Eye structure and amphibious foraging in albatrosses

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Anterior eye structure and retinal visual fields were determined in grey-headed and black-browed albatrosses, *Diomedea melanophris* and *D. chrysostoma* (Procellariiformes, Diomedidae), using keratometry and an ophthalmoscopic reflex technique. Results for the two species were very similar and indicate that the eyes are of an amphibious optical design suggesting that albatross vision is well suited to the visual pursuit of active prey both on and below the ocean surface. The corneas are relatively flat (radius *ca.* 14.5 mm) and hence of low absolute refractive power (*ca.* 23 dioptres). In air the binocular fields are relatively long (vertical extent *ca.* 70°) and narrow (maximum width in the plane of the optic axes 26–32°), a topography found in a range of bird species that employ visual guidance of bill position when foraging. The cyclopean fields measure approximately 270° in the horizontal plane, but there is a 60° blind sector above the head owing to the positioning of the eyes below the protruding supraorbital ridges. Upon immersion the monocular fields decrease in width such that the binocular fields are abolished. Anterior eye structure, and visual field topography in both air and water, show marked similarity with those of the Humboldt penguin.

Keywords: albatross; *Diomedea*; Procellariiformes; vision, amphibious; eye structure; visual fields; foraging

1. INTRODUCTION

The diet of procellariiform sea birds inhabiting the Southern Ocean have been extensively studied (Croxall & Prince 1980; Croxall 1987; Reid *et al.* 1996) and an understanding of how common food resources are differentially exploited by sympatric species is beginning to emerge (Croxall *et al.* 1997). In a number of species dietary segregation seems to depend in part upon differences in the foraging techniques that are employed in pursuit of similar food items (Prince 1980; Price & Jones 1992; Croxall & Prince 1994; Huin 1994; Prince *et al.* 1994). However, little is known of the sensory bases of these birds' foraging. Such information can give clues to the limitations and constraints upon behaviour, which may throw further light on the mechanisms underlying ecological segregation (Lythgoe 1979).

Black-browed albatrosses, *Diomedea melanophris*, and grey-headed albatrosses, *D. chrysostoma*, visit large areas of ocean in pursuit of similar diets consisting mainly of squid and fish (Reid *et al.* 1996; Prince *et al.* 1997). Compared with sympatric procellariiforms (Croxall *et al.* 1997), these albatrosses take relatively large prey items in small numbers (approximately eight items of 75–150 g each per day (Huin & Prince 1997)). However, it is not clear whether albatrosses take this food at the surface or at depth, or whether food is taken alive or scavenged (Croxall & Prince 1994). There is evidence that black-browed and grey-headed albatrosses dive regularly (Prince *et al.* 1994; Hedd *et al.* 1997; Huin & Prince 1997). They reach moderate depths (average 2–5 m) suggesting

that these birds propel themselves underwater, perhaps in pursuit of prey (Hedd *et al.* 1997; Huin & Prince 1997).

Differences in the sensory tasks of detecting and taking prey (whether alive or dead) from either the sea surface or at depth are quite marked. Although olfactory cues can bring procellariiform birds to a foraging area (Hutchison & Wenzel 1980; Bang & Wenzel 1985; Verheyden & Jouventin 1994; Nevitt *et al.* 1995), experimental evidence suggests that olfaction is not an important foraging cue among albatrosses (Verheyden & Jouventin 1994; Nevitt *et al.* 1995). It seems likely therefore that albatrosses must rely upon visual cues to detect individual items whether they are taken from the surface or during dives.

Visual guidance to items at depth presents different problems to those faced when taking the same items at the surface. In particular, an eye that functions both in air and in water must be able to compensate for the loss upon immersion of its corneal refractive power (Sivak 1978).

This paper describes the visual fields and anterior optical structure in the eyes of black-browed and grey-headed albatrosses. It is shown that these eyes exhibit amphibious features that are very similar to those of a penguin. This suggests that the vision of these albatrosses is well suited to the visual pursuit of prey both at and below the water surface.

2. METHODS

(a) Subjects

Two adult black-browed albatrosses and two adult grey-headed albatrosses were taken from among the non-breeding

birds associated with nesting colonies on Bird Island, South Georgia in December 1995 to January 1996. The birds were carried to a laboratory and held in semi-darkness until measurements were completed. The birds were then returned to the place in the colony whence they had been obtained. The total time in captivity for each birds was 2–3 h.

