal (50 mg/ml) by an initial intramuscular (pectoral) injection of 0·17 ml/100 mg body weight. Throughout the experiment a satisfactory level of anaesthesia was maintained by supplementary injections of Sagatal (0·08–0·15 ml) as required. A cannula was inserted into the trachea to permit artificial respiration and a unidirectional flow of air was established by allowing circulated air to escape from an incision in the abdominal air sac.

Orientation of the bird

The head was fixed in each vertical plane by two horizontally opposed ear bars, attached to a head holder. The ear bars fitted neatly into a cartilaginous recess near the entrance to each ear canal. Separation of the tips of the ear bars ranged between 13·1 and 14·3 mm. The orientation of the head was fixed in the horizontal plane by a short metal rod rigidly attached to the bone of the dorsal skull. The rod was attached to the head with an acrylic glue (Eastman 910) and the head was fixed in a natural position (bill tip to centre of ear canals = 25° from horizontal; taken from a photograph of a free-standing bird).

Implantation of electrodes

An opening in the bone was made in the infero-lateral quadrant formed by the intersection of two semicircular canals (Schwartkopff & Bremond, 1963). After the removal of some superficial trabeculae, the recessus tympani was visible, including an edge of the round window membrane. These two areas border a small channel in the bone through which the columella and footplate attachment to the oval window can be seen. A No. 24 gauge syringe needle was used to manually bore a small hole immediately behind the round window. A second hole was made further along the cochlea duct (or occasionally in the side of the closest ampullary crista). Two short pieces of Teflon-coated silver wire (diam. 200 μm) with ends bared to 1 mm were inserted into the perilymph through these holes. The position of the recording wires was fixed with dental cement by filling up the opening in the skull through which they were inserted.

After implantation of the electrodes, the ear bars were removed and the whole preparation, with rod attached to the skull, was transferred to an anechoic chamber. The bird was placed on a small elevated platform in the centre of the room. The head was secured by clamping the vertical section of the attached rod (which descended directly in front of the head) in the midline axis.

Acoustic stimuli and recording procedure

Acoustic stimuli consisted of continuous pure tones with frequencies between 160 and 12 kHz. These tones were broadcast from a baffled loudspeaker (Goodmans Twin Axiom 8). Details of the acoustic field did not differ from those given in Hill *et al.* 1980 (but see also this paper, Fig. 1). The sound source was then rotated horizontally about the preparation at a radius of 1·05 m from the quail head. The centre of rotation of the speaker was vertically above the intersection of the ear axis and midline. In each preparation a pointer on the end of a plumbline (suspended from the speaker boom pivot joint), was made to just touch a horizontal cotton line stretched between the centre of the speaker diaphragm and the boom counterweight. The 'centre of the head' was then positioned directly underneath the plumbline pointer.

After head positioning, the electrode wires protruding from the cement plug in the skull were connected to the differential input of a Neurolog voltage-following device, located at the side of the body. A small Faraday cage which was acoustically transparent and did not modify the sound field, was placed over the platform.

Cochlear potentials (CM) were fed from the voltage follower to the input of a Neurolog AC preamplifier (Model NL 103) and amplified × 1000 on a bandpass of 100–20 kHz (50 Hz notch filter in). The amplified signals were connected to the direct input of a measuring amplifier (Bruel and Kjaer 2107) via a ⅓-octave filter (Bruel and Kjaer 1612). During the experiment both the CM, and the output of a ¼ in. microphone (Bruel and Kjaer 4135) placed at the ear canal entrance, were displayed on an oscilloscope screen. Possible waveform distortions were periodically checked on unfiltered signals. Voltages of the CM and sound pressure level (SPL) of the microphone (dB re 0·00002 N/m^2) were both measured as the root-mean-square (RMS) value. The validity of the CM was tested by holding a thick book in front of the speaker when the CM was seen to decrease. Further, at the termination of the experiment the CM disappeared.

RESULTS

(A) *Monaural CM directivity patterns*

(1) *Definitions*

A single sound source was moved around the quail's head in the horizontal plane with 0° defined as ipsilateral to the recorded ear. Directly in front of the head was 90°. The response of a microphone placed at the ipsilateral ear canal (to measure diffraction effects) and the CM amplitude were both referenced to 0 dB at 90° for standardization. In polar response curves, decreasing amplitude (sensitivity) is represented *towards* the centre of rotation.

(2) *Effects of the head on the sound field*

The effects of the quail head on phase and intensity at the ear canal, in a uniform sound field, have already been described in Hill *et al.* (1980). In the present study, the directional effects of the bird's head on sound intensity arriving at the ipsilateral ear have been replicated so as to provide a direct and simultaneous comparison with the directional response of the CM. Fig. 1 (and cf. Fig. 4) shows the maximum directional effect of the microphone (average of seven) for the most effective angles of sound incidence from 200 Hz to 10 kHz. The free-field and head diffraction measurements are very similar. Clearly the presence of the quail's head in the sound field has very little effect. If the same criterion is applied to both head shadow and free field measurements, then head shadow is an insignificant parameter from 200 Hz to about 4 kHz ($\leqslant$ 4 dB). Above 4 kHz the maximum head shadow produced by diffraction can approach 6–8 dB, e.g. at 6·3 kHz. Three frequencies which show the greatest effect of the head on the sound intensity at the recorded ear are shown in Fig. 1 as polar curves for 5, 6·3, and 8 kHz. Only small losses in sound intensity occur for contralateral positions of the speaker, and the patterns are nearly symmetrical about the ear axis.

