DIRECTIONAL HEARING IN THE PLAINS-WANDERER, *PEDIONOMUS TORQUATUS*

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INTRODUCTION

One of the most stimulating impacts on research into the mechanisms of directional hearing has come from the work on the barn owl by Konishi and his collaborators (see review in Konishi, 1983). A number of findings of general significance have emerged from apparently esoteric details of the neural mechanisms by which the barn owl can so accurately localise sound sources. The first of these is the midbrain “computational” map of sound source location (review in Knudsen et al., 1987). The second is the parallel processing of time and intensity information, taken from the same acoustic nerve fibre into two separate pathways, a finding with a long anatomical history (Ramón y Cajal, 1909) now given physiological meaning (Takahashi et al., 1984, Carr and Konishi, 1988). The particular role played by time processing in the assessment of sound source azimuth in the barn owl may be generalisable to mammals, since it also seems to be present in the cat (Aitkin et al., 1985).

Not all birds require such accurate auditory localisation as the barn owl, but other avian species can nevertheless provide important insight into some aspects of directional hearing. Diurnal birds of prey, for example, show some specialisations for auditory localisation in the horizontal plane, without the vertical discrimination shown by the barn owl (Calford et al., 1985). Hawk owls (Family Strigidae as distinct from the Family Tytonidae to which barn owls belong) also have good horizontal localisation without the vertical ability (Calford, 1988, Volman and Konishi, 1988). Even pigeons have neurons which can localise low-frequency sounds in azimuth (Lewald, 1988).

In the present study we examine the directional hearing of an unusual Australian bird, the Plains-wanderer, *Pedionomus torquatus*. The Plains-wanderer has an unlikely acoustic ability. It can locate species-specific sounds whose wavelengths are orders of magnitude larger than its own head! We first briefly describe the unusual biology of this remarkable bird, including its vocalisations. We then give an account of neurophysiological studies of its directional hearing. Finally we give an account of the role of the avian interaural canal in the directional hearing of the Plains-wanderer.

A BRIEF BIOLOGY OF THE PLAINS-WANDERER

Gondwanan Inland Waders. Plains-wanderers are plump birds around 17 cm (male) to 20 cm long (female). They resemble rails except for their prominent heads and their tendency to stand very erect while they survey the landscape. Restricted to sparsely vegetated plains in the inland of Eastern Australia, the Plains-wanderer is the sole member of its Family Pedionomidae, whose closest living relatives are the Seed Snipes, Family Thynocorididae, an unusual family of waders (Charadriiformes) living on the Andean steppes of South America. Although many bird books place the Plains-wanderer close to the Button Quails, Family Turnicidae, and therefore by implication within the Charadriiformes, there is now compelling evidence from osteology (Olson and Steadman, 1981) and from DNA-DNA hybridisation (Sibley and Ahlquist, 1985, Sibley et al., 1988) that the Plains-wanderer is a member of the Charadriiformes. In other words it is an aberrant wader. Like the Seed Snipes, Plains-wanderers are probably an ancient branch of the waders which have become adapted to inland conditions by feeding on seeds as well as invertebrates.

Camouflage. The plumage provides a remarkable degree of camouflage. In the natural habitat it is virtually impossible to visualise a crouching bird at one’s feet. In combination with the camouflaging crouch, a speedy gait enables the Plains-wanderer to escape undetected from danger and has caused great problems for biologists attempting a census. A reliable census can be carried out only at night, from a vehicle moving at a crawl and equipped with a spotlight which enables the characteristic silhouette of the erect bird to be picked out.

Arhythmic Circadian Cycle. Although some activity such as calling may take place at night, careful observation of captive colonies has failed to confirm suspicions that they are primarily nocturnal (Baker-Gabb, 1988). The eye is like that of most other waders with optics indicative of arhythmic (i.e. diurnal-crepuscular), rather than predominantly nocturnal, function. At first sight the pupil appears to be irregular with a shape like a base-down triangle. Closer examination reveals that the bright yellow iris has a zone of black pigmentation which is confined to the lower half next to the margin of
the pupil. Observation with an ophthalmoscope shows that the entrance pupil has the conventional circular shape (unpublished observations of J.D.P.).

