What is binocular vision for? A birds' eye view

Graham R. Martin

School of Biosciences, University of Birmingham,
Birmingham, UK

It is proposed that with the possible exception of owls, binocularity in birds does not have a higher order function that results in the perception of solidity and relative depth. Rather, binocularity is a consequence of the requirement of having a portion of the visual field that looks in the direction of travel; hence, each eye must have a contralateral projection that gives rise to binocularity. This contralateral projection is necessary to gain a symmetrically expanding optic flow-field about the bill. This specifies direction of travel and time to contact a target during feeding or when provisioning chicks. In birds that do not need such control of their bill, binocular field widths are very small, suggesting that binocular vision plays only a minor role in the control of locomotion. In the majority of birds, the function of binocularity would seem to lie in what each eye does independently rather than in what the two eyes might be able to do together. The wider binocular fields of owls may be the product of an interaction between enlarged eyes and enlarged outer ears, which may simply prevent more lateral placement of the eyes.

Introduction

It is nearly 70 years since Walls (1942) published his encyclopedic survey of the adaptive radiation of the vertebrate eye. Walls posed many key functional questions that have remained central to visual science. The answers that were proffered by Walls were sometimes conjectural, but they usually drew widely upon available comparative data and brought together information from diverse areas (anatomy, physiology, behavior, and ecology) in a stimulating mix of ideas. Such an approach requires data drawn from a wide comparative base. The demand for such comparative data may in fact be insatiable; there may always be evidence from another species that can support or disprove a hypothesis. For this reason, it has often proved easier and more intellectually rigorous to focus upon mechanistic rather than functional questions in visual science. However, the answers to functional questions that are based upon comparative data remain both fascinating and capable of stimulating further enquiry.

One intriguing set of questions that Walls raised concerned the function of binocular vision. All vertebrates have two eyes, and it seems that there is always some overlap in the visual fields of each eye. Thus, binocularity (a portion of the world around an animal's head viewed simultaneously by its two eyes) can be regarded as a ubiquitous property of vertebrate visual systems. Walls' conclusions as to the function of this overlap of visual fields were characteristically forthright. "Vertebrates have had a powerful incentive to develop binocularity wherever their snouts and their beaks and their requirements for periscopy would permit" (p. 326), and, "two eyes are better

than one, and that vertebrates in general have seemingly striven to enlarge binocular fields at the expense of uniocular ones. Animals which have clung to strong laterality have done so in obedience to powerful factors, such as defencelessness or total absence of cover in the environment which makes the retention of periscopy vitally important. The various degree of partial frontality are compromises between the urge for binocularity and the need for periscopy" (p. 291). He further argued that an animal "would gain absolutely nothing from binocularity if they saw the object diplopically; so if they see the object singly with two separate eyes, they must have fusion of the two images of the object. If they have fusion, they have parallactic localization of the object in space; and if they have fusion of their disparate right-eyed and left-eyed view of a solid object, they have a percept of solidity" (p. 327).

The argument that there is an "urge for binocularity" and "a powerful incentive to develop binocularity," that "vertebrates in general have seemingly striven to enlarge binocular fields," and especially the idea that these are concerned with "a percept of solidity" has become subsumed in the large body of literature on the judgment of distance, the phenomenon of binocular fusion, the properties of global and local stereopsis, and the common mechanisms that are thought to underlie them.

Although the comparative base of evidence for binocular fusion and stereopsis is very narrow, the assumption that these are widespread and provide a general functional explanation of binocularity in vertebrates seems established. Stereopsis has been investigated in only a narrow range of species that share the characteristic of a relatively wide frontal binocular field produced by eyes that are typically widely spaced and forward-facing, with parallel

axes and conjugate movements. However, these are significant features of the visual system in only a small proportion of extant vertebrates, most notably primates, and may be a highly specialized rather than general arrangement. In the majority of vertebrates, eye positions, eye movements, and binocular fields are quite different.

In birds, the eyes are placed close together, nearly touching in the median sagittal plane of the skull, and they always project laterally to some degree. This is true even in owls (Strigiformes) with their apparent eye frontality (Figure 1). With the exception of owls, binocular fields in birds are typically small, vertically long and narrow, and make up only a very small portion of the total visual field (Martin, 2007). In some bird species (some ducks, Anatidae; Martin, Jarrett, & Williams, 2007; and some shorebirds, Scolopacidae; Martin, 1994), binocularity extends from just above the bill to behind the head thus providing total panoramic vision in the horizontal plane and comprehensive coverage of the celestial hemisphere (*periscopy* to use Walls' term). Furthermore, due to relatively large amplitude and non-conjugate eye movements, binocular fields in many bird species can be spontaneously abolished or made asymmetric (Martin, White, & Butler, 2008). What are the functions of binocular vision in such species? Do they give clues to more general functions of binocularity in vertebrates, especially in species in which the optic axes are not parallel?

Although a possible neural substrate for global stereopsis has been described in an owl, *Tyto alba,* Tytonidae (van der Willigen, Frost, & Wagner, 1998), and stereopsis was behaviorally demonstrated in a falcon *Falco sparverius,* Falconidae, 40 years ago (Fox, Lehmkuhle, & Bush, 1977), these demonstrations have not been replicated or extended more generally among bird species. The presence of global stereopsis in other bird species is based upon conjecture. McFadden (1994) found some behavioral evidence of local stereopsis in pigeons; however, these results did not support the presence of global stereopsis. Furthermore, although binocular cells have been reported in the Wulst of pigeons (Micheli & Reperant, 1982; Perisic, Mihailovic, & Cuenod, 1971) and chickens (Wilson, 1980), they are relatively scare and are not thought capable of supporting global stereopsis. A deliberate search for disparity sensitive cells in Wulst of pigeon *Columba livia* yielded negative results (Frost, Goodale, & Pettigrew, 1983), and while this negative result was originally attributed to anesthetic procedures, a further series of investigations also failed to find such neurons (Frost, Wylie, & Wang, 1994). Despite this conflicting evidence, the assumption that global stereopsis is a primary general function of binocularity in birds seems to be widely held. Thus, Iwaniuk and Wylie (2006) stated recently, "Although the role of the Wulst in stereopsis has yet to be definitively proven, the available neural evidence from owls suggests that the Wulst mediates stereopsis"…"it is conceivable that Wulst enlargement underlies functional global stereopsis." Furthermore, based
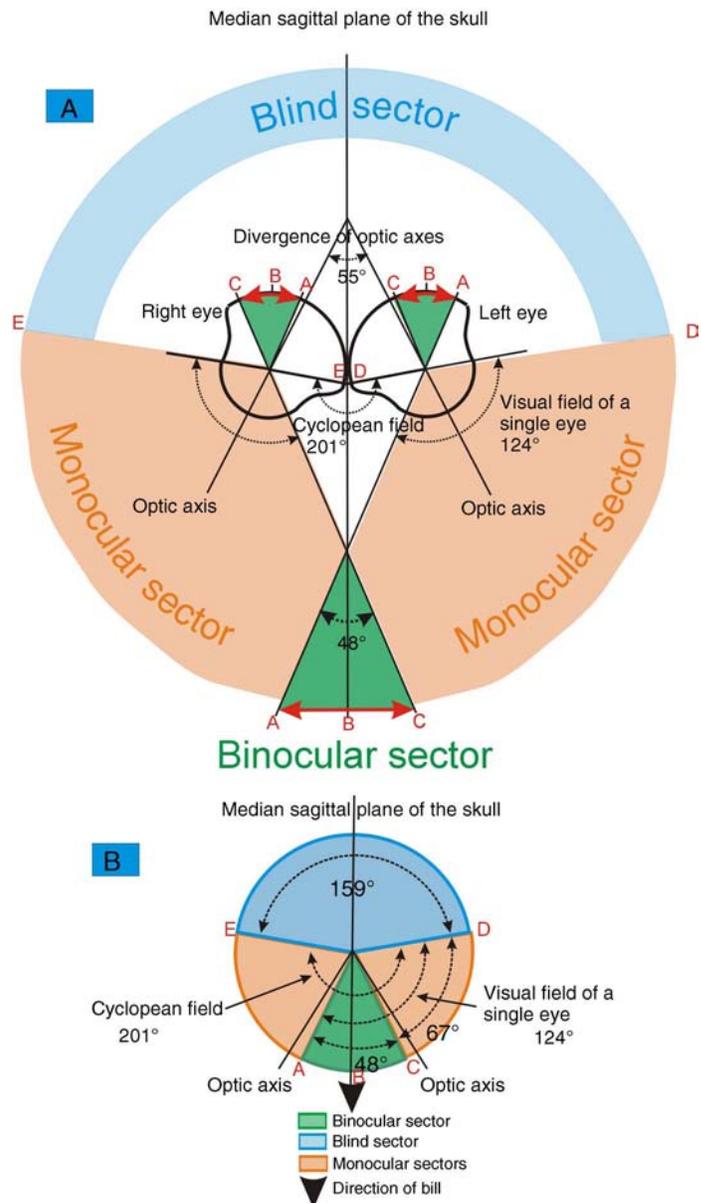

Figure 1. Diagrammatic representations of visual fields in a bird species with non-parallel optic axes, based upon data for tawny owls. (A) Horizontal sections through the eyes and the associated visual fields. Eyes meet at the median sagittal plane of the skull and their axes diverge by 55°. The binocular sector of the visual field projects to the peripheral (temporal) retina in each eye such that the image of point A, which is at the limit of the visual field of the left eye, falls within the central portion of the retina of the right eye and vice versa. Point B falls on the median sagittal plane. In species in which optic axes are parallel (such as primates), the images of points A to C would fall at equivalent positions in the retina of each eye. (B) Schematic horizontal section through the same visual field based upon the assumption that the field has a central viewpoint.

upon extrapolation from owls, a further assumption that binocular vision is associated with nocturnality and predation also appears to be widely held. Thus, Schwab and Hart (2003) asserted that, "This evolutionary position [of frogmouths Podargidae] between the swifts and the owls, visually, illustrates the binocular imperative for sophisticated nocturnal predation."