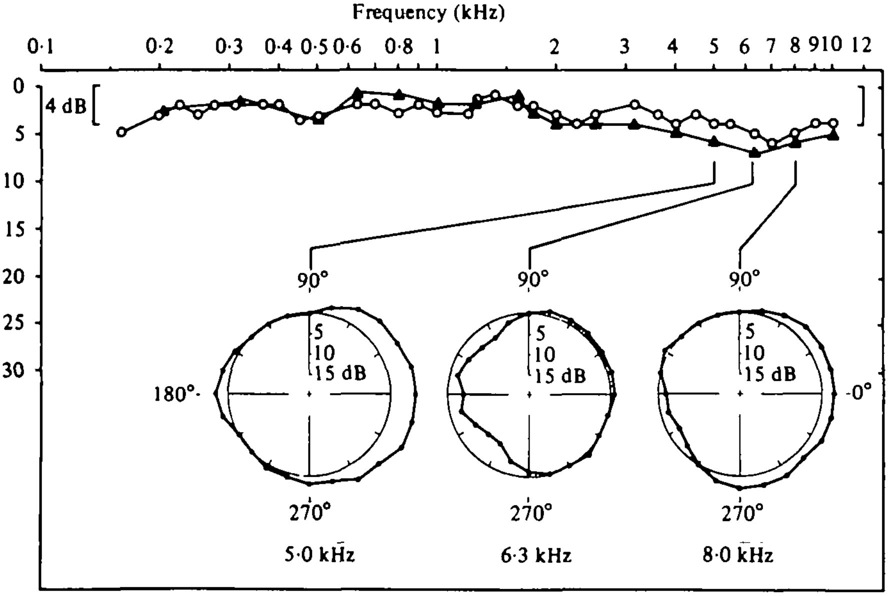

Fig. 1. Maximum change in SPL (dB) during 360° rotation of the sound source in the horizontal plane, as a function of frequency. Average of seven birds. ○, Free field measurements; ▲, Pressure field fluctuations measured by a microphone at the ear canal entrance. Examples of most pronounced head diffraction shown in polar form. For definitions of polar orientations see text. Curves are referenced to 0 dB at 90°, attenuation of SPL is towards centre of rotation. Threshold for significant directionality is 4 dB (indicated).

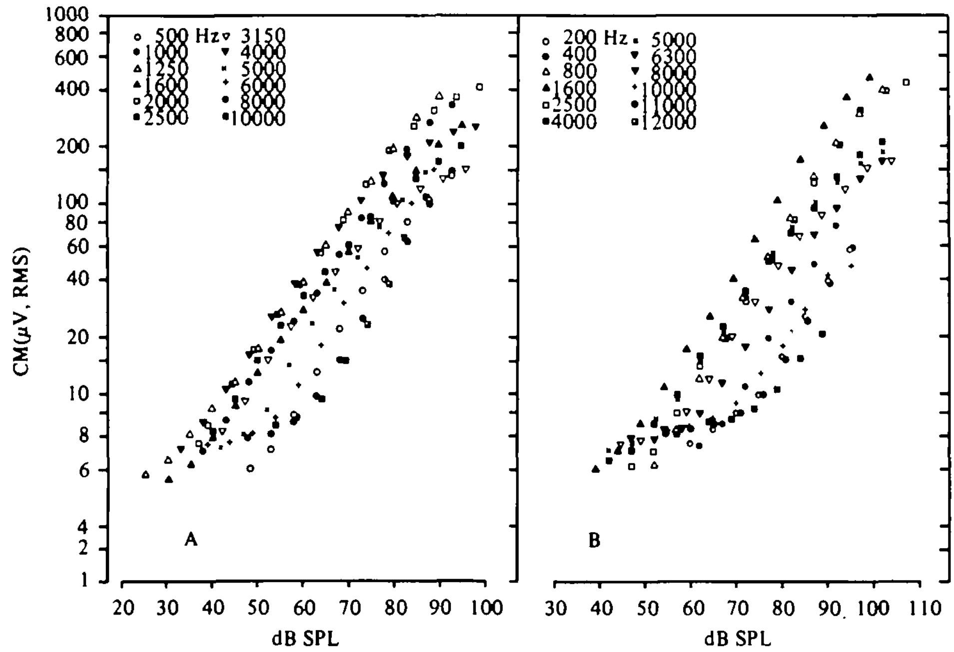

Fig. 2. Relationship between CM amplitude (μV, RMS) and SPL (dB re. 0·00002 N/m²) for selected frequencies between 200 Hz and 12 kHz in two separate experiments. Average linear slope is 0·7 (input re. output).

(3) *CM intensity function*

To monitor the changes in sensitivity of the CM as a function of the direction of the sound source, the relationship between SPL and CM amplitude was established for a speaker position at 0°. Two series of input–output curves are shown in Fig. 2 for selected frequencies between 200 Hz and 12 kHz. The CM functions have a familiar linearity and provide an approximate dynamic range of 50 dB. An important feature of this relationship is that the slope of the function is not unity. In mammals, the slope of the CM function generally has a value of one (Dallos, 1973). However in some non-mammalian vertebrates the slope is significantly less than one (Necker, 1970). In this study, a tenfold change in CM amplitude (20 dB) is produced by a change of 28 dB in SPL. This average value (28 dB) was calculated for 30 CM functions at selected frequencies (e.g. in Fig. 2) and showed little variation (27–29 dB).

The two examples in Fig. 2 show maximum CM amplitudes close to 400 μV (RMS), typical for sound intensities approaching 100 dB SPL. CM potentials of up to 1 mV were obtained in some experiments. Because of such CM sensitivity, stimuli exceeding 90 dB SPL were not used, thus avoiding the upper plateau of the CM curves where distortion effects occur. The lower limit of the CM was about 4–5 μV (30–40 dB SPL), reflecting the noise limitations of the ⅓-octave filters. The most sensitive frequencies occurred between 1 and 4 kHz. The frequency sensitivity range of the CM, for a constant CM voltage was 35 dB (e.g. 20 μV, see Fig. 2).

The linear relationship between voltage (SPL) and the output voltage (CM) was used as a measure of cochlear sensitivity (relative dB) to changing the angle of sound incidence. The relative changes in CM sensitivity were calculated from the average slope of the CM function (0·7), the sound intensity being constant at the source.

(4) *Frequency-dependent changes of CM directional sensitivity*

The maximum change in CM sensitivity with a change in sound direction at a single frequency was 26 dB. The range of maximum change in CM sensitivity with changing sound direction (for any angle) as a function of frequency is shown for two birds in Fig. 3A. The most prominent directional effects in these examples are a peak of 24 dB in the fluctuation of CM sensitivity at 315 Hz; another peak of 26 dB at 2 kHz; and smaller peaks of between 13 and 24 dB from 4 to 8 kHz.