**Sexual Dimorphism.** Plains-wanderers show reverse sexual dimorphism. Females are more brightly coloured, with a black necklace dotted with white as well as a bright chestnut breast patch or gorget, neither of which is seen in the male. Females are also heavier than males and are suspected to be polyandrous since the territory maintained by one female during the breeding season includes a number of incubating males and since there is an excess of males over females in the adult population (Harrington et al., 1988).

**Figure 1.** “Oom” call of female Plains-wanderer. A. Amplitude envelope of call; note the increasing amplitude of successive calls (both bird and microphone were stationary); repetition rate is about 0.5 Hz. B. Sonogram (frequency-versus-time analysis); note that each call has two harmonics around 360 Hz and 550 Hz; the higher overtone was 20 dB less intense than the dominant harmonic at 360 Hz and therefore shows up better on the later, louder calls; on some recorded calls there was also a lower harmonic at around 180 Hz (not shown).

**Species-specific Calls.** From the point of view of the present study, the vocal repertoire is perhaps the most interesting aspect of the Plains-wanderer’s biology. Four different calls have been recorded, 2 from the female and 2 from the male. Only call 1 is sufficiently loud to be audible under field conditions. The other 3 calls have been recorded only at close quarters between interacting, captive birds:

- **Call 1:** (The “oom” call): Given by the lone female, often at night, this call has some similarity to the repeated “oom” calls of other birds, such as the kakapo, or owl parrot, *Strigops habroptilus*, a nocturnal lekking parrot (Merton and Empson, 1989) and the tawny frogmouth. The dominant harmonic of the Plains-wanderer’s “oom” is between 300 and 350 Hz (depending on the individual), with both low frequency (150-180 Hz) and high frequency (450-570 Hz) harmonics. The female recorded in the sonogram of Fig. 1B came from the Riverine Plains area of N.S.W. and has a dominant harmonic at 360 Hz with a higher harmonic at 570 Hz. The low frequency harmonic is not evident in the sonogram of Fig. 1B. Another female recorded from the Diamantina Plains of Western Queensland had a dominant harmonic at 300 Hz with harmonics at 150 Hz and 450 Hz. The “oom” call is repeated at around 0.5 Hz and, like the “oom” call of the Tawny Frogmouth, gradually increases in amplitude over successive syllables (see Fig. 1A). This call has been elicited by gently releasing a recently-captured pair at night during the breeding season, whereupon the male retreats while the female holds her ground and calls after a minute or so.

- **Call 2:** An agonistic, broad spectrum (0.5 - 1.4 kHz) “uk”, briefly repeated at around 2 Hz by the female when first confronted with another female or when played the “oom” call.

- **Call 3:** A “peep” call given by the male on close visual or auditory contact with the female. This call is of such low intensity that it can be heard only with difficulty, even at a distance of one metre from the bird. The major frequency component of this call is around 1.4 kHz.

- **Call 4:** A very low intensity call, repeated in the presence of the female, by the male with a repetition rate of 4 Hz, a duration of 70 msec and two frequency components at 175 Hz and 350 Hz. Despite the similarity in these two components to those of the female’s “oom” call, there is no higher overtone (at around 500 Hz as in the “oom” call of the female) and the short duration makes it difficult, for the human ear at least, to recognise any affinity with the female’s call.

Much work remains to be done on the significance of these calls and on the mechanism by which such long wavelengths can be produced from tiny vocal tracts. From the point of view of the present study it is sufficient to note the predominance of low frequencies (inclusive range is 150 - 1400 Hz) in all the recorded calls of the Plains-wanderer.