The general argument

There is now a growing body of comparative data on visual field topography in birds that can be used to examine these general assumptions concerning the function of binocularity. Data are available on visual field topography in a range of species which differ in their behavior, ecology, and evolutionary origins (34 spp; 21 families; 14 orders; Appendix A). These data have been collected with a standard technique and therefore provides a base for interspecific comparisons. It is used here to argue that the general function of binocular vision in birds is not associated with stereopsis, the "percept of solidity," or judgments of distance. It is also argued that among birds there is no evidence to support the idea that "vertebrates in general have seemingly striven to enlarge binocular fields" (Walls, 1942, p. 291) and no general binocular imperative associated with either nocturnality or predation. The answer to the central question "What is binocular vision for?" has two parts. A functional answer describing the behaviors that binocular vision may be specifically used to control, and an answer concerned with the information that binocularity provides for the control of those behaviors. Contrary to Walls' (1942, p. 327) suggestion that birds "would gain absolutely nothing from binocularity if they saw the object diplopically," it is argued here that vision in birds may indeed be diplopic and that they do indeed gain important information from this arrangement. Finally, it is argued that it may be more appropriate to discuss the role of *contralateral vision* (which gives rise to binocularity) rather than *binocular vision* itself since the latter term brings with it assumptions of function that do not have evidential support.

Evidence for the function of binocular vision in birds

Data drawn mainly from the comparative studies of visual fields in birds that are listed in Appendix A, and other studies concerning the functions of vision especially in both lateral and binocular fields provide eleven principal pieces of evidence which are grouped here under two main headings to answer the question "What is binocular vision for?" This evidence is diverse. Some is derived from detailed comparative arguments concerning visual fields, behavior, and ecology; others draw upon straightforward observations and conclusions published previously. No single piece of evidence answers the functional question but this body of evidence can be used to build a series of arguments that challenge the general assumptions of the functions of binocularity that Walls and subsequent workers have presented. The approach is discursive, in the intellectual or rational sense, rather than statistical.

The statistical comparative method is a useful tool for testing functional hypotheses about the evolution of behavioral and morphological traits. It can be used to look for correlations between traits while controlling for phylogenetic relationships among species. It would thus seem appropriate for an investigation of this kind. However, while Appendix A provides data from a sample of species chosen because they encompass particular behavioral and ecological traits or taxonomic relationships (especially differences within families), the sample is not large. Properly measured visual fields are known only for a relatively small number of avian species (34 species drawn from ∼10,000 extant species), and thus it would seem inappropriate to use the statistical comparative method at this time. However, work continues in building the avian visual field database, and it is hoped that this review will also stimulate others to collect further data so that at some point the data base is sufficiently large to apply the statistical comparative method where it may provide appropriate tests of some of the arguments presented here. It is also noteworthy that avian phylogeny, especially at the higher taxonomic levels, is far from settled (del Hoyo, Elliott, & Sargatal, 1992; Hackett et al., 2008; Livezey & Zusi, 2007), and it is not clear which of the current phylogenies would be appropriate for a statistical comparative approach at this time. The arguments presented here rest mainly upon differences within families and between well-established avian orders and thus avoid some of problems of arguing from a relatively small comparative database.

In what follows, when a particular species or species group are mentioned, the citations supporting data on their visual fields are found in Appendix A where species are listed in the taxonomic orders and sequence employed by del Hoyo et al. (1992) in the various volumes of the *Handbook of the Birds of the World*. These citations also give information on the behavior and ecology of the species. To reduce a clutter of citations, evidence on ecology and behavior of particular species are not cited here but can be found in the relevant paper listed in Appendix A for each species. "Recommended English Names" (Gill & Wright, 2006) are used throughout and scientific names for species, families, and orders are given in Appendix A.

Observations on the nature of binocular fields in birds

Maximum binocular field widths show a high degree of interspecific convergence

With the exception of owls, kiwi, some ducks, and some shorebird species (see Binocular vision and the control of bill position section), the maximum width of frontal binocular fields recorded to date typically fall within the narrow range of 15°–30° while vertical extent may vary between 80° and 180°. Maximum binocular field widths in the 15°–30° range are found in birds that differ markedly in their behavioral ecology and phylogeny. Among species in which this is found are pigeons, starlings, herons, albatrosses, penguins, eagles, cormorants, shorebirds, ostriches, blue ducks, hornbills, nightjars, oilbirds, wigeon, and flamingos. Furthermore, this apparent convergence upon similar binocular field width is independent of the extent of the lateral fields in these species (Martin & Katzir, 1999).

Such a marked similarity across a wide range of taxa suggests that this narrow range of maximum binocular field widths is likely to be the result of ecological convergence that represents an optimal solution to a common set of visual challenges. These common visual challenges could arise from two similar and frequently conducted tasks that are under visual control.

a. Tasks associated with locomotion: these would involve avoidance of obstacles during flight or when running and the estimation of target position and time to contact a surface or perch when landing.
b. The accurate placement of the bill with respect to a target. The most frequent targets are likely to be items of food, but would also include the open mouths of chicks when provisioning them before their independence and the seizure of items used for nest building. Accurate bill placement in foraging would apply whether the food items are taken by pecking, lunging, or seizing from a surface of from within the airspace. Raptorial birds typically take prey in their feet and this seems to involve direct approach of the head/bill toward a target with the feet brought up into the binocular field just prior to prey capture (Martin & Katzir, 1999).

There are two important elements for the visual control of these visual challenges: the correct positioning of the bill or feet with respect to the target and the correct prediction of time to contact the target. The latter is important for the control of bill (or foot) opening and closure when seizing an item, or for bill opening when releasing an item during chick provisioning or nest building.

Starlings present an interesting variant of this apparent convergence toward maximum binocular field width of 15°–30°. When the eyes adopt their resting position, the binocular field in starlings is as described above. Similar to other birds, starlings have large amplitude eye movements and can spontaneously abolish binocularity (see Binocular fields can be spontaneously abolished section). However, although these birds peck at targets and collect nest material apparently under visual control, they employ a specialized foraging technique: open-bill probing. In this, the bill is placed into the surface of a substrate and opened wide to push material aside to allow examination for invertebrate prey hidden just beneath the surface (Beecher, 1978; Feare, 1984). With the bill wide open, the eyes are swung further forward and achieve a binocular field width between the opened mandibles comparable to that of owls (≈50°). The function of this is not clear. However, items examined with this wider degree of binocular overlap will be at a close fixed distance, i.e., within the length of the bill. These more forward eye positions may be a way of using more central portion of the visual field of each eye to visually inspect items at close range when the bill is inserted in the substrate. This would obviate the need to turn the head to use lateral vision to examine objects with one eye (see Lateral and binocular vision section). Such lateral viewing brings more central optics to examine an object and is seen in other ground feeding Passerines, such as thrushes (Montgomerie & Weatherhead, 1997) and Zebra Finches *Taeniopygia guttata* (Bischof, 1988), and also in non-passerines such as Pigeons *Columba livia* (Bloch, Jäger, Lemeignant, & Martinoya, 1988) and domestic chicks (Dharmaretnam & Andrew, 1994), all of which take items by detecting them when standing and pecking them from a surface.

Binocular vision is peripheral vision

Lateral placement of eyes in the skull inevitably means that forward/binocular vision is achieved by the peripheral portion of the visual field and hence the peripheral retina of each eye (Figure 1). This is in contrast to the situation in species with parallel optic axes (such as primates) in which it is the central portion of each eye's visual field/retina that mediates forward/binocular vision. There are two consequences of this:

a. Since the highest optical quality in any imaging system is usually found along the optical axis, forward/binocular vision in birds and other lateral eyed vertebrates is likely to be served by relatively lower quality images compared with central vision, thus reducing the amount of information potentially available within the binocular field of view compared with information that can be extracted from the laterally projecting regions of the visual fields about the optic axes of each eye. This poor optical quality in the far periphery may be linked to the failure to maximize functional binocular field widths within the limits imposed by the available optical field (see Binocular field widths are not maximized section).

b. Neural pathways that could potentially link points of correspondence in the binocular portions of the two eyes must be more complex than in species with parallel optic axes. This is because an image point in the far retinal periphery of one eye will correspond with one that is more centrally placed in the retina of the other eye.

In Figure 1, the image of point A (at one margin of the binocular field) projects to the far peripheral retina in the left eye but projects to the central retina in the right eye, and vice versa for point C. This was overlooked in the original schematic description of possible neural pathways serving binocular vision in owls (Pettigrew, 1979; Pettigrew & Konishi, 1976). It was assumed that the configuration of the eyes would be similar to those of primates (or other animals with parallel optic axes) in which corresponding images fall on similar locations in the retinae of each eye. In primates, corresponding points in the two retinae are brought together through partial decussation of the optic nerves, and that representation of the binocular field is divided about a vertical meridian (which lies in the median sagittal plane of the skull) and that each half of the visual field projects to and is spatially mapped in the ipsilateral visual cortex. In birds, there is total decussation of the optic nerves and so similar mapping of the binocular field cannot occur in them. Possible solutions in the avian thalamofugal visual pathways require a partial decussation of the neural pathways between the lateral geniculate nucleus (LGN) and the visual Wulst (hyperpallium; Figures 2 and 3). It would also require that the representation of the binocular field in the Wulst takes one of two forms:

   a. The representation of the binocular field is separated about a vertical meridian (which as in primates lies in the median sagittal plane of the skull) such that information from each half of the binocular field is processed separately in the contralateral, left, and right visual Wulst (Figure 2). However, this would mean that each Wulst would process information only from the left or right visual hemifield rather than the full visual field of the contralateral eye.
   b. The complete binocular field is represented in both the left and right visual Wulst (Figure 3). This would ensure that each Wulst would process information from the full visual field of the contralateral eye as seems to be the case (Rogers, 2008) but means that the binocular field has two representations in the brain.