CM directionality expressed in this manner was not averaged across experiments since marked variations occurred in the precise frequencies at which maximum directionality was elicited. Between directionally effective frequencies there were frequency bandwidths which consistently yielded poor directionality. Ineffective bandwidths (i.e. those in which the maximum directional sensitivity did not exceed 4 dB) were determined for each animal. Although the frequencies investigated were not continuous, the bandwidths were divided into ⅛ octaves and the number of birds which failed to show directionality in these intervals was determined. The results are represented as histograms (Fig. 3B). The distribution falls into two populations with means of 820 Hz and 3·5 kHz. In all but one experiment there is a region close to 820 Hz for which directionality is essentially non-existent. The mean bandwidth for this region is about ½ octave between 600 and 980 Hz. For the higher frequencies,

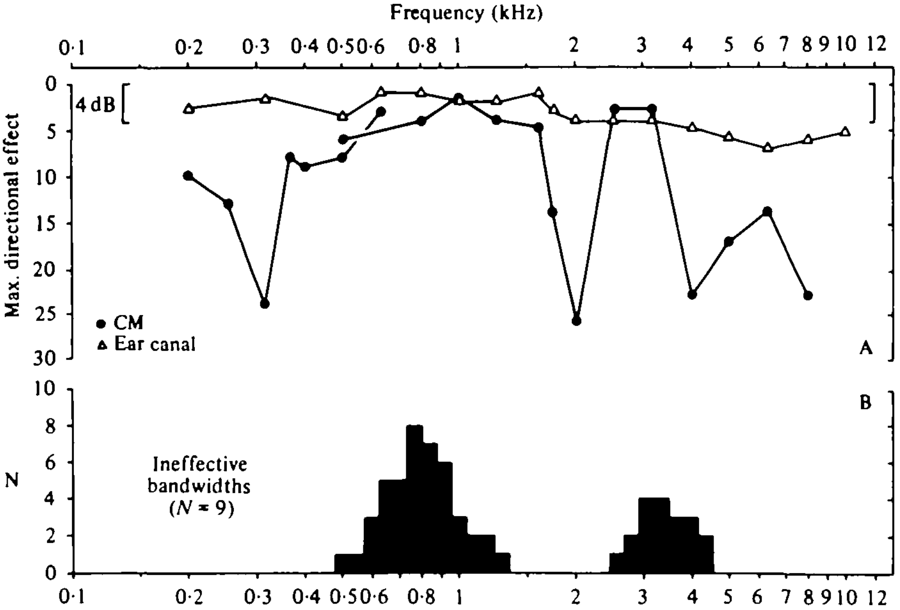

Fig. 3. In A, the physical effect of the quail head is replotted from Fig. 1 (△: ear canal) and can be compared to the maximum change in CM directional sensitivity (dB). CM results (●) obtained from two experiments with overlapping ranges extending from 200 Hz to 8 kHz. Effective directionality occurs for CM sensitivity ranges up to 26 dB. In B, frequencies (⅓ octave intervals) which failed to exceed threshold (4 dB) are termed directionally ineffective and summed for nine experiments, forming two distributions (lower mean, 820 Hz; upper mean 3·5 kHz).

the mean ineffective ranges extend for ⅓ octave between 3 and 3·8 kHz. The two distributions of ineffective bandwidths divide the frequency spectrum into three directionally effective regions.

(5) *CM directivity patterns*

The voltage levels resulting from CM directional sensitivity were usually very stable in each experiment and data points were accurate to ± 0·5 dB. Therefore it was unnecessary to assign any variability to these points.

A variety of directivity patterns resulted from angular variations in CM sensitivity with frequency. These patterns were not always symmetrical about the midline or ear axes. Nevertheless, a series of regular and familiar polar curves emerged. Fig. 4 shows seven highly distinctive directivity patterns generated by the CM. Each of these polar curves has a number of features in common. With the rotation of the speaker about the head, changes in sensitivity occur which appear as one or more lobes and 'nulls'. Lobes may be termed major or minor, depending on their relative contributions to the curve. *Nulls represent spatial positions around the head for which the ear is relatively insensitive to sound.* Highly specific nulls and lobes were seen and classified into the following types:

(*a*) *Cardioid*: comprising a single lobe with a null located about 180° from the peak (Fig. 4A, B).