(b) *Measurements*

Measurements of retinal visual fields were made in alert birds using an ophthalmoscopic reflex technique and procedures similar to those used previously with other bird species. For a detailed description of the apparatus and methods, see Martin & Katzip (1994). Briefly, each bird was held in a foam rubber cradle with its head held in position at the centre of a visual perimeter by a specially manufactured bill holder. The perimeter's coordinate system followed conventional latitude and longitude with the equator aligned vertically in the birds' median sagittal plane, and this coordinate system is used for the presentation of visual field data (figure 1). The head was positioned with the bill tip pointing downwards such that the tip projected 30° below the horizontal. This position was used as it approximated that which the birds adopted spontaneously when held in the foam cradle of the apparatus. This head position was also recorded in photographs and video sequences of birds sitting on nests, walking, and in flight. Heads in this position are depicted in figure 1.

The eyes were examined using an ophthalmoscope mounted on the perimeter arm. For each eye, the visual projections of the following were determined as a function of elevation in the median sagittal plane at 10° intervals: (i) the limits of the retinal visual field, (ii) the edges of the pecten, and (iii) the optic axes. From these data (corrected for viewing from a hypothetical viewing point placed at infinity) a topographical map of the visual field and its principal features was constructed. (These features are (i) monocular fields, the visual field of a single eye; (ii) binocular field, the area where monocular fields overlap; (iii) cyclopean field, the total visual field produced by the combination of both monocular fields; (iv) projection of the optic axes, the directions of the approximate axis of symmetry of the optical components of each eye; (v) divergence of the optic axes, the angular separation of the optic axes; and (vi) nasal and temporal hemifields, two sectors into which the monocular field is divided by the optic axes in an approximately horizontal plane.) Owing to the intrusion of the bill and of the holding apparatus it was not possible to measure visual field parameters more than 30° below the horizontal in the frontal field (see figure 1). To the rear of the head, measurements were made at all elevations down to the horizontal.

Established procedures (such as light tapping sounds and flashes of light in the periphery of the visual field) were employed to determine the maximum amplitude of eye movements at each elevation. These procedures have readily elicited eye movements in other bird species when birds have been positioned in similar apparatus (e.g. common starlings, *Sturnus vulgaris* (Martin 1986a); Manx shearwaters, *Puffinus puffinus* (Martin & Brooke 1991); and herons, Ardeidae (Martin & Katzip 1994)).

Measurements of corneal curvature were made using a keratometry technique (Bennett & Francis 1962), which involved taking calibrated photographs of the anterior of the eye in the direction of the optic axis employing a modified ring-flash attachment. Corneal diameter was measured from these same photographs. Separation of the eyes in the skull was determined from calibrated photographs.

3. RESULTS

All measurements for the two individuals of each species were similar and are combined in the results. The results for the two species were similar, but are presented separately. For ease of comparison, tables 1 and 2 present various eye structure and visual field parameters, and figures 1 and 2 show aspects of visual fields diagrammatically in the two species.

Figure 3 shows that in both species the eyes are placed laterally in the skull, suggesting that these birds have a wide cyclopean visual field but a narrow frontal binocular field. The frontal view of the head shows that each eye appears to be set deep within the skull below a prominent supraorbital bony ridge, suggesting that these birds have an extensive blind region above their heads.

(a) *Eye movements*

The techniques employed readily elicited eye movements. These eye movements were complex, involving both rotation and lateral displacement, but were quantified by the maximum amplitude of the lateral movement of the projections of the retinal margins at each elevation. Such a measure allows the quantification of changes in the extent of visual field components, particularly the binocular field width, which are due to eye movements. In both species, maximum eye-movement amplitude of 20–25° occurred in the region of the frontal binocular field, i.e. 30° below to 30° above the horizontal. Above the head, although the eyes could be seen to move, no quantifiable changes in the position of the field margins occurred between 30° anterior to 30° posterior to the vertical. To the rear of the head (from the horizontal to approximately 50° above) eye-movement amplitude was 6–9°.

(b) *Visual fields*

(i) *Binocular field*

In both species, when the eyes are in their maximum forward (converged) position, the region where binocular vision occurs is relatively long and narrow with the bill placed close to the centre (figure 1). In both species the bill intrudes into the binocular field and limits its extent 30° and more below the horizontal. The maximum width in both species is approximately 30° and occurs over a 30° range about the plane containing the optic axes.

(ii) *Monocular fields*

In both species the optic axes lie in the plane 10° below the horizontal (figure 1), and in this plane the monocular retinal fields equalled approximately 150° (figure 2). The field of each eye is approximately symmetrical about its optic axis.

(iii) *Cyclopean field*

Lateral placement of the eyes in the skull (optic axes diverge by 120°), coupled with the 150°-wide monocular fields and the relatively small, 30° binocular overlap, provide the albatrosses with a cyclopean field of 270° in the horizontal plane (figure 2). There is an extensive blind area both above and to the rear of the head (figures 1 and 2). Above the head the margins of the fields were seen to

Figure 1. Visual fields of (a) grey-headed and (b) black-browed albatrosses. Each diagram shows a perspective view of an orthographic projection of the binocular field when the eyes are converged (maximum binocular field width). The projections of the pectens, optic axis and bill tip are also shown. The lowest limit (30° below the horizontal in the frontal field) at which visual field measurements were made is indicated by the dashed line. The diagrams use a conventional latitude and longitude coordinate system with the equator aligned vertically in the median sagittal plane of the bird (grid at 20° intervals). The birds' heads are shown in the correct orientation for the coordinate system, which was also the head position employed when measurements were made.

coincide with the feathering of the supraorbital ridges. In the frontal field, and to the rear of the head, feathering did not coincide with the visual field margins.