Neither arrangement would seem likely. In species with non-conjugate eye movements (see Binocular fields can be spontaneously abolished section), solution a is unlikely because the projections onto the retinae (and then their mapping onto the LGN) of a point lying on the median sagittal plane (point B in Figures 1, 2, and 3) are not fixed
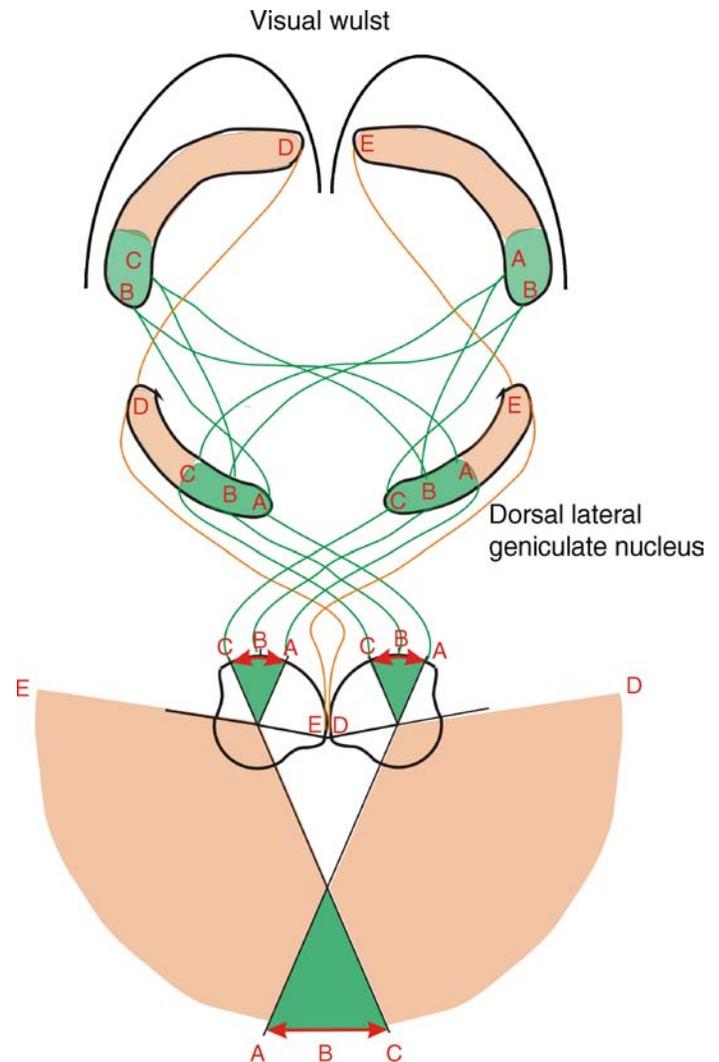

Figure 2. Schematic representation of neural pathways that could potentially link points of correspondence in the binocular portions of the two eyes. In birds, there is total decussation of the optic nerves and spatial mapping on to the lateral geniculate nucleus (LGN). To achieve mapping of corresponding portions of the retina in the visual Wulst (VW) requires complex partial decussation between the LGN and VW. In this schematic, it is assumed that the binocular field is split into left and right halves about a vertical meridian in the visual field corresponding to point B of the binocular field. Thus, each Wulst maps the contralateral visual hemifield. This is similar to the arrangement in species with parallel optic axes and conjugate eye movements such as primates, but in them the mapping of visual fields in the higher visual centers is of the ipsilateral visual hemifields. However, in birds that have non-conjugate eye movements, the projection of the image of point B in the visual field onto the retina is not fixed. Therefore, the mapping of points A–B or B–C cannot be fixed.

(i.e., unlike the situation in primates there is not a fixed vertical meridian represented in the retina) and so what constitutes a "binocular portion" of the retina, and hence its projection through the optic nerve, is not fixed.
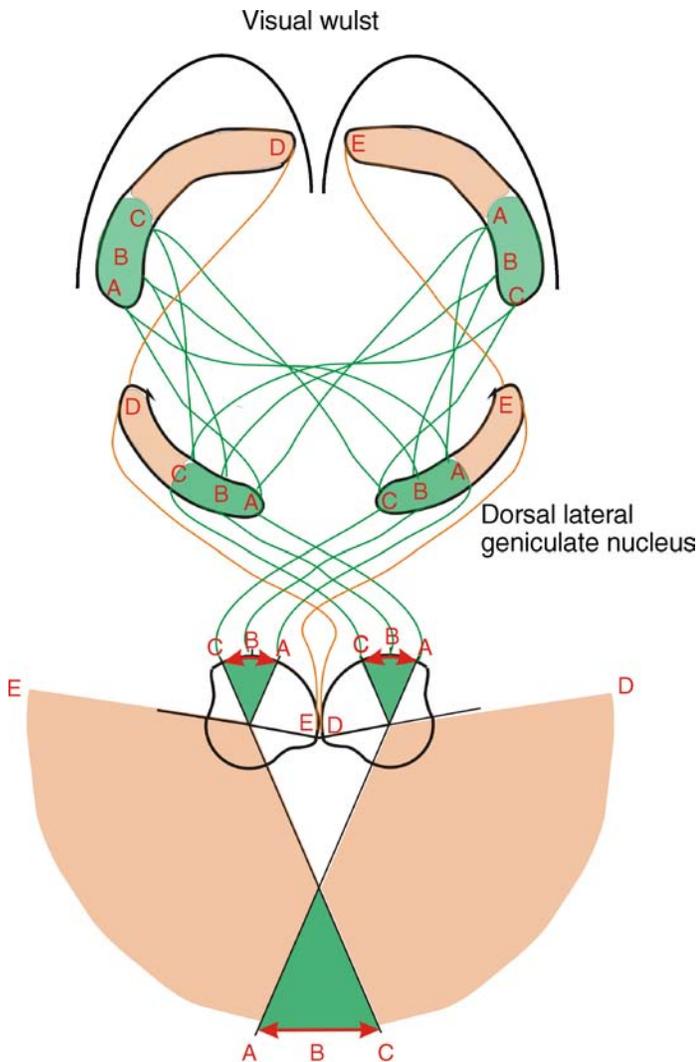
Figure 3. As Figure 2, but in this case it is assumed that the binocular field is not split about a vertical meridian in the visual field corresponding to point B. In this case, the whole of the binocular portion of the visual field is mapped in each visual Wulst. Thus, each Wulst maps the complete visual field of the contralateral eye. However, this means that the binocular portion of the visual field is mapped in both halves of the visual Wulst. Also eye movements would mean that images of the points A, B, and C would fall on changing sectors of the retinas and although each Wulst could represent the visual field of the contralateral eye, the binocular portion of it would change. Therefore, corresponding points cannot be mapped as they could be in species without eye movements or in species with parallel optic axes.

It may be more parsimonious to assume that both eyes project to the left and right hyperpalliums, as suggested by the work of Rogers (2008) and colleagues, but that these projections do not map onto each other in the binocular region, i.e., there are no projections in the brain where information from the binocular portions of the visual fields are mapped together. As shown in Figure 3, if the binocular portions of both eyes mapped to each hemisphere, there would then be two areas in the Wulst where the binocular field projects rather than a unique projection which combines input from the two eyes within the binocular region.

It is also noteworthy that projections of the left and right eyes in the thalamofugal pathways to the hyperpallium are quantitatively asymmetric (Rogers, 2008). Thus, in the brains of domestic chicks, greater numbers of fibers project from the left LGN (which receives input from the right eye) than project from the right LGN (which receives input from the left eye). Whether this asymmetry of projections extends equally throughout the visual field of each eye is unknown but clearly it could pose additional problems for any mapping of corresponding points since the same location viewed binocularly could be more heavily represented in the hyperpallium from one eye than from the other.

Binocular field widths are not maximized

In a number of bird species, binocular fields could be twice the size that they functionally are. This occurs because full use is not made of the available optical field at the frontal margin of the visual field. This gives rise to the impression from casual observation that binocular fields are wider than they actually are. Thus, while it is possible to see into the eye through the pupil at the frontal margin of the optical field and thus gain the impression of a wide binocular field, there may not be any retina serving that part of the optical field, i.e., there is a blind optical margin (Figure 4).

In tawny owls, short-toed eagles, and herons, the widths of the bind optical margins are such that the functional (retinal) binocular field could be twice the width actually found if full use were made of the available optical fields of each eye. In the case of owls, this failure to maximize retinal field width within optical limits could be explained by the "tubular" shape of the eye which may prohibit extension of the retina into the far optical periphery (the tubular shape itself can be regarded as an adaptation to achieve a long focal length combined with a large entrance aperture while reducing the overall bulk of the eye as a means of weight reduction and/or minimizing the width of the head; Martin, 1982). However, such an explanation does not apply to both the eagle (Figure 4) and the herons which do not have tubular eyes. This would seem to suggest that the width of the frontal binocular field has simply not been maximized within the constraints of the optical system. This may be related to the possible poor quality optics of the peripheral visual field of the eye that projects forward and constitutes the binocular field (see Binocular vision is peripheral vision section). However, it is noteworthy that full use of peripheral optics in these same eyes is achieved at the lateral margins of the visual field. Thus, both the optical and retinal margins coincide in the part of the visual field that serves vision to the rear of the head (Figure 4). This suggests that

within the constraints of the optical system, visual field extent is maximized to the rear but not to the front of the head, indicating that vision at these different margins of the visual fields are probably serving different functions.

Binocular fields can be spontaneously abolished

In the majority of birds, eye movements are present. Many birds exhibit eye movements of large enough amplitude to significantly affect the configuration of the visual field. In particular, the configuration of the region of

binocular overlap can be significantly altered and may in fact be completely abolished. Eye movement amplitude varies with elevation in the sagittal plane, and typically maximum excursion occurs close to the plane in which maximum binocular field width is achieved (e.g., hornbills, cormorants, herons, starlings). Eye movements are complex rotations such that while they achieve maximum displacement of field margin projections (typically 15°–18° in amplitude) to the front of the head, they have little effect on the projection of field margins to the rear of the head (this has been described most comprehensively in hornbills and cormorants).

A further notable feature of eye movements in birds is that unlike the situation in animals that have parallel optic axes and in which eyes are moved conjugately (as in primates), these movements are independent. The result of these large independent movements is that the degree of binocular overlap is not fixed and binocularity can be spontaneously abolished. Thus, it is possible to observe a binocular field that is symmetrical with respect to the median sagittal plane of the head, but a moment later the binocular field may take up an asymmetric shape, or there may be a complete absence of binocularity (Figure 5). Such eye movements and the spontaneous abolition of binocularity may occur frequently and rapidly.