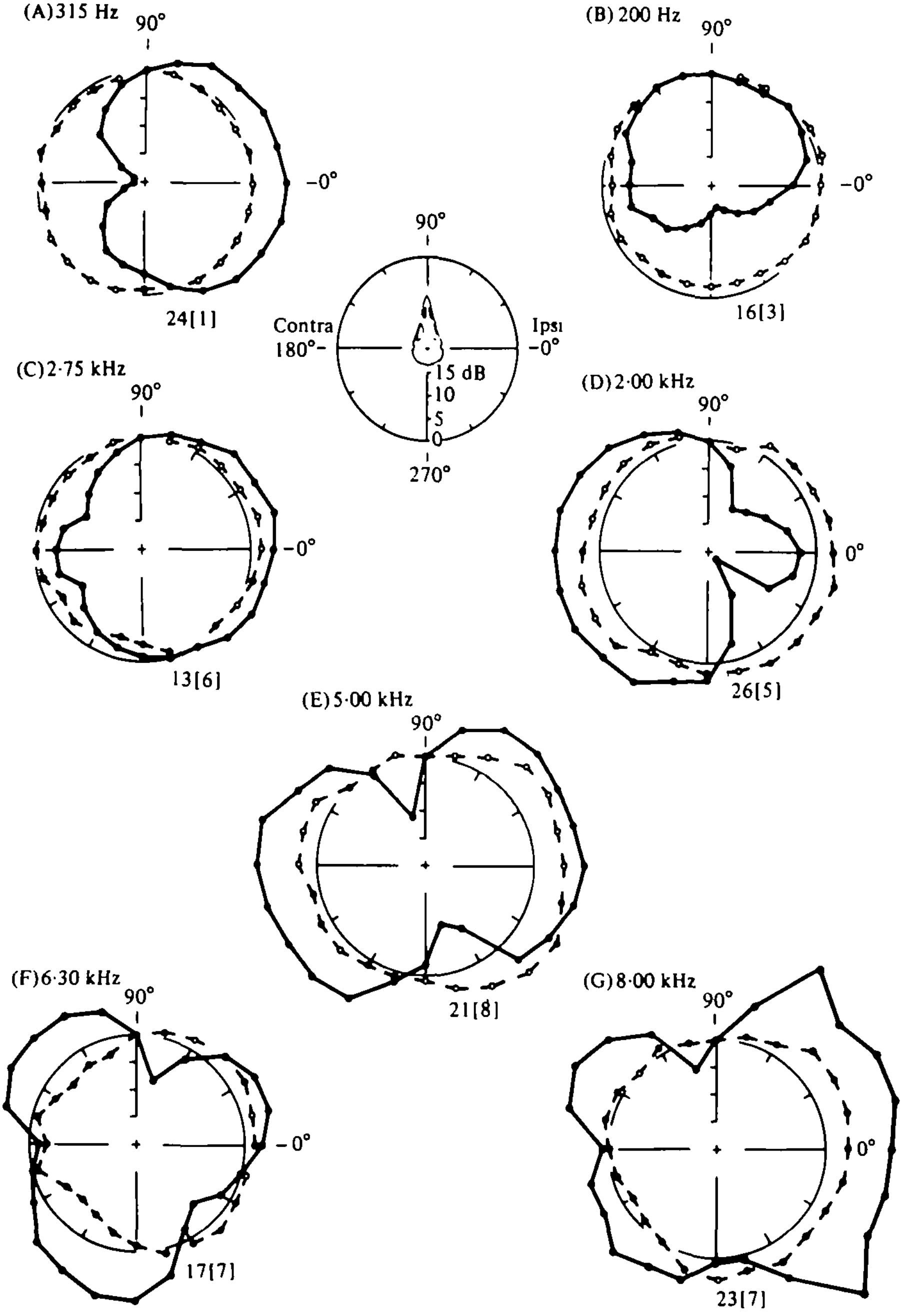

Fig. 4. Polar curves of CM sensitivity (●) from various experiments referenced to 0 dB at 90° (anterior) showing characteristic forms. (A, B) Cardioid; (C, D) supercardioid; (E) figure-of-eight; (F) tripartite; (G) multilobed. Polar plots of incident sound intensity measured at the entrance to the meatus of the recorded ear (○) and referenced to 0 dB at 90° are also shown. The numbers below each figure give the maximum range of CM sensitivity and (in parentheses) the maximum range of the microphone readings.

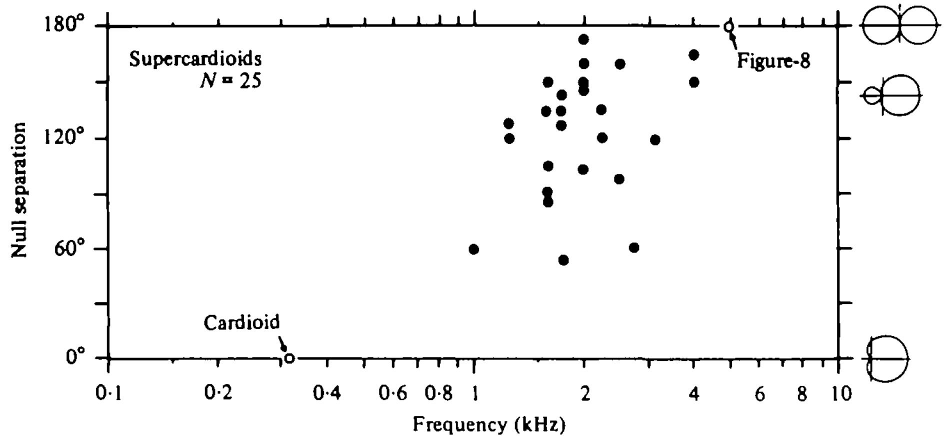

Fig. 5. Measurement of null separation (in degrees) for a sample of supercardioids ($N = 25$) distributed between 1 and 4 kHz. Two limiting cases are shown: cardioid at 315 Hz (single null) and a figure-of-eight at 5 kHz (nulls 180° apart). Extreme right-hand column shows polar response curves, similar to CM directivity patterns but derived mathematically from a first-order limaçon series (see Beranek, 1954).

(*b*) *Supercardioid*: comprising a major and a minor lobe with two nulls whose angular separation is less than 180° (Fig. 4C). A rotated form is shown in Fig. 4D, and is essentially a mirror image of the first supercardioid.

(*c*) *Figure-of-eight*: comprising two lobes of approximately equal magnitude separated by two nulls 180° apart (Fig. 4E). This pattern is the limiting case of the supercardioid since here the two nulls have the maximum possible separation.

(*d*) *Tripartite*: comprising three lobes of equal or unequal size, associated with three nulls (Fig. 4F).

(*e*) *Multilobed*: comprising many lobes and nulls of varying proportions (Fig. 4G).

Polar curves for frequencies between 200 and 800 Hz indicate that, even at these low frequencies, highly directional CM plots occur. There are CM sensitivity ranges between 8 and 24 dB, with a cardioid pattern occurring at 315 Hz (shown in Fig. 4A). The sound directions with greatest effect can occur on either side of the head but are predominantly contralateral to the sound source. These experiments indicate that the single null, cardioid type directivity pattern predominates at lower frequencies; 1 kHz was the highest frequency for which this type of pattern could be clearly detected. At higher frequencies the CM directional sensitivity varies considerably and produces many forms of polar curves (see Fig. 4).

Fig. 5 shows that it is possible to define supercardioids by the separation between their (two) nulls and the frequency for which these effects are produced. A sample of 25 supercardioid patterns taken from a series of experiments suggests that they cluster in the mid-frequency region. Nineteen (76%) of the supercardioids occur in an octave band from 1·4 to 2·8 kHz. This region corresponds to the greatest sensitivity of the CM to sound frequency (independent of direction). There is some additional clustering of data points indicating patterns with wide null separation (mean = 123°). Two boundary conditions exist: in one case a figure-of-eight pattern will be formed for 180° separation; in the second case, null separation approaches 0°, producing a cardioid.