(iv) Eye structure

Based upon the measured separation of the corneal vertices, the divergence of the optic axes and the assumption that the eyes meet in the median sagittal plane of the skull, it is possible to calculate the approximate axial

length of a bird's eye. Such calculations show that the albatross eyes are relatively large, with an axial length of 37–39 mm (table 1). Their corneas are relatively flat, radius of curvature of 14.4–14.7 mm, and hence of low refractive power in air, 22.3–22.8 dioptres (D; table 1). (The refractive power of any optical element may be defined as the reciprocal of its focal length, and when focal length is in metres the power is in dioptres; corneal refractive power was calculated assuming that the cornea is a single

Figure 2. Sections through the visual fields of (a) grey-headed and (b) black-browed albatrosses in the plane containing the optic axes. Top, eyes converged to produce maximum binocular field width; bottom, eyes diverged resulting in the abolition of the frontal binocular field. The widths in degrees of the following topographical features are shown: binocular, monocular and cyclopean fields, the blind areas and the divergence of the optic axes. The margins of the visual fields of the left and right eye are differentiated by hatching.

curved surface separating the aqueous humour (refractive index 1.334) from air.)

4. DISCUSSION

These results show that albatross eyes can be considered amphibious in their optical design and suggest that albatross vision is well suited to the visual pursuit of active prey both on and below the ocean surface. The results also demonstrate how comparative knowledge of sensory systems can clarify ecological questions concerning diet and foraging behaviour.

(a) *Binocular field and foraging*

The vertically long and narrow binocular field with the bill placed below its centre (figure 1) is a similar topography to that found in a range of bird species of quite different ecology and phylogeny (Martin & Katzir 1995). It has been argued (Martin & Katzir 1995) that this is a convergent feature of species that feed using visual information to guide pecking or the procurement of larger items directly in the bill. It occurs independently of the width of monocular and cyclopean visual fields, eye size and separation in the skull, as well as differences in phylogeny and ecology (Martin & Katzir 1995). Bird

Figure 3. Photographs of the head of (a) grey-headed albatross and (b) black-browed albatross. Top, lateral view; bottom, frontal view approximately in the plane containing the optic axes.

species whose foraging is guided primarily by non-visual cues have binocular fields with quite different topography (Martin 1994, 1996).

(b) *The amphibious nature of albatross eyes*

Penguins (Sphenisciformes) feed exclusively underwater but conduct all other aspects of their lives in air (Williams 1995). Their corneas are relatively flat, and hence of low refractive power, compared with those of non-aquatic bird species. It is argued that such low-powered corneas are an important feature of an amphibious eye as it serves to reduce the effects of the loss of corneal refraction upon immersion (Sivak 1976; Sivak & Millodot 1977; Martin & Young 1984). Table 1 shows that the corneas of the albatrosses are in fact of lower refractive power than that of the Humboldt penguin, *Spheniscus humboldti*, although corneas of even lower power have been found in other penguin species (Sivak & Millodot 1977). It is not unreasonable, therefore, to suggest that albatross eyes might be amphibious in their function.

Further support for this comes from consideration of how visual fields alter upon immersion. The loss of corneal refraction upon immersion has the result that monocular visual field boundaries shrink towards the optic axes. This decrease in monocular visual field size results in a decrease in both binocular and cyclopean field sizes. The size of these decreases can be calculated from knowledge of the monocular field in air, the curvature of

the cornea and the corneal diameter (Bennett & Francis 1962; Martin & Young 1984). Thus, it can be calculated that upon immersion the monocular fields of the grey-headed and black-browed albatrosses shrink by 26.6° and 28° , respectively.

Table 2 compares visual field parameters in the plane containing the optic axes, in air and in water in the two species of albatross and in Humboldt penguins. It is clear that visual field topography in all three species is very similar both in air and in water. In all three species binocularity is just retained when the eyes enter water, suggesting that visual field topography is such that upon diving, comprehensive visual coverage of the frontal field is just retained, although binocularity is lost. This would allow the birds when foraging underwater to retain visual guidance of the bill towards prey items, but they would do so without the benefit of extensive binocularity.