Not all birds exhibit eye movements and the spontaneous abolition of binocularity. Eye movements do not occur in owls and other species which have eyes that are relatively large compared with the size of their skull. These include nocturnally active species such as plovers, oilbirds, stone-curlews, and nightjars, in which increased eye size is correlated with increased absolute visual sensitivity. In all of these species, eye size appears to have increased such that they fit either tightly in the orbit or that they do not fit within the orbit and (as in the case of plovers) are firmly anchored to specialized structures of the skull (Martin & Piersma, 2009) from which they bulge.
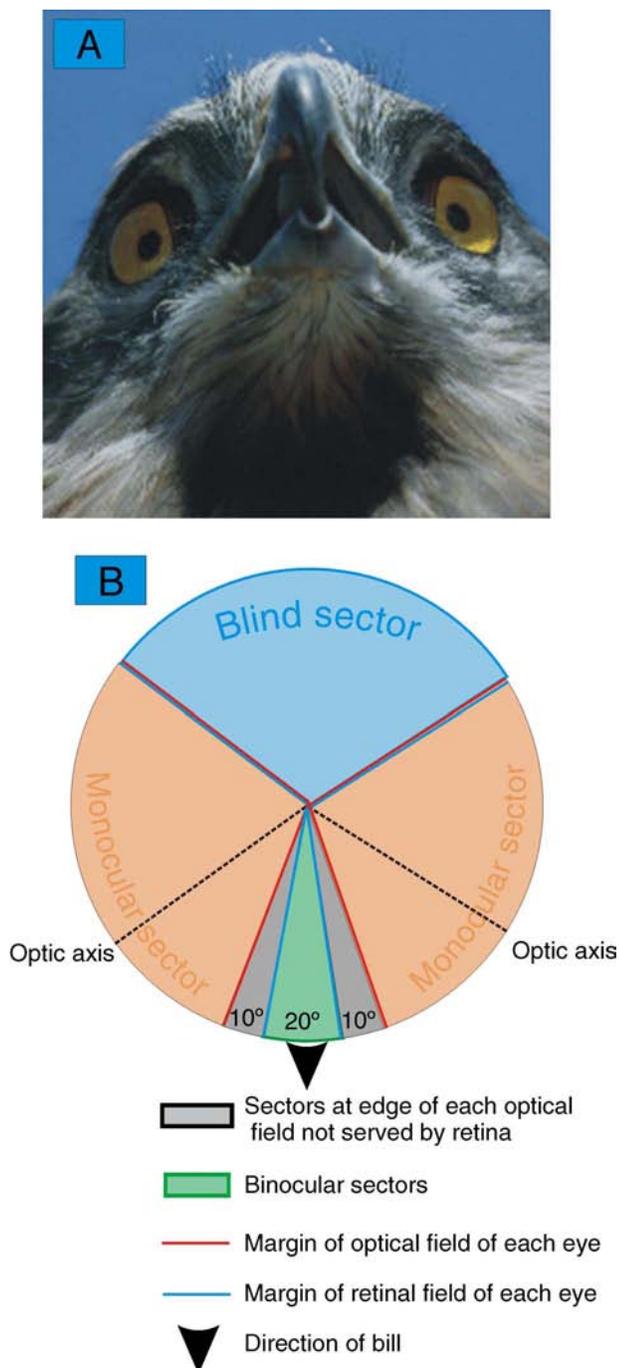
Figure 4. The disparity between optical and retinal margins of the visual fields in frontal vision. This is illustrated by data from short-toed eagles. (A) Photograph of an eagle taken at an elevation where the bird appears to have a binocular view of the camera. However, mapping the visual fields shows that although it is possible to see into the eye from this viewpoint (the pupils are visible and so the camera is looking into the posterior of the eye), there is in fact no retina serving vision. Thus, the bird cannot in fact see the camera. (B) Schematic section through the visual field in an approximate horizontal plane, the margins of the optical field and of the retinal field in each eye are shown. To the rear of the head, the margins coincide and so full use is made of the available optical field. However, to the front of the head, there is a 10° wide margin between the optical field and the retinal field. Thus, the functional binocular field is 20° wide but the potential binocular field is 40°. Therefore, within the constraints of the eye's optical system, the width of the binocular field is not maximized.
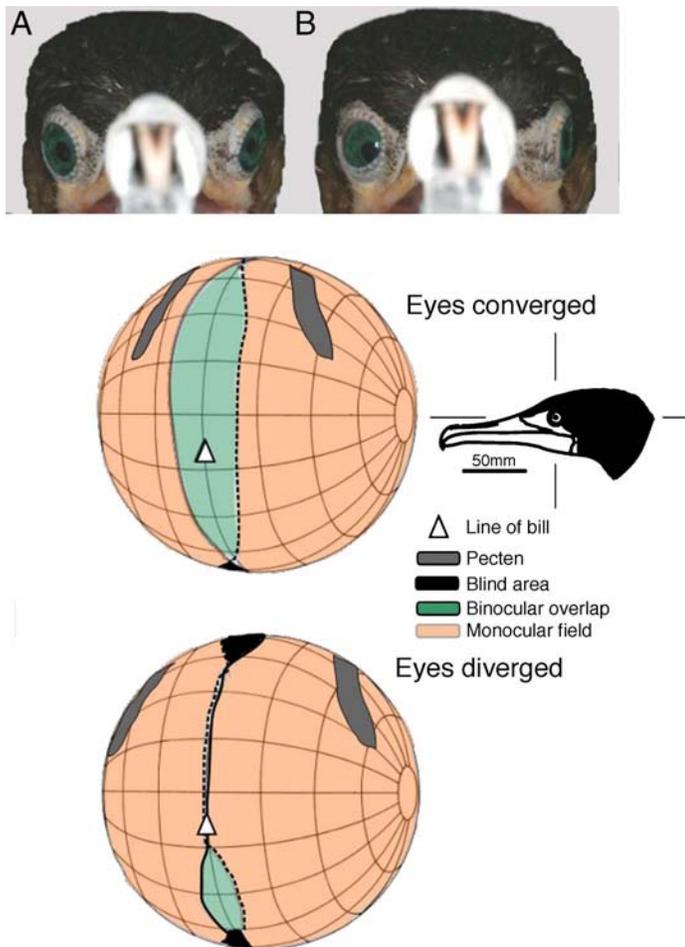
Figure 5. The effect of eye movements on visual fields illustrated by data from great cormorants. (A) The eyes have adopted a symmetrical position with respect to the median sagittal plane of the skull; in panel B, one eye has rotated more forwards and the other eye has rotated toward the rear of the head. Such eye movements occur spontaneously although they do adopt an apparent symmetrical "resting" position. (C, D) Presentation of the visual fields in which features are mapped onto the surface of a globe using conventional latitude and longitude coordinates (grid at 20° intervals). It should be imagined that the bird's head is at the center of the sphere and the visual field features are mapped onto the globe surface. In panel C, the eyes are converged and the binocular field is symmetrical about the median sagittal plane with the bill projecting centrally below the horizontal; in panel D, the eyes are fully diverged; binocularity is abolished although the visual field margins of the two eyes just meet and so vision to the front of the head is maintained; there is a small area of binocularity retained below the bill.

Binocular fields and giant retinal ganglion cells

A study of the characteristics and distribution of retinal ganglion cells in Manx Shearwaters *Puffinus puffinus* (Hayes, Martin, & Brooke, 1991) showed a distinct area within the peripheral retina comprised of large and widely spaced cells. It was shown that this area projected exclusively into the lower half of the binocular field. The function of such large and widely spaced ganglion cells is unclear but they certainly suggest that visual resolution is low and it was conjectured that their function is primarily concerned with the detection of movement. Although there have been many descriptions of retinal ganglion cell distributions in birds, these have typically concentrated upon central regions serving vision in lateral visual fields. However, an investigation of retinal ganglion cells in the peripheral retinas of chicks of pigeons, domestic chicken, and quail *Coturnix coturnix* (Campaña & Suburo, 1981) also reported "giant" ganglion cells to be present, although the visual projections were not known. Clearly it would be of value to know whether large ganglion cells projecting into the binocular region are found more generally in bird retinas. Certainly their presence suggests that visual capacities of the binocular field are different from those of lateral visual fields and may be more associated with the detection of movement rather than resolution.

Binocular vision and behavior

Binocular vision and the control of bill position

As noted above (Maximum binocular field widths show a high degree of interspecific convergence section), there are exceptions to the general finding that maximum binocular field width across most avian taxa lies between 15° and 30°. In owls, maximum binocular field widths are larger, typically close to twice this width and an explanation for these wider binocular fields is discussed below. However, maximum binocular field widths about half those found in the majority of birds occur in some species. In these birds, maximum binocular field widths ≤10° occur, eye movements are absent, and the projection of the bill falls outside (below) the visual field. The binocular field width at the horizontal in front of the head (when the head is held in its resting posture or in the approximate position adopted during flight) may be as narrow as 5°. Such maximum binocular field widths have been described in a number of duck species (mallards, northern shovelers, pink-eared ducks) and in some long bill shore birds (woodcocks).

Although the ducks and shorebirds are phylogenetically quite distinct (Hackett et al., 2008), a factor that is common to these particular ducks and to woodcocks is that they do not employ vision in the guidance of foraging. These ducks are primarily filter feeders; woodcocks employ tactile cues received from touch receptors clustered around the bill tip to detect invertebrates buried in soft substrates. Furthermore, these birds do not provision their young or build elaborate nests. Both shorebirds and wildfowl hatch chicks that are precocial self-feeders, and their nests are usually simple scrapes, perhaps lined with loose material, that does not require visually guided construction using the
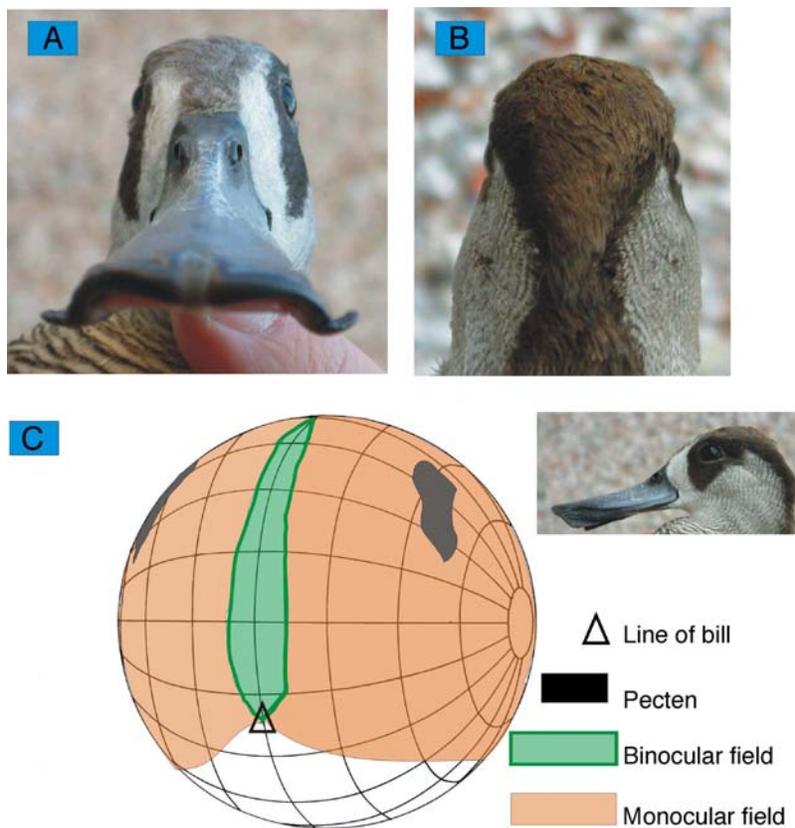
Figure 6. Eye position and visual fields in a species whose visual fields provide total panoramic vision of the space around the head (periscopy), illustrated by data from pink-eared ducks. (A and B) Frontal and rear views of the head on the horizontal plane showing that the eyes are placed high and laterally in the skull. To the rear of the head, the eyes can be seen. This arrangement of the eyes produces a narrow binocular field that extends from just above the bill through more than 180° to behind the head. (C) Presentation of the anterior portion of the visual field showing that the projection of the bill falls at the periphery (i.e., the birds may be able to just see their bill tip), and the narrow binocular field which extends through the full extent of the fontal region and continues behind the head.