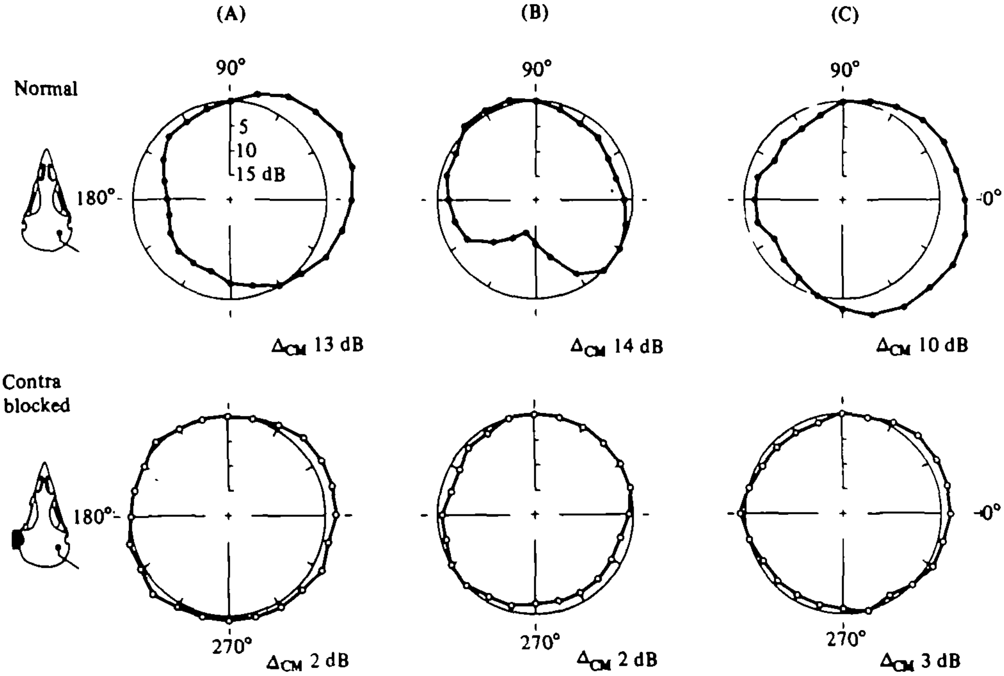

Fig. 6. Three examples of blocking the ear (meatus) contralateral to the recorded ear (right ear) on CM directional sensitivity. (Max. range at bottom right of each curve.) Taken from Table 1 and plotted in polar form.

(8) *Head diffraction and directivity patterns*

The incident sound intensity was routinely measured at the entrance to the meatus of the recorded ear, simultaneously with the CM. Fig. 1 shows that head diffraction effects become increasingly significant at higher frequencies. However, maximum directional effects (in dB) give no indication of the shapes of the microphone and CM directivity patterns. These two types of polar plots are given together in Fig. 4 for selected frequencies. There is little or no correlation between the head diffraction curves and the CM directionality; this is particularly true for directions producing nulls in the CM. Clearly, the overall CM directivity patterns must be derived from both diffraction and pressure gradient effects but the predominant influence appears to be that of a pressure gradient system.

(9) *Effects of blocking the contralateral ear*

Blocking the ear canal contralateral to the recorded ear has a significant effect on the directional sensitivity of the CM. Table 1 indicates the change in the maximum directional effect after contralateral occlusion. The simplest approach to blocking was to saturate a small wad of cotton wool with water and insert it firmly into the contralateral canal. Table 1 shows that the CM directional sensitivity tested with this type of block, in two separate experiments at 2·5 and 6·3 kHz, was significantly reduced. In one case, at 2·5 kHz (Fig. 6C), the blocking effect is expressed as a polar curve illustrating the result more clearly. The CM becomes essentially non-directional after blocking.

Table 1. *The effect of blocking the meatus* contralateral *to the recorded* (*ipsilateral*) *ear expressed as the maximum change in CM sensitivity* (*dB*)

(The results from a, b, c, are shown in Fig. 6 as polar curves.)

		CM range (dB)		
Expt.	Freq. (Hz)	Normal	Contra block	Type of block
Q28[a]	200	13	2	Eastman 910
Q28[b]	1000	14	2	
Q22	2000	14	4	
Q20[c]	2500	10	3	Wet cotton wool
Q9	6300	19	9	

Blocking the contralateral ear with glue (Eastman 910) produced a very effective abolition of CM directionality. Some results are shown for three test frequencies in Table 1, where directionality was completely lost. Again, two of these results are shown in polar coordinates. In Fig. 6B a directivity pattern at 1 kHz, generated by a prominent null behind the head at 255°, is completely lost after blocking the contralateral ear. Similar effects are shown at 200 Hz in Fig. 6A.

(B) *Binaural directional cues*

Sensitivity changes of a single ear can be the result of a change in sound direction or distance of the source (or both) and such changes are potentially ambiguous. One method of achieving an unequivocal directional cue is to compare the sensitivities of two directional receivers, i.e. a binaural comparison. There are two ways in which such a comparison can be made, based on the sum or difference between directivity patterns. A sum pattern still remains ambiguous for direction since it is *intensity dependent* and can produce the same output at different directions for different intensities. In contrast, a difference pattern is *intensity independent*. Therefore, if two acoustic receivers have similar properties, a difference between their directional sensitivities will provide an unambiguous cue of spatial position (within the limits of linearity). We suggest that a comparison of the difference between cochlea activity is the most suitable method by which the direction of a sound stimulus can be coded. The summation of activity simply provides a reference level by establishing the average binaural intensity. In physical systems, sum and difference patterns are used extensively in radar and sonar applications (Skudrzyk, 1971). These ideas have not been previously applied to directional hearing in birds but Goldberg & Brown (1968), for example, suggested that the sum and difference properties of binaural cells in the mammalian auditory brainstem could establish a neural code for spatial location. Many schemes have been proposed (see Erulkar, 1972).