(c) *Diving and visual acuity*

Huin & Prince (1997) demonstrated that grey-headed albatrosses dive deeper around midday (maximum depth 6 m) and rarely dive at night. One explanation suggested for this is that increased diving depth results in lower ambient light levels which may limit the visual acuity of the foraging birds (Huin & Prince 1997). It is worth noting that albatrosses forage in clear oceanic waters: optical types II and III in the Jerlov (1976) classification. At a depth of 10 m, beyond the depth of most albatross

Table 1. *Axial eye length (mm) and corneal refractive power (D) in black-browed albatross, grey-headed albatross, Humboldt penguin, tawny owl, rock pigeon, European starling and human*

(Axial eye length and corneal radius and diameter in the albatrosses were measured as described; values for other species are from schematic eye models (Bennett & Francis 1962; Martin 1982, 1986a; Martin & Young 1984; Martin & Brooke 1991).)

	axial length (mm)	corneal radius (mm)	corneal power (D)
grey-headed albatross	37.0	14.7	22.8
black-browed albatross	39.0	14.4	23.3
Humboldt penguin	18.7	11.3	29.0
tawny owl	35.7	9.42	28.5
rock pigeon	11.6	3.55	95.9
European starling	7.9	2.69	124.6
human	24.0	7.8	43.1

Table 2. *Visual field widths in black-browed albatross, grey-headed albatross and Humboldt penguin*

(Field widths are those in the plane containing the optic axes (values rounded to the nearest integer in degrees) when the eyes are converged. Values in air were measured using a similar technique in all three species. Values in water were calculated as described in the text. Data for the penguin from Martin & Young (1984).)

	black-browed albatross	grey-headed albatross	Humboldt penguin
optic axes divergence	120	121	116
visual field widths			
air			
binocular	32	26	28
monocular	151	148	155
nasal hemifield	76	73	72
temporal hemifield	75	75	83
cyclopean	271	270	282
water			
binocular	4	0	0
monocular	124	122	123
nasal hemifield	62	60	58
temporal hemifield	62	62	65
cyclopean	243	243	246

dives, incident irradiation in these water bodies is attenuated by between 0.3 and 0.5 log₁₀ units (Jerlov 1976). This is a relatively modest change in ambient light levels. For example, it is quite within the range produced when the sun is obscured by cloud (US Navy 1952). Luminance-acuity functions for both nocturnal (tawny owl, *Strix aluco*) and diurnal (rock pigeon, *Columba livia*) birds suggest that this change in luminance, whether it occurs at day- or night-time ambient levels, would not lead to a marked decrease in visual resolution (Martin & Gordon 1974; Hodos & Leibowitz 1977). It seems unlikely therefore that the ability of albatrosses to forage for their food items at these depths will be significantly limited by visual acuity compared with foraging near the surface under the same ambient light conditions.

(d) *Eye movements*

Eye movements in the albatrosses are of such an amplitude that binocularity in the frontal field can be completely abolished (figure 2), and spontaneous abolition of the binocular field was observed a number of times during measurements. The function of this, which has been observed in other species (for example, herons (Ardeidae; Martin & Katzir 1994)), is not understood. In albatrosses it seems unlikely to be concerned with reducing the extent of the blind area above and to the rear of the head. This is because eye movements are not simply translational within a given plane. Thus a large amplitude eye movement which abolishes binocularity in the frontal region is not associated with an equal amplitude gain of visual coverage to the rear of the head (figure 2). In addition, above the head the extent of the blind area is unaffected by eye movements and appears to be limited by the position of the eyes with respect to the supraorbital ridges.

(e) *Phylogenetic affinities of penguins and albatrosses*

The similarities in the eyes' anterior optical structures and visual fields in albatrosses and in a penguin raise the question of whether these are the result of ecological convergence or phylogenetic relatedness. That these similarities occur despite a near twofold difference in absolute eye size could suggest that ecological convergence has been an important factor in the evolution of these amphibious eyes. Until recently, morphological differences between penguins and albatrosses were considered evidence that these bird groups had quite distinct evolutionary origins, and this was recognized by placing them in separate avian orders: penguins, Sphenisciformes, Spheniscidae; albatrosses, Procellariiformes, Diomedidae (Campbell & Lack 1985). However, classification based upon DNA-DNA hybridization now suggests a closer affinity between penguins and albatrosses (Sibley & Monroe 1990). They are placed in the same order (Ciconiiformes) with albatrosses in a subfamily of the Procellariidae and penguins retained in the Spheniscidae. This proposed closer affinity between these two groups could suggest that the similarities in eye structure and visual fields are not the result of convergence, but are a feature retained from a common amphibious ancestor.

I thank Simon Berrow, Dirk Briggs, Richard Humpidge and Dom McCafferty for help in obtaining the study birds and providing working space at Bird Island. Peter Prince arranged the logistics and necessary support for the visit to the British Antarctic Survey Research Base at Bird Island, South Georgia, and also made valuable comments on a draft of this paper. This work was supported in part by the Royal Society.

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