bill. Thus, these birds appear to be freed from the requirement of placing the bill accurately with respect to a discrete target. The result is that natural selection appears to have favored the evolution of eyes that are positioned high in the skull providing comprehensive visual coverage of the celestial hemisphere (periscopy). This is achieved through narrow binocular overlap that extends throughout the median sagittal plane from close to the horizontal in front of the head to the horizontal behind the head (Figure 6).

It should be noted that not all ducks or shorebirds have such visual field topography even though they have precocial chicks and do not build elaborate nests. However, those ducks and shorebirds that lack periscopy employ visual cues in their foraging. Thus, in blue ducks, which forage on invertebrates within the water column or on rock surfaces, which presumably requires accurate visual guidance of the bill toward individual items, the eyes are more forwardly placed. A 20° wide binocular field is found and periscopy is absent. Wigeons have a similar visual field topography to blue ducks but these birds require accurate visually guided bill placement to mediate their feeding which involves selective grazing of ground

vegetation. Other longer billed shorebirds, such as red knots, which also employ tactile cues from their bill tips to find buried prey, do not have periscopic vision and their bill tip projects centrally within the binocular field as in other visually guided foragers. This is explained by the fact that when breeding, these birds switch to visually guided foraging of surface and aerial insects, a feeding technique which presumably requires accurate visual guidance of the bill (Martin & Piersma, 2009). Thus, these species reinforce the contention that frontal binocular fields of between 15° and 30° in maximum width, and in which the bill projects approximately centrally, have their prime function in the accurate visual guidance of the bill.

Flamingos are also an instructive species concerning the role of binocular vision in accurate bill positioning. These birds are well known for their technique of filter feeding in which the head is held inverted close to the feet. In effect, a feeding flamingo walks forwards with its inverted head facing backwards. It was predicted that such a technique would favor the evolution of periscopy since this would allow the birds to effectively see "forwards," i.e., behind the back of the head, when moving with the head upside

down. This, however, is not the case; flamingos have a visual field of similar topography to those of precision pecking species discussed in the Maximum binocular field widths show a high degree of interspecific convergence section. The interpretation of this visual field arrangement in flamingos is that although accurate bill position is not necessary for adult birds when feeding themselves, it is necessary for the provisioning of chicks. Young flamingos have a long period (up to 12 weeks) of dependence upon the adults during the time when the filter-feeding bill structures are developing. During this period, chicks are fed by the adults dripping "esophageal milk" into the chick's open mouth. This drip feeding requires highly accurate bill positioning by both adult and chick, and this would seem to be achieved through similar visual field topography to that required for accurate pecking or lunging.

Binocular vision and the control of flight

While the above examples and arguments make the strong case that frontal binocular field topography in birds is primarily associated with the accurate visual control of bill position during foraging or chick provisioning, the examples of the filter-feeding ducks and woodcocks make an equally strong case that the 15°–30° width of the binocular visual fields seen in the majority of birds is not primarily associated with the control of locomotion. Thus, filter-feeding ducks and tactile-feeding woodcocks have very narrow binocular fields of only 5°–10° maximum width. However, they often fly within structurally complex habitats. Furthermore, mallards and shovelers have high wing loadings and consequently are among some of the fastest birds in level powered flight and they takeoff and land at high velocity. Woodcocks nest on the ground and forage within woodlands. They fly beneath the canopy but they have a relatively low wing loading, consequently their velocity at takeoff and when landing and the velocity of level flight are lower than those of the ducks. Mallards typically nest on the ground under scrub but they may also place their nests in trees. Thus, it can be concluded that frontal binocular fields less than 10° wide and even as narrow as 5° are sufficient for the control of flight and landing at relatively high velocities and in structurally complex (e.g., woodland) habitats.

Binocular vision and nocturnality

The principal evidence linking nocturnality, predation, and the degree of binocularity is based upon observations of owls which are noted for their nocturnal hunting of vertebrate and invertebrate prey. Casual observations give the impression that these birds have forward facing eyes and a frontal binocular field of large horizontal width. However, it is clear that although the binocular field widths of owls are probably the widest described in any bird species, the binocular fields (48° in tawny owls; Figure 1) are narrower than appears from casual observation and do not match those of primates with which they are often compared. Also it is clear that unlike primates the optic axes are far from parallel (Figure 1) as has often been assumed (see for example Pettigrew and Konishi's, 1976, diagram of eye placement in barn owls). The most important comparisons are with other birds that are strictly nocturnal in their activity. Oilbirds and Kiwi are the most nocturnal of all bird species but they do not have "owl-like" visual fields.

Oilbirds live in caves by day from which they emerge after dusk and return before dawn, thus they never see daylight. Their eyes exhibit retinal adaptations (tiered rod receptors) and optical adaptations (low f-number, large entrance pupil area), which suggest that their sensitivity is close to the theoretical limit for vertebrate eyes. However, the eyes are laterally placed (optic axes diverge by 140°) and the binocular region is vertically long and narrow with a maximum width of 30° occurring close to the horizontal plane.

Kiwi are nocturnal and flightless, yet their binocular fields are the smallest yet recorded in a bird and quite unlike those of owls. They are only 60° in vertical extent and with a narrow maximum width of 10°. There is evidence that the kiwi visual system is evolutionarily regressive with olfactory, tactile, and possibly auditory cues being used to guide foraging and general behavior rather than vision. However, the involvement of non-visual cues to guide prey detection and foraging is a common feature of strictly nocturnal bird species with audition complementing vision in owls, and olfaction and audition are used by oilbirds.

Three groups of nocturnally foraging birds that appear to be guided primarily by visual cues are plovers, nightjars, and night herons. Plovers (Charadridae) are a taxon of shorebirds which forage for soil or surface invertebrates typically at night apparently using visual cues for their detection. As in oilbirds and owls, the eyes of plovers are enlarged, which is readily interpreted as an adaption to maximize sensitivity (Land & Nilsson, 2002; Martin, 1982), such that they do not fit wholly within the orbits and protrude from the skull and are unable to move. In the case of golden plovers, specialized wings of bone, apparently unique to the Charadriidae, extend above the orbit as an anchor for the eyes (Martin & Piersma, 2009). All of these adaptations suggest that high-sensitivity vision plays an essential role in these birds' nocturnal behavior. However, the binocular field of golden plovers exhibit marked similarity to those of a wide range of species that use visual guidance in their foraging (pecking or lunging at individual items) at higher daytime light levels (e.g., pigeons, red knot, cormorants), with a vertically long and narrow (maximum width ≈20°) binocular field in which the bill projects approximately centrally.

Another group of nocturnally active birds that use vision to guide their foraging are nightjars (Caprimulgidae). These birds take aerial insects and are aided in their visual detection of prey items by an enlarged gape and a system of

rictal bristles surrounding the gape which may act like a net to enlarge the catchment zone (Martin, 1990). Visual fields in these birds are vertically long and narrow, achieving a maximum width ≈20°, and are quite similar to species that use vision to control foraging using pecking or lunging. Thus, although nightjars are strictly nocturnal they do not show "owl-like" binocular visual field configurations that are distinct from those of diurnally active birds that employ vision to guide their foraging.

Night herons (*Nycticorax* spp. Ardeidae), as their name implies, forage primarily at night yet their visual fields show high similarity to those of herons that forage during day time and do not exhibit "owl-like" features (Katzir & Martin, 1998).

King penguins forage by both night and day. When foraging during the day, they do so at pelagic depths (200–300 m) where light levels are equivalent to those of night time at the surface. They too have large eyes and a low f-number that can be interpreted as an adaption to low light levels, but they too have a binocular field that is similar to those of diurnally active birds whose foraging is visually guided.

These comparisons among nocturnally active birds certainly suggest that there is not a simple relationship between the nocturnal habit and visual field topography. A wider frontal binocular field may occur in owls but it is not a common feature of nocturnally active birds and its occurrence in owls would seem to require an explanation beyond the correlation with nocturnal activity (this is discussed in more detail below).

Binocular vision and predation

The assumed association of a wide frontal binocular field with the predatory habit is also not supported by comparative evidence. Eagles (Accipitridae) are regarded as exemplars of the predatory habit during day time. Short-toed eagles are diurnal predators that are described in handbooks as having forward facing eyes and a wide binocular field. However, appearances are deceptive (Figure 4). The functional binocular field of these birds is vertically long and relatively narrow (maximum width 20°), a topography similar to those found in a wide range of birds, such as pigeons, common starlings, penguins, and cormorants, which forage using vision to guide pecking or lunging at prey. Video of prey capture shows that short-toed eagles take prey in their feet which are swung up into the binocular field just prior to prey seizure. Although this evidence is from a single species of diurnal raptor and further comparative data are required, it does show clearly that a simple correlation between a wide binocular field and the predatory habit does not occur in birds. Certainly it is clear that this eagle does not have visual fields with the same characteristics as owls (compare Figure 1 with Figure 4) and the assumption that both nocturnality and the predatory habit result in similar binocular field characteristics is erroneous.