(1) *The directional index*

We define the *directional index* (DI) as the contrast in sensitivity between the ears (in dB). It is generated at various spatial positions around the head and forms the basis for a difference pattern. The magnitude of the DI provides a series of directional or spatial cues around the head.

In the present study it is assumed that each ear produces a similar directivity

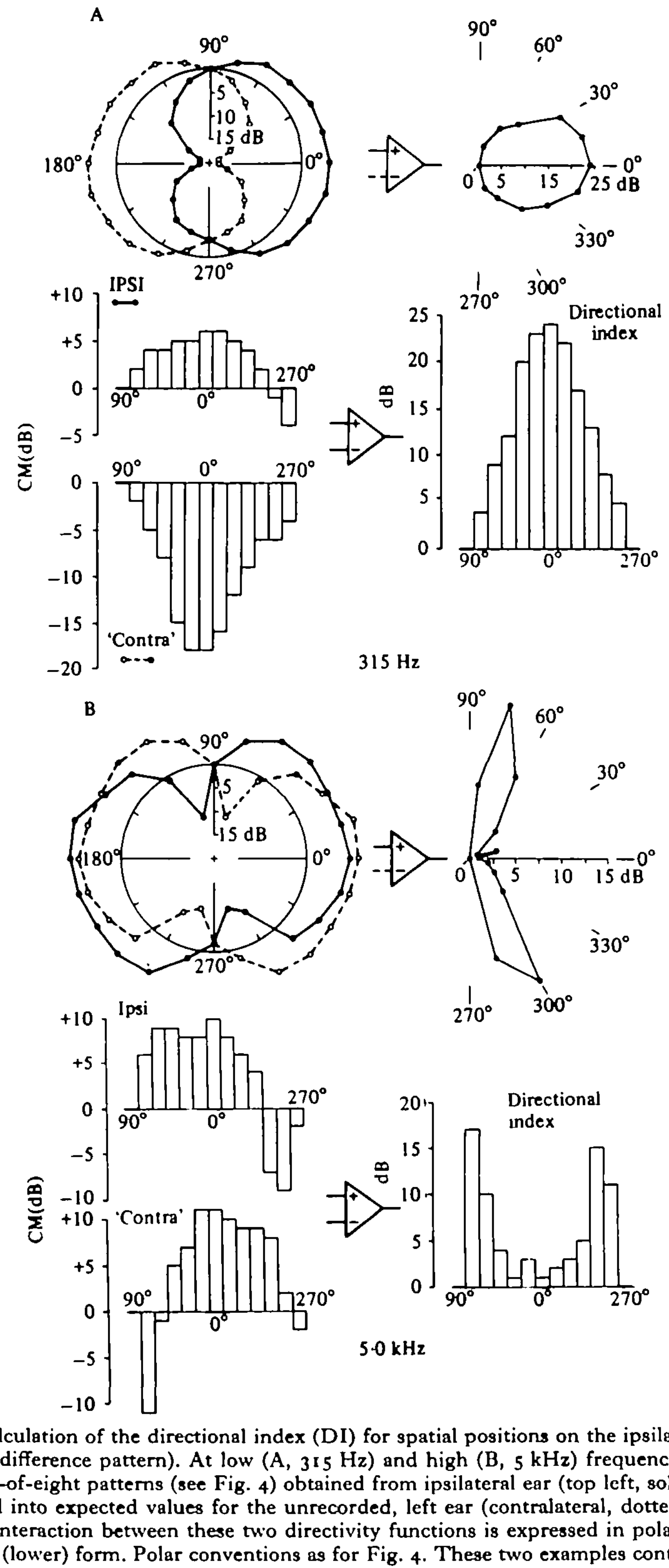

Fig. 7. Calculation of the directional index (DI) for spatial positions on the ipsilateral side of the head (difference pattern). At low (A, 315 Hz) and high (B, 5 kHz) frequencies, cardioid and figure-of-eight patterns (see Fig. 4) obtained from ipsilateral ear (top left, solid lines) are transposed into expected values for the unrecorded, left ear (contralateral, dotted line). The resultant interaction between these two directivity functions is expressed in polar (upper) or histogram (lower) form. Polar conventions as for Fig. 4. These two examples contrast a single broad peak in the DI (cue) near the ipsilateral ear for low frequencies with sharp double peaks towards the front and rear of the head at higher frequencies.

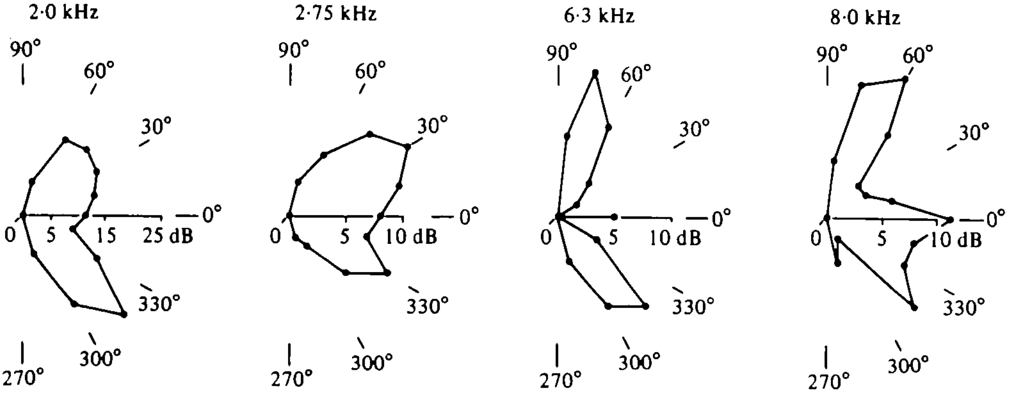

Fig. 8. Difference patterns in polar form, derived as in Fig. 7 using monaural directivity patterns from Fig. 4. Magnitude of directional index in dB at 15° intervals.

pattern for a given stimulus condition. This assumption is quite reasonable in the quail (and most birds), since the middle and outer ears are symmetrically placed about the midline. Nocturnal owls with asymmetric external ears are probably an exception (Payne, 1971; Konishi, 1973*a*; Norberg, 1977).