**Localisation of Calls.** No formal behavioural study has determined how well the Plains-wanderer can localise its own species-specific calls, but we can infer that the male must show fairly accurate acoustic orientation to the female’s “oom” call because of the difficulties of visual orientation at long range when the bird is similar in size to the vegetation and when
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calling seems to take place mostly at night. Our own efforts at playback experiments in the field were strongly suggestive that males orient to the "oom" call, but more work is needed to establish a suitable behavioural assay for these laconic birds.

NEUROPHYSIOLOGICAL METHODS

We studied 6 birds, 4 females (59 - 88 g, mean = 71 g) and 2 males (44 - 60 g). The birds had been hand-netted at night with spotlight on sparsely-vegetated Mitchell grass plains 2 Km north of Nails Creek and about 20 Km west of the Diamantina River on Davenport Downs station in western Queensland. Four birds were examined in the St. Lucia laboratory and 2 were investigated with similar techniques under field conditions on the plains of the bird's natural habitat about 1-2 km from the capture site.

The general experimental set-up has been described in detail elsewhere (Calford et al., 1985). Briefly, the birds were anaesthetised with an intramuscular injection of a mixture of Ketamine (40 mg/Kg) and Xylazine (3 mg/Kg) and then single unit and unit cluster recordings were carried out from the auditory midbrain while sound stimuli were presented with different intensities, frequencies and source locations. We used a sound-attenuating, anechoic chamber fitted with a hoop to change the location of the sound source in the laboratory studies (see Knudsen et al., 1977, Calford et al., 1985). We monitored sound pressure level continuously with a small probe microphone (Briel & Kjaer type 4170) near the meatus contralateral to the recording site as a check on the occurrence of standing waves. There was evidence for such effects at the lowest frequencies and highest intensities which we found to be necessary to activate some neurons. It was for this reason that we carried out some field studies with a specially-constructed rotating turntable which carried the bird-holder and microelectrode holder. The turntable was arranged so that the axis of rotation was centered on the bird's head and there was no obstruction to the sound field or visual field for 150° to either side of the bird's zero azimuth. The turntable was mounted on a tripod so that the bird's head was 150 cm from the ground, level with a loudspeaker similarly-mounted at a distance of 100 cm. Cables from the microelectrode preamplifier and to the loudspeaker were connected to the main bank of recording and sound presentation equipment in the back of a truck at a distance of 30 m. The main equipment bank was powered by a generator in a trench at 100 m. One of us advanced the microelectrode while listening for acoustically-driven unit activity using a small battery-operated audio monitor converted from a portable radio; the same person was also responsible for changing the azimuthal angle of the turntable and bird-holder with respect to the sound source. The second person operated the oscillator, attenuator, oscilloscope, tape recorder and protocol book in the back of the truck.

RESULTS

Audiogram. The Plains-wanderer had an unusual audiogram, particularly when one considers its small head (Fig. 2). Peak sensitivity was in the region between 0.5 and 1 kHz. Sensitivity was poor, with thresholds around 30 dB SPL in the best neurons. There was no difference that we could detect between the sexes. High frequency roll-off was steep above 2 kHz. We found no neurons with best frequencies above 4 kHz. The unusual pattern of high threshold, best frequencies around 0.5 kHz and high frequency roll-off above 2 kHz shown for one bird in Fig. 2 was also seen in three other birds. The total number of points sampled within the nMLD was 819 in 19 different tracks. We therefore do not think that the audiogram can have arisen by some kind of sampling error. The low

![Diagram](image-url)

Figure 2. Neurophysiological Audiogram of Plains-wanderer, Pedionomus torquatus. Dots indicate sample points taken in nMLD (the avian midbrain auditory nucleus) from single units or multi-unit clusters. The thin lines indicate tuning curves taken from two units found in the central part of the nucleus where they were broadly tuned for direction but sharply tuned for frequency. Note the relative insensitivity of the units and the low best frequencies observed. These data were obtained from one bird. The same features were observed in 3 other birds tested.
frequencies represented in the audiogram are mirrored by the low frequencies of the species-specific calls.