Pecking and landing accuracy without binocular vision

In a series of experiments that involved assessing the accuracy with which a pigeon could peck a target in an operant conditioning task, Jäger and Zeigler (1991) showed that accuracy did not deteriorate when one eye was used compared to the accuracy achieved with the simultaneously use of both eyes.

Davies and Green investigated the visual information associated with accuracy of landing behavior in Pigeons and Harris Hawks (*Parabuteo unicinctus*; Davies & Green, 1994). Their principal conclusion was that a landing bird may employ a range of depth information (perhaps accommodation, convergence, tau, or binocular disparity) at close range to visually guide these behaviors but that global stereopsis is unlikely to be involved. This is because higher order processing that leads to the gain of relative depth information is a relatively slow process, and they argue that this is not fast enough to cope with the rapidly changing scene and speed of movements that are required as a flying bird prepares to land upon a target. Exactly how birds do control their behavior when landing is still not clear but Davies and Green (1994) suggest that a complex of multiple sources of information that may provide birds with distance cues to close objects are available to birds when using only one eye and thus do not involve binocularity.

Lateral and binocular vision

Attempting to ascribe possible functional specialization to binocular vision also needs to take account of the function of lateral vision and how visual control of behavior may be switched from lateral to frontal vision. Does binocular vision do things that lateral vision cannot do, and vice versa? Typically lateral vision has been seen as serving the detection of predators or conspecifics (Fernandez-Juricic, Erichsen, & Kacelnik, 2004) and indeed this was the prime function ascribed to it by Walls (1942) when he argued for factors that have resulted in "the retention of periscopy" (p. 291). However, it is now clear that lateral vision in birds has a prime role in sophisticated aspects of foraging and predator detection tasks, including the response to novel stimuli and the reliable separation of pertinent from distracting stimuli (Rogers, 2008). Moreover, it is also clear that the avian brain is functionally lateralized in the conduct of such tasks and that these are revealed by birds preferentially using their left and right eyes for different tasks (Rogers, 2008). This use of lateral vision is seen clearly in tasks where birds chose to examine different types of objects and scenes preferentially with the left or right eye rather than binocularly (Dharmaretnam & Andrew, 1994; Franklin & Lima, 2001; Koboroff, Kaplan, & Rogers, 2008; Mench & Andrew, 1986; Rogers, 1991). Moreover, even the task of a falcon stooping upon it prey seems to be under the control of lateral rather than frontal/binocular vision in that the birds approach along a curving path, which allows the prey

object to be kept in the central (lateral) vision of one eye until the final closure upon the prey object (Tucker, 2000; Tucker, Tucker, Akers, & Enderson, 2000). This use of lateral vision to detect an object and the control of behavior passing to the frontal field only when the object is in close proximity is similar to that already described above in thrushes (Montgomerie & Weatherhead, 1997), zebra finches (Bischof, 1988), pigeons (Bloch et al., 1988), and domestic chicks (Dharmaretnam & Andrew, 1994), all of which take items by detecting them when standing and pecking them from a surface. All of the above examples suggest that lateral and binocular visions are used for specific tasks and are not interchangeable in their function.

What is binocular vision for?

Behavioral functions of binocular vision

Evidence presented above suggests that the primary function of binocular fields in birds lies in the extraction of information used in the control of bill position and the timing of its opening in the final approach to a target, especially during feeding. In both ground feeding birds which are always close to their food items or falcons stooping upon prey from a distance, lateral vision appears to be used for the detection of items with behavioral control assigned to the binocular field only close to the moment of seizure (Bischof, 1988; Montgomerie & Weatherhead, 1997; Rogers, 2008; Tucker et al., 2000).

Visual control of pecking, snatching, or lunging

The visual control of bill position using the binocular field applies regardless of whether food procurement involves pecking at items on a surface (e.g., pigeons, ostriches, stone-curlews, starlings), snatching items from a surface (e.g., shearwaters, albatrosses, prions), lunging at prey items in air (e.g., nightjars), lunging at items on a surface (e.g., eagles, hornbills), lunging at items through a water surface (e.g., herons), or lunging at items within a water column (e.g., cormorants, penguins, blue-ducks). All of these feeding techniques require an accurate assessment of the position of an object as it is approached and an accurate estimate of time to contact that object in order to time the opening of the bill or feet.

Non-visual control of feeding: Tactile cues and filter feeding

In species that do not feed in these ways, the frontal binocular fields are very much reduced in width and the projection of the bill falls outside the visual field and these species have gained periscopy. This arrangement is found in species that filter feed (e.g., certain species of ducks) or in those that depend upon tactile cues to detect hidden prey (e.g., woodcocks and kiwi). These foraging modes do not require vision for the control of bill position with the consequence that natural selection has not favored the evolution of a binocular field of 15°–30° width in which the bill projects centrally or just below the center.

Nest construction and chick provisioning

Accurate visual control of bill position is necessary for activities other than feeding. Nest construction typically requires the procurement and manipulation of material using the bill. Provisioning chicks typically requires accurate visual assessment of the position of the chick's mouth and control of the bill in relation to the approach toward it. The case of the specialized chick feeding technique in the filter-feeding flamingos provides positive evidence for this role of binocular vision in the control of bill position during chick feeding. In many bird species, nests are simple scrapes which do not require elaborate construction, and chicks are precocial self-feeders that are not provisioned by their parents. Among those species with simple nests and precocial chicks are ducks (Anatidae) and shorebirds (Scolopacidae). This lack of a requirement for chick provisioning and elaborate nest construction in the filter-feeding ducks and in the tactile guided woodcocks provides evidence that when freed of the need for visual information for the guidance of the bill (for foraging, provisioning of chicks, and for nest construction), binocular fields do not encompass the projection of the bill. Furthermore, in these species, the width of the binocular field is reduced and periscopic vision has evolved. However, in those species of ducks and waders that require visual guidance of the bill in foraging, broader binocular fields surrounding the bill are present and periscopy is absent. This is despite these birds not needing visual guidance for chick provisioning or nest building. This also reinforces the argument that binocular vision is primarily concerned with the control of bill position in foraging.

Binocular vision and locomotion

Filter-feeding ducks and tactile-feeding woodcocks also provide evidence that the wider binocular fields of most birds are not associated primarily with the control of locomotion. These ducks and woodcocks are capable of rapid flight in complex habitats, yet they have frontal binocular overlap of less than 10° width. In the case of woodcocks, binocular field width is only about 5° in the horizontal plane, which defines the direction of travel in flight.

Visual inspection of items held in the bill

A further more specialized role for binocular vision may lie in the inspection of items held in the bill. In many species, although the bill tip projects approximately

centrally within the binocular field, it does not in fact intrude into the visual field, i.e., the birds cannot see their own bill tip. This is demonstrated clearly in ostriches that feed by accurate pecking. Despite the large size of their bill, it does not intrude into the visual field; binocularity starts just beyond the bill tip (Figure 7).

In some species, however, the bill does clearly intrude into the binocular field. This implies that the bird will be able to see what is held within the bill. This has been demonstrated in cormorants, black skimmers, hornbills, and starlings. Although these species are phylogenetically distinct and have quite different feeding techniques, they share a common problem in that they may procure potential food items with their bill before they know what they are, or in the case of starlings actually search for items between the
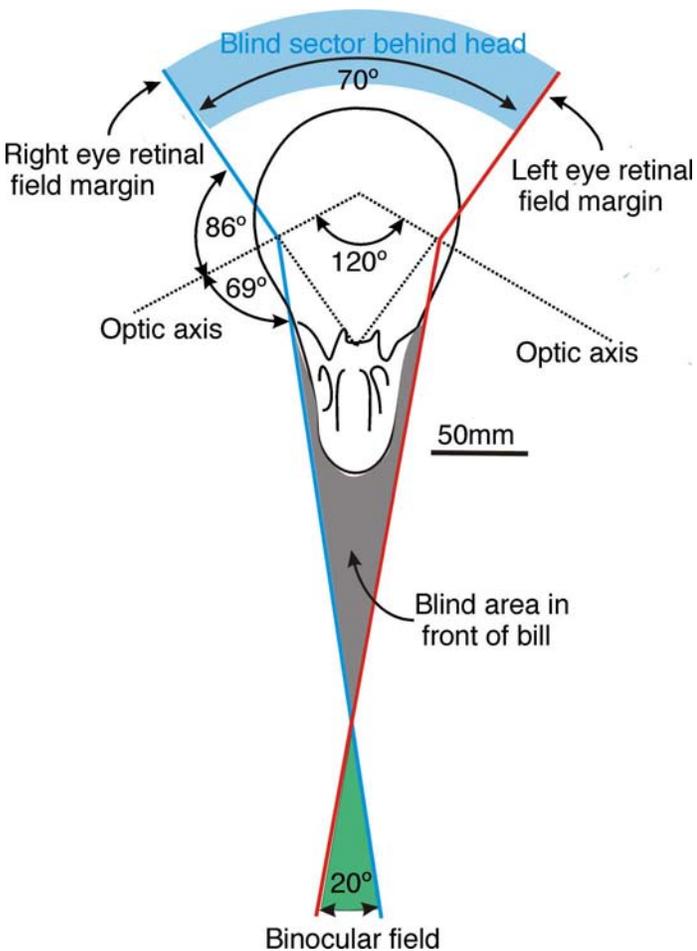

Figure 7. Schematic section through the head and visual fields showing how in some birds, although they have binocular vision about the bill, they cannot actually see their own bill tip. This is illustrated here by data from ostriches whose foraging technique involves precision pecking. It can be seen that the margins of the visual field of each eye only intersect about 150 mm beyond the bill tip. Thus, ostriches cannot see their own bill tip, and pecking is in fact ballistic with the eyes usually closed as the bill approaches its target.

opened mandibles. Thus, visually inspecting the procured items after capture or inspecting items that lie between the opened mandibles may be an essential facet of their feeding technique. In the case of cormorants, it is proposed that they often lunge at and capture prey at short range but they must do this before it is possible to fully identify the target. In effect, these birds lung at an escaping blur (White, Day, Butler, & Martin, 2007). Although such items have a high probability of being a food item, this can only be verified when brought to the surface in the bill and visually inspected (Martin et al., 2008). Black skimmers forage using a tactile technique in which the mandible is lowered into the water during flight, and bill closure is triggered when an object hits the mandible. This frequently results in non-edible items being caught and thus visual inspection of caught items is necessary before ingestion (Martin, McNeil, & Rojas, 2007).