Based on this assumption the polar curves of the recorded ear can be transposed into values expected for the opposite ear. This can be done relative to the ear axis The polar curves can be superimposed on each other and a difference pattern obtained. Two examples of this procedure are given in Fig. 7. When a difference pattern is plotted on polar or orthogonal coordinates, symmetrical patterns of difference exist on both sides of the midline. It is assumed that each ear acts effectively at the centre of the head (since wavelengths are longer than the interaural distances) and the midline always yields a difference of zero. If the whole monaural directivity pattern is symmetrical about the midline it will yield poor DI values, even if the monaural pattern is highly directional. This situation was rare; most of the monaural patterns were not symmetrical about the midline and they usually resulted in DI values close to those of the CM range. From 98 polar curves studied between 160 Hz and 8 kHz, 92% yielded a maximum DI within 4 dB of the maximum CM sensitivity range.

If we further assume that the quail can detect sidedness, then the DI pattern need only be represented for the left or right side. We have chosen to represent the magnitude of the DI for the right side of the head only, since it was the recorded side in the present study.

In Fig. 7A the difference pattern yields a DI function with a single broad peak of 24 dB very close to 0° (shown in both polar and histogram form). This DI pattern at 315 Hz indicates a unidirectional capacity since the greatest binaural contrast occurs in only one direction. Another monaural CM directivity pattern at 5 kHz (Fig. 7B) has also been analysed in terms of the DI. Two sharp peaks occur at 75° (17 dB) and 300° (15 dB). Inspection of both CM polar curves in Fig. 7 emphasizes the importance of the null regions for the production of large DI values. When polar curves contain more than one null, they may code bi-directional information when analysed by a difference pattern. Since several nulls occurred in CM directivity patterns in the mid- to high-frequency regions, further examples of polar DI patterns

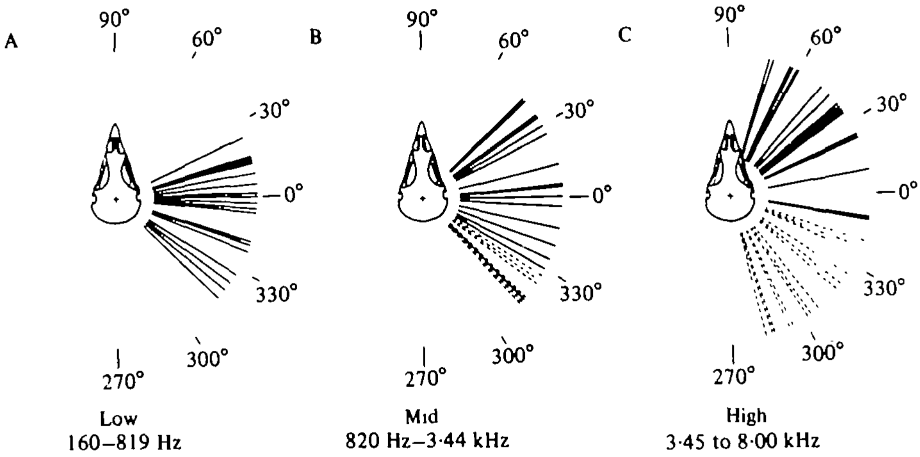

Fig. 9. Estimation of 'best' directional cues taken from 54 difference patterns in nine experiments and divided into low-, mid- and high-frequency groups (see Fig. 3). Primary best directions shown in solid lines, secondary best directions are in dotted lines. Further details in text.

are shown in Fig. 8. Each of these examples is derived from the appropriate CM directivity patterns shown in Fig. 4.

(2) *Relationship between DI and frequency*

The ability of the DI to code for various spatial positions may show some correlation with frequency, particularly peaks in the DI distributions. To quantify this relationship, the mean angle of peaks in DI distributions were calculated from their 4 dB down point ($Q_{4\ \mathrm{dB}}$). This angle reflects the confidence with which a significant peak in the DI pattern can provide the quail with a 'preferred' or 'best' direction at different frequencies. Best directions were considered *primary* for either a single peak in the DI pattern or for the greater peak in bimodal or multimodal distributions, and *secondary* for the smaller of two DI peaks for a given frequency. The results are shown in Fig. 9 for 54 DI patterns and have been divided into three bandwidths based on the poor CM directionality seen near 820 Hz and 3·5 kHz (Fig. 3). The distribution of best directions overlap between each frequency group but there is a tendency for higher frequencies to produce best directional cues closer to the anterior midline. The secondary best directions of the DI are also indicated and these effects are usually produced towards the rear of the head. They occur to a small extent at mid frequencies and commonly at high frequencies.

DISCUSSION

The well-defined directional sensitivity of the CM at most frequencies contrasts sharply with the largely insignificant pressure field fluctuations at the entrance to the ear canal (Fig. 4). We have considered that directional effects are only significant above a 4 dB change in CM sensitivity. In the horizontal plane, the positions of the sound source which contribute most to directionality are mainly those regions of relative insensitivity that appear as discrete minima or nulls in the polar response curve. Large directional effects reflect the ability to detect nulls in the polar response curves. Some of these nulls are exceedingly sharp, resulting in the complete disappearan of the CM; sensitivity changes of 20–26 dB produce highly directional effects. These effects appear for frequencies between 160 Hz and 8 kHz, with noted exceptions near 820 Hz and 3·5 kHz.

Some CM directivity patterns are highly distinctive, with the number of nulls and lobes increasing with frequency. Their polar forms are frequency dependent and elements of an asymmetrical, first-order, pressure gradient system can be seen up to 5 kHz. Characteristic patterns comprising cardioid, supercardioid and figure-of-eight are established. However, this series is not continuous because non-directional patterns occur near 820 Hz and (more variably) near 3·5 kHz. Above 5 kHz directivity patterns associated with second-order and higher-order pressure gradients are established up to 8 kHz.

The present study supports the calculated, first approximation predictions outlined in Paper I (see fig. 8, Hill *et al.* 1980). However, the physiological results more closely approach the real situation and show higher-order polar plots which are not predicted by the data taken in Paper I. The interaural distances at the frequencies investigated are always below one wavelength. Thus, supercardioids should be the most complex forms found. Certainly, above 4 kHz diffraction effects become increasingly more significant and these effects must interact in a complex fashion with the pressure gradient system. But, it is unlikely that higher-order polar curves are produced because of such interactions, and we have no explanation, at present, why such higher-order effects should occur.