The narrow range of hearing in the Plains-wanderer may explain the extraordinary tolerance shown by these birds to noise in captivity. So long as they were visually isolated from transients (we provided them with their own large room), we found that they remained calm and continued to feed unconcernedly in a noisy University animal house situation despite the clanging of pans, the vocalisations of sheep and bats and constant traffic.

**Directional Neurons.** The midbrain auditory nucleus, nMLD, was proportionately large in the Plains-wanderer (as large in relation to the midbrain as it is in the barn owl, Tyto alba and the inland dotterel, *Pelekhanus australis*) and subdivided functionally into medial and lateral subdivisions. The medial subdivision had neurons which were sharply-tuned for frequency and arranged into well-defined iso-frequency laminae with a low-to-high progression in best frequency as one passed dorsoventrally in the nucleus. These medial neurons showed no preference for a particular sound source location (Fig. 3). The lateral subdivision had neurons which were broadly tuned for frequency, but which showed preferences for particular sound source locations. Most of these neurons had preferences for locations in the contralateral sound field. Of particular interest was the fact that these neurons showed directional behaviour for remarkably low frequencies. One example, where the stimulus was a pure tone at 300 Hz, is shown in Fig. 4. It can be seen that this neuron has dramatic directional behaviour despite the long wavelength of the stimulus.

![Figure 3. Omnidirectional neurons from the central part of nMLD in Plains-wanderer: Note that the response to a pure tone stimulus (at the CF or characteristic frequency indicated) in the case of each unit is unaffected by changing the azimuthal location of the sound source (contrast with unit in Fig. 4). In each case the stimulus strength was 20 dB above the unit's threshold determined at 60° contralateral.](image)

![Figure 4. Directional unit recorded from the lateral part of nMLD of Plains-wanderer: Note that responses were strongest when the pure tone stimulus was located in the contralateral part of the bird's space. The 300 Hz sinusoidal stimulus was shaped into a trapezoidal shaped pulse with 100 msec duration and 50 msec rise time.](image)

**A Basis for Directionality?** At 1.5 cm in width, the Plains-wanderer's head is not an appropriate antenna for the interception of sound waves 1 m in length. Yet the bird's most important call, at 350 Hz, has this wavelength. Our surmise from behavioural considerations that this call can be localised by the bird is confirmed by the neurophysiology. Single neurons can localise pure tone stimuli at 300 Hz with an accuracy which would ensure that the whole bird could find the source (Fig. 4).

How is this achieved? Of the two binaural cues which are generally considered in this context, interaural intensity differences should be nonexistent because of the failure of such a small object as the 1.5 cm head to diffract the 1 m wave. Interaural time cues will also be very small, about 30 μsec for the best case when the sound source is at 90° azimuth. Detection of such small time intervals has been reported by some nervous systems, but even the barn owl's legendary abilities in this regard might not be sufficient; barn owls can detect time disparities in the range 20 - 60 μsec corresponding to azimuths which range from close to zero to 90°. Is it likely that our unspecialised Plains-wanderer has acoustic time processing machinery to handle small intervals as accurately as a barn owl? If the Plains-wanderer has a sound localisation ability around 25° like that recently reported for other small birds such as the zebra finch, budgerigar...
Directional Hearing in the Plains-Wanderer and canary (Park and Dooling, 1989), one would have to postulate the detection of time disparities around 10 μsec.

Fortunately it is not necessary to postulate such extreme values because of the role played by the interaural canal, a structure which has heroic dimensions in the Plains-wanderer (Calford, unpublished) and which may play a pivotal role in sound localisation by small birds.

**Interaural Canal.** The avian interaural canal is a phylogenetically ancient structure found in dinosaurs (personal observations) and crocodiles (Wever and Vernon, 1957) as well as all birds (Schwartzkopff, 1952). An interaural canal has also apparently been invented independently by insects, such as crickets and cicadas, which have similar problems to the Plains-wanderer in locating with their relatively tiny bodies the long wavelength acoustic signals of con-specifics (Fletcher and Hill, 1978, Larsen et al., 1989).