Conclusion

The primary behavioral function of binocular vision in birds would appear to be for the control of bill position with respect to objects at close quarters and the control of bill opening when seizing or releasing those objects. The tasks in which these functions are employed are foraging, feeding young, and the manipulation of nest material. Secondarily, in some species, binocularity may be used for the visual inspection of objects held in the bill. Thirdly, binocular vision has a role in the control of locomotion (avoidance of more distant objects, preparation for landing) and this can be achieved with a binocular overlap as small as 5°.

Informational functions of binocular vision

The behaviors with which binocularity is associated would seem to require information that identifies an object as a target or an obstacle and information about the location of the target with respect to the animal, especially how location changes over time due to relative movement between target and animal.

The identity of a target is likely to have a significant cognitive component especially with respect to food objects, chick feeding, and nest materials, and this may be achieved primarily through lateral vision (Rogers, 2008). Target location, however, requires more generic information. This could be derived from a "percept of solidity" based upon binocular fusion and stereopsis. However, apart from the evidence of binocular neurons and stereopsis in owls, there is little evidence to support the idea that birds in general have either binocular fusion or stereopsis. Much of the evidence presented above argues against the assertion that birds have either global or local stereopsis. In particular, the finding that birds with eye movements frequently and spontaneously abolish their

binocular fields and that uniocular vision can control pecking as accurately as binocular vision suggests that birds' eyes may function independently (and indeed the left and right eyes may process information differently; Rogers, 2008) and that higher order information is not extracted from the simultaneous view of the same object by the two eyes. Thus, rather than try to find evidence of binocular fusion and stereopsis, it might be more parsimonious to consider what the function of binocularity could be if birds viewed objects diplopically within their binocular fields.

Binocular vision and optic flow-fields

For any bird, the vital information beyond recognition of an object is the accurate identification of its position and, if there is relative speed between the object and the observer, to gain information on time to contact. The actual distance of an object from a bird may be of little importance compared with knowing its direction and the time it may take to make contact with it. Such information is available from optic flow-fields (Lee, 1980; Lee & Lishman, 1977). Furthermore, it has been shown that gannets *Morus bassanus* and Hummingbirds (Tochilidae), when carrying out maneuvers that require accurate visual information regarding speed of approach to a target, appear to employ flow-field information (Lee & Reddish, 1981; Lee, Reddish, & Rand, 1991). In mammals, optic flow-field information is analyzed in the accessory optic system (Giolli, Blanks, & Lui, 2006) and pretectum (Gamlin, 2006), and a similar accessory system has been identified in birds (McKenna & Wallman, 1985; Pakan & Wylie, 2006).

Flow-field information is potentially available from any pattern of optical flow across the retina; it is not necessarily associated with binocular portions of a visual field. However, information on direction of travel toward a target and time to contact a target can be derived most efficiently when travel is directly toward a target. This will result in an optical flow-field that expands symmetrically about the image of the target. This would seem to be the situation in the key tasks described above. For example, when pecking or lunging at an object, both position and time to contact need to be accurately specified. The essential consideration, however, is that a flow-field that symmetrically expands about an object directly ahead of the bird can only be achieved if the visual field of each eye extends contralaterally, i.e., across the median sagittal plane of the bird (Figure 1). Thus, the important consideration is *contralateral* vision, not *binocular* vision. Binocular vision can be seen simply as a by product of the need to have eyes that look forward across the median sagittal plane, not as an adaptation that has evolved specifically to achieve simultaneous views of the same object from slightly different positions. Binocular vision is perhaps irrelevant; what is important is contralateral vision.

From this perspective, other questions flow:

a. Do two eyes retrieving information from almost identical flow-fields provide more information than one eye? The evidence of apparently equal pecking accuracy using one and two eyes in pigeons (Jäger & Zeigler, 1991) suggests that the gain may not be significant; it may add little beyond redundancy.

b. Why does there appear to be convergence upon binocular fields of 15°–30° (perhaps more appropriately described as contralateral projections of 7.5°–15°)? This may represent the minimum symmetrical flow-field diameter necessary for accurate determination of time to contact at close quarters. The diameter of the flow-field for the control of flight alone, that is with respect to objects more remote from the bird, appears to be less than half this. The contralateral visual field projection in woodcocks is only 2.5°, but clearly this is sufficient to control these birds' gross body maneuvers with respect to obstacles.

Information is assumed to be extracted from "optic elements" within the flow-field (Gibson, 1986), and there may be an optimal density or number of elements for the extraction of specific information. However, the density and the number of elements would be ultimately determined by acuity or ganglion cell density as well as velocity of flow across the retina. Thus, unraveling the factors underlying the degree of contralateral projection of the visual field would require analysis of acuity (or ganglion cell density), the degree of contralateral projection, and the velocity of pecking/lunging movements. This relationship between resolution and optic elements that contribute to the flow-field may also explain why full use is not made of the available optic visual field to maximize the degree of contralateral projection (Figure 4; Evidence for the function of binocular vision in birds section). As suggested above, it is possible that the optical quality of peripheral optics (which serve frontal/binocular/contralateral vision) is low. Extension of the retinal field into the far periphery of the contralaterally projecting optical field (thus gaining a wider binocular field) would not provide additional information to enhance the accuracy of direction of travel or of time to contact.

Finally, the existence of giant widely spaced ganglion cells in the far periphery of the retina that project into the binocular field, admittedly described in detail in only a few species but of quite different phylogeny and ecology, also suggests that binocular/contralateral vision is concerned primarily with the detection of movement or flow-field information rather than resolution.

Binocularity in owls

Owls (Strigiformes) may be an exception. It was argued above that comparison of owl visual fields with those of

other nocturnally active birds and with other predatory birds strongly suggests that the wider binocular fields of owls are not a simple correlate of nocturnal activity or of the predatory habit. Although flow-field information would similarly be available to these birds as it is to others, binocularly driven neurons seem to be unique to owls (Iwaniuk & Wylie, 2006). They may have arisen in these birds because their specific behavioral ecology of nocturnality and predation is also associated with their unique possession of elaborate outer ears. The function of these ear structures in the accurate auditory localization of prey seems to be key to their ability to take active prey at night (Martin, 1986b). This was first described by Payne (1971) in barn owls *Tyto alba* and subsequently demonstrated and further investigated in a range of owl species (Konishi & Knudsen, 1979; Martin, 1986b; Norberg, 1978). In owls, it seems possible that the more frontal eyes (though note that they are still laterally placed and binocular vision is still peripheral vision, Figure 1) can be seen as the result of selection for large eyes (Martin, 1986b, 1990), alongside selection for large and elaborate outer ear structures (Norberg, 1978). These enlarged eyes and ears must be accommodated within a small skull; indeed it is possible to see part of the back of the eye through an owl's ear openings, indicating that eyes and ears are very tightly packed within the skull. Rhetorically, it can be asked, "Where else can the eyes be positioned?" The enlarged outer ears may simply prevent more lateral placement of the eyes and it is this which has resulted in greater binocularity. It may be that these eyes' fixed positions have provided the substrate for neurons that are binocularly driven and frontally projecting. In other birds, eye mobility is retained, prohibiting the evolution of binocularly driven neurons with fixed visual fields. Where enlarged eyes are fixed in the skulls of other nocturnal forms (such as some of the plovers and oilbirds), there are no elaborate outer ear structures that prohibit more lateral placement of eyes with the result that extensive lateral visual fields and narrower frontal fields occur.

General conclusion

Binocular vision in birds would appear to be primarily for the control of bill or feet position in foraging (pecking, lunging, taking prey) and/or in the feeding of young. Secondarily, in some species binocularity may be used for the inspection of items held by the bill or lying between the opened mandibles. Only thirdly is binocular vision used for the control of locomotion (flight, obstacle avoidance, and landing). These functions are placed in this order since in species which do not use vision for the control of bill or feet position during foraging, or for provisioning their young, frontal binocularity is very much reduced and periscopy is achieved by having binocular vision from in front to directly behind the head. If there is an "urge" or "imperative" in visual field topography among birds, it is for periscopy (more comprehensive visual coverage of the space around the head), not for binocularity.

The second answer to "What is binocular vision for?" is that binocularity functions to provide information on the direction of travel and time to contact a target. However, this information can be provided by each eye independently, and for this reason it might be more appropriate to refer to "contralateral vision" rather than "binocular vision" since the latter brings with it assumptions concerning the percept of solidity and stereopsis with which binocular vision in birds does not appear to be associated. Thus, in the majority of birds, the function of binocularity would seem to lie in what each eye does independently (i.e., diplopically) rather than in what the two eyes might be able to do together.

Appendix A

Bird species in which visual fields have been determined using the ophthalmoscopic reflex method (14 orders; 21 families; 34 spp.). Species are listed in the orders and taxonomic sequence of del Hoyo et al. (1992) in the *Handbook of the Birds of the World*. English names are those recommended by Gill and Wright (2006). Type 1 fields are those with maximum binocular field widths of 15°–30° in which the bill projects approximately centrally and there is a blind sector behind the head. They are associated with foraging that involves pecking, lunging, or snatching items. Type 2 fields are those with maximum binocular field widths of ≤10° in which the bill projects outside (below) the visual field; there is a binocular field that extends from directly in front to directly behind the head providing total visual coverage of the hemisphere about the head (periscopy). Type 3 fields are those with a maximum binocular field widths of ≈50° and a substantial blind area behind the head; to date they have been described only in owls. Type 4 fields are those reported to date only in Kiwi, in these the binocular field has a maximum width of ≈10° but there is a substantial blind area behind the head.