Blocking the unrecorded ear canal produces substantial losses in directional sensitivity. This is mainly due to the elimination of insensitive regions in the polar response curves. This implies that the cancelling effect produced by the instantaneous sound pressure acting on each surface of the membrane contralateral to the sound source has been destroyed. Previous blocking experiments failed to show a significant effect on CM directionality in the bullfinch, although it was recognized that sound transmission across the head may occur (Schwartzkopff, 1952).

Use of directional cues

Directional hearing achieved by binaural comparisons have been studied extensively in the mammalian auditory system (see Erulkar, 1972). It is now known that the avian auditory midbrain for example, possesses similar binaural cell types (principally EI and EE) and in equivalent proportions (Coles & Aitkin, 1979). Since it is suggested here that spatial cues are produced by a difference pattern, these cues would be ideally processed by binaural cells whose response properties reflect a differential input, i.e. EI cells. EE cells would therefore assess the absolute (average) binaural intensity by virtue of summed inputs. These types of binaural interactions have not been studied in specific relation to the neural coding of auditory space in birds, although spatial receptive fields do exist (Knudsen, Konishi & Pettigrew, 1977; Knudsen & Konishi, 1978*a*).

No behavioural audiogram has been reported for the Japanese Quail but it is likely to approximate to that of the pigeon (Heinz, Sinnott & Sachs, 1977) where the best frequency sensitivity occurs between 800 Hz and 4 kHz. It is well known that the CM can be recorded for frequencies beyond the normal range of hearing. Therefore, the pressure gradient effects studied here potentially provide more directional information than the quail may actually use during sound localization. Gatehouse & Shelton (1978) have investigated sound localization in the Bobwhite Quail. Although their results are limited, they indicate that as speaker separation decreases, the errors of location increases; tones at 1 kHz were more poorly located than those at 2 kHz. Poor sound localization at 1 kHz in the Bobwhite Quail may correspond to the poor CM directionality observed near 820 Hz in the Japanese Quail. Our present study shows that close attention must be paid to frequency and to the direction around the head at which minimum audible angles are assessed (Mills, 1958).

Highly significant DI's occur across most of the audible spectrum. As frequency increases the sharper peaks in the difference patterns imply that, behaviourally, spatial acuity may increase. It is also apparent that the 'best' directional cues move towards the midline at higher frequencies. At low frequencies, the broadness of the DI distribution suggests that directional acuity may be less precise than for higher frequencies although the *magnitude* of the directional cue may still be large. The higher-order pressure gradient effects occurring above 5 kHz provide substantially sharper DI peaks suggesting an improvement in directional acuity compared to the first-order effects. However, at higher frequencies, the difference patterns indicate that bidirectional cues may be manifest as front-to-rear errors during sound localization.

Comparative aspects

To date, most of the important information concerning the neurophysiology and behaviour of directional hearing in birds comes from studies in the barn owl (Konishi, 1973*a*, *b*; Knudsen *et al.* 1977; Knudsen & Konishi, 1978*a–c*). The barn owl is highly specialized for sound localization, but a number of observations relate specifically to the present study.

In both the forebrain (Knudsen *et al.* 1977) and midbrain (Knudsen & Konishi, 1978*a–c*) of the barn owl, auditory neurones have been found with spatial receptive fields either space-dependent (limited field units), space-preferring or space-independent. Interestingly, space-dependent neurones have spatial properties which are largely independent of sound intensity, whilst the other types are intensity dependent. The present study suggests that neurones with space-dependent, but intensity-independent, spatial fields are likely to result from a differential binaural comparison. The position of spatial receptive fields would relate specifically to DI peaks in the difference patterns and may well be a property of EI cells (discussed above and by Coles & Aitkin, 1979). Auditory neurones with spatial receptive fields dependent on intensity are likely to be derived from binaural summation seen in EE cells. One consequence of applying an excitatory and inhibitory interaction (as in EI cells) to the generation of the difference pattern would be to yield receptive fields with a central excitatory region of space (DI peaks) bordered by inhibitory regions (see Fig. 6A, B). Such a centre-surround organization for auditory receptive fields has in fact been reported for the barn owl (Knudsen & Konishi, 1978*c*).

In their recordings from auditory neurones in the midbrain, Knudsen & Konishi (1978*b*) report that it was possible, under certain conditions, to introduce a secondary auditory receptive field behind the owl's head. Precisely the same effects are seen from the DI peaks which arise from bimodal difference patterns in the quail. Such coincidence between the quail and the barn owl may seem surprising in view of their diverse auditory capacities but such an observation helps to strengthen the present results in terms of a general application to birds. We share the view of these authors that there are conditions under which front-to-rear errors should occur during sound localization in birds. Such errors are common during human sound localization (Stevens & Newman, 1934) but are only now being considered for birds.

In essence, the suggested mechanism for directional hearing in birds relies on *null detection*. Nulls are very sensitive measures of changes in stimulus position and can be suitably exploited for directional hearing. Payne (1971) was well aware of the property of nulls in his consideration of directional hearing in the barn owl. Although he succeeded in finding spatial regions with very low pressure (nulls), he was unable to produce a cohesive theory of directionality. Payne assumed that the barn owl localized sound by maximizing intensities at all frequencies. We propose that this view is now untenable. Instead, it is suggested that maximizing the binaural DI may be more appropriate, resulting from frequency and direction dependent nulls produced in each ear.

Finally, the present view of directional hearing may provide some new insights into the functional properties of bird sounds. Marler's (1955, 1957) original interpretation of the properties of locatable and non-locatable sounds was based on the traditional mammalian ideas for sound localization. The present study suggests that sources of very low or very high frequencies may be readily located by birds. It should be borne in mind that the ability to localize sound sources is likely to be a function of, not only audibility of their spectral components, but also their actual spatial position. It is therefore important to determine the extent to which biologically significant acoustic signals have a strategic directional value for birds.

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