![Diagram](image)

**Figure 5.** Schematic account of enhancement of time and intensity cues provided by interaural canal: Right ear (closest to source) and behaviour at right tympanum are shown as solid lines; left ear and tympanic behaviour are shown as dotted lines; A. (Top traces) Outside each tympanum, pressure changes at right tympanum precede those at left, but amplitudes are similar because head does not diffract the long sound wave. B. (middle traces) Inside each tympanum pressure changes in left ear precede those at right because of direct path provided through the interaural canal. C. (resultant shown in bottom traces) Actual tympanic motion has both time cue enhancement (cf. D2 with D1) and amplitude enhancement (cf. AM2 with AM1). SP = sound pressure.

The interaural canal is less well-developed in the passerines and the owls than it is in most non-passerines (Moisell and Komishi, 1981). The largest canals (measured as canal bore in relation to head width in a series of 25 families of birds) were found by us in the pheasant coucal (Centropus phasianinus) and in the Plains-wanderer.

The canal has two effects, both of which facilitate the bird’s attempts to localise a sound source (Fig. 5). The first effect is well-known for pressure difference receivers (into which the tympanic membrane is converted by the interaural canal) and consists of a pattern of vibration which is highly dependent upon both the location of the sound source and its frequency. At low frequencies this effect could provide a strong interaural intensity cue concerning the location of the sound source, as has already been argued for diurnal raptors (Calford et al., 1985). The second effect is not well-known. It consists of a magnification of the interaural time cue (Calford and Piddington, 1988). This effect surprised us when it came out of one of Bob Piddington’s calculations, but it has now been rigorously tested in both a computer model and in live birds (Calford and Piddington, 1988). Over a range of frequencies which depends on the length of the canal, there is as much as a five-fold magnification in the time cue. In the case of the Plains-wanderer, the time difference which would have to be detected to discriminate a 350 Hz source at 0° azimuth from 90° azimuth then exceeds 200 μsec, which easily brings the task within the physiological range which has been reported in vertebrate auditory pathways (reviewed in Irvine, 1986).

**CONCLUSION**

Explanations of the very low frequency call used by the Plains-wanderer have usually turned on the acoustical properties of its flat habitat. We were ourselves quite impressed by the sound-attenuating properties of the cracked-soil plains where they lived and wondered whether the “oom” call was an adaptation to maximise sound transmission across the plain. But there is another class of explanation altogether which is raised by the properties of the interaural canal. Is it possible that this bird is using low frequencies because these are the frequencies at which it can outperform other species without such large canals, particularly predators? We know that the enhancing effects of the canal on the interaural cues for directional hearing are greatest for low frequencies (Calford, 1988, Calford and Piddington, 1988). Given a large canal, Plains-wanderers may have specialised their central auditory processing, and perhaps also their acoustic communication signals, at the low frequencies most appropriate for the operation of this peripheral acoustic aid.

Humans often express surprise on discovering that so small a bird has such a deep voice and that it can, moreover, localise wavelengths as...
long as those it produces. Perhaps surprise is experienced by other predatory creatures which try to locate the Plains-wanderer acoustically!

Acknowledgements. We are indebted to David Stewart who obtained the Plains-wanderer calls from which we constructed the spectrogram in Fig. 1. Brett Jordan wrote the sound analysis program we used to edit the calls. Bob Piddington supplied some calculations and the basis for Fig. 5. David Milgray provided helpful logistical support during our work on Davenport Downs station where he was the Manager. The research was supported by a Commonwealth Special Research Centre Grant from the Australian Research Council and a National Health and Medical Research Council grant to J.D.P. O.N.L. was supported by a Danish Natural Science Research Council Grant (M11-6083) and a University of Queensland Travel Grant.

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