Struthioniformes
Struthionidae
Ostrich *Struthio camelus* (Type 1) (Martin & Katzir, 1995)
Apterygidae
Brown Kiwi *Apteryx mantelli* (Type 4) (Martin, Wilson et al., 2007)
Great Spotted Kiwi *Apteryx haastii* (Type 4) (Martin, Wilson et al., 2007)
Sphenisciformes
Spheniscidae
Humboldt penguin *Spheniscus humboldti* (Type 1) (Martin & Young, 1984)

King Penguin *Aptenodytes patagonicus* (Type 1) (Martin, 1999)

Procellariiformes
Diomedeidae
Black-browed albatross *Diomedea melanophris* (Type 1) (Martin, 1998)

Grey headed albatross *Diomedea chrysostoma* (Type 1) (Martin, 1998)

Procellariidae
Manx shearwater *Puffinus puffinus (Type1)* (Martin & Brooke, 1991)

White-chinned petrel *Procellaria aequinoctialis* (Type 1) (Martin & Prince, 2001)

Antarctic prion *Pchyptila desolata (Type1)* (Martin & Prince, 2001)

Pelecaniformes
Phalacrocoracidae
Great Cormorant *Phalacrocorax carbo (Type1)* (Martin et al., 2008)

Ciconiiformes
Ardeidae
Cattle egret *Bubulcus ibis (Type1)* (Martin & Katzir, 1994a)

Reef heron *Egretta gularis (Type1)* (Martin & Katzir, 1994a)

Squacco heron *Ardeola ralloides (Type1)*(Martin & Katzir, 1994a)

Black-crowned night heron *Nycticorax nycticorax (Type1)* (Katzir & Martin, 1998)

Phoenicopteriformes
Phoenicopteridae
Lesser Flamingo *Phoeniconaias minor (Type1)* (Martin, Jarrett, Tovey, & White, 2005)

Anseriformes
Anatidae
Mallard *Anas platyrhynchos* (Type 2) (Martin, 1986c)

Northern Shoveler *Anas clypeata* (Type 2) (Guillemain, Martin, & Fritz, 2002)

Wigeon *Anas penelope* (Type 1) (Guillemain et al., 2002)

Blue Duck *Hymenolaimus malacorhynchos* (Type 1) (Martin, Wilson et al., 2007)

Pink-eared Duck *Malacorhynchus membranaceus* (Type 2) (Martin, Wilson et al., 2007)

Falconiformes
Accipitridae
Short-toed snake eagle *Circaetus gallicus* (Type 1) (Martin & Katzir, 1999)

Charadriiformes
Burhinidae
Stone-curlew *Burhinus oedicnemus* (Type 1) (Martin & Katzir, 1994b)

Scolopacidae
Woodcock *Scolopax rusticola* (Type 2) (Martin, 1994)

Red knot *Calidris canutus (Type1)* (Martin & Piersma, 2009)

Charadriidae
European golden plover *Pluvialis apricaria (Type1)* (Martin & Piersma, 2009)

Laridae
Black skimmer *(Type1) Rynchops niger* (Martin, Wilson et al., 2007)

Columbiformes
Columbidae
Pigeon *Columba livia* (Type 1) (Martin & Young, 1983)

Strigiformes
Strigidae
Tawny owl *Strix aluco* (Type 3) (Martin, 1984)

Caprimulgiformes
Steatornithidae
Oilbird *Steatornis caripensis* (Type 1) (Martin, Rojas, Ramirez, & McNeil, 2004)

Caprimulgidae
Paraque *Nyctidromus albicollis* (Type 1) (Martin, Rojas, Ramirez Figueroa, & McNeil, 2004)

Coraciiformes
Bucerotidae
Southern Ground Hornbill *Bucorvus leadbeateri* (Type 1) (Martin & Coetzee, 2004)

Southern Yellow-billed Hornbill *Tockus leucomelas* (Type 1) (Martin & Coetzee, 2004)

Passeriformes
Sturnidae
European Starling *Sturnus vulgaris* (Type 1) (Martin, 1986a)

Acknowledgments

References

Beecher, W. J. (1978). Feeding adaptations and evolution in the starlings. *Bulletin of the Chicago Academy of Sciences, 11,* 269–298.

Bischof, H.-J. (1988). The visual field and visually guided behavior in the zebra finch (*Taeniopygia guttata*). *Journal of Comparative Physiology A, 163,* 329–337.

Bloch, S., Jäger, R., Lemeignant, M., & Martinoya, C. (1988). Correlations between ocular saccades and

headmovements in walking pigeons. *The Journal of Physiology, 406,* 173.

Campaña, H., & Suburo, A. (1981). The periphery of the avian retina: Specializations of the layer of ganglion cells and their axons. *Revue Canadienne de Biologie Experimentale, 40,* 187–194.

Davies, M. N. O., & Green, P. R. (1994). Multiple sources of depth information: An ecological approach. In M. N. O. Davies & P. R. Green (Eds.), *Perception and motor control in birds: An ecological approach* (pp. 339–356). Berlin: Springer-Verlag.

del Hoyo, J., Elliott, A., & Sargatal, J. (1992). *Handbook of the birds of the world* (vol. 1). Barcelona: Lynx Edicions.

Dharmaretnam, M., & Andrew, R. J. (1994). Age-and stimulus-specific use of right and left eyes by domestic chick. *Animal Behaviour, 48,* 1395–1406.

Feare, C. J. (1984). *The starling.* Oxford: Oxford University Press.

Fernandez-Juricic, E., Erichsen, J. T., & Kacelnik, A. (2004). Visual perception and social foraging in birds. *Trends in Ecology & Evolution, 19,* 25–31. [PubMed]

Fox, R., Lehmkuhle, S. W., & Bush, R. C. (1977). Stereopsis in the falcon. *Science, 197,* 79–81. [PubMed]

Franklin, W. E., III., & Lima, S. L. (2001). Laterality in avian vigilance: Do sparrows have a favourite eye? *Animal Behaviour, 62,* 879–885.

Frost, B. J., Goodale, M. A., & Pettigrew, J. D. (1983). A search for functional binocularity in the pigeon. *Society for Neuroscience Abstracts, 9,* 823.

Frost, B. J., Wylie, D. R., & Wang, Y. C. (1994). The analysis of motion in the visual systems of birds. In M. N. O. Davies & P. R. Green (Eds.), *Perception and motor control in birds: An ecological approach* (pp. 248–269). Berlin: Springer-Verlag.

Gamlin, P. D. (2006). The pretectum: Connections and oculomotor-related roles. *Progress in Brain Research, 151,* 379–405. [PubMed]

Gibson, J. J. (1986). *The ecological approach to visual perception.* Hove: Erlbaum.

Gill, F., & Wright, M. (2006). *Birds of the world: Recommended English names.* London: Christopher Helm.

Giolli, R. A., Blanks, R. H., & Lui, F. (2006). *Progress in Brain Research, 151,* 407–440.

Guillemain, M., Martin, G. R., & Fritz, H. (2002). Feeding methods, visual fields and vigilance in dabbling ducks (Anatidae). *Functional Ecology, 16,* 522–529.

Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C., Braun, E. L., Braun, M. J., et al. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science,* 1763–1768. [PubMed]

Hayes, B., Martin, G. R., & Brooke, M. D. L. (1991). Novel area serving binocular vision in the retinae of procellariiform seabirds. *Brain, Behavior and Evolution, 37,* 79–84. [PubMed]

Iwaniuk, A. N., & Wylie, D. R. W. (2006). The evolution of stereopsis and the Wulst in caprimulgiform birds: A comparative analysis. *Journal of Comparative Physiology A, 192,* 1313–1326. [PubMed]

Jäger, R., & Zeigler, H. P. (1991). Visual field organization and peck localization in the pigeon (*Columba livia*). *Behavioural Brain Research, 45,* 65–69. [PubMed]

Katzir, G., & Martin, G. R. (1998). Visual fields in the Black-crowned Night Heron *Nycticorax nycticorax*: Nocturnality does not result in owl-like features. *Ibis, 140,* 157–162.

Koboroff, A., Kaplan, G., & Rogers, L. J. (2008). Lateralization and antipredtor behaviour in Australian magpies (*Gymnorhina tibicen*). *Brain Research Bulletin, 76,* 304–306.

Konishi, M., & Knudsen, E. I. (1979). The Oilbird: Hearing and echolocation. *Science, 204,* 425–427. [PubMed]

Land, M. F., & Nilsson, D.-E. (2002). *Animal eyes.* Oxford: Oxford University Press.

Lee, D. N. (1980). The optic flow field: The foundation of vision. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 290,* 169–179. [PubMed]

Lee, D. N., & Lishman, R. (1977). Visual control of locomotion. *Scandinavian Journal of Psychology, 18,* 224–230. [PubMed]

Lee, D. N., & Reddish, P. E. (1981). Plummeting gannets: A paradigm of ecological optics. *Nature, 293,* 293–294.

Lee, D. N., Reddish, P. E., & Rand, D. T. (1991). Aerial docking by Hummingbirds. *Naturwissenschaften, 78,* 526–527.

Livezey, B. C., & Zusi, R. L. (2007). Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy: II. Analysis and discussion. *Zoological Journal of the Linnean Society, 149,* 1–95.

Martin, G. R. (1982). An owl's eye: Schematic optics and visual performance in *Strix aluco* L. *Journal of Comparative Physiology A, Sensory, Neural, and Behavioral Physiology, 145,* 341–349.

Martin, G. R. (1984). The visual fields of the tawny owl, *Strix aluco* L. *Vision Research, 24,* 1739–1751. [PubMed]

Martin, G. R. (1986a). Sensory capacities and the nocturnal habit of owls (Strigiformes). *Ibis, 128,* 266–277.

Martin, G. R. (1986b). The eye of a passeriform bird, the European starling (*Sturnus vulgaris*): Eye movement amplitude, visual fields and schematic optics. *Journal of Comparative Physiology A, Sensory, Neural, and Behavioral Physiology, 159,* 545–557.

Martin, G. R. (1986c). Total panoramic vision in the mallard duck, *Anas platyrhynchos*. *Vision Research, 26,* 1303–1306.

Martin, G. R. (1990). *Birds by night*. London: T & A D Poyser.

Martin, G. R. (1994). Visual fields in woodcocks *Scolopax rusticola* (Scolopacidae; Charadriiformes). *Journal of Comparative Physiology A, Sensory, Neural, and Behavioral Physiology, 174,* 787–793.

Martin, G. R. (1998). Eye structure and amphibious foraging in albatrosses. *Proceedings of the Royal Society of London B: Biological Sciences, 265,* 1–7.

Martin, G. R. (1999). Eye structure and foraging in King Penguins *Aptenodytes patagonicus*. *Ibis, 141,* 444–450.

Martin, G. R. (2007). Visual fields and their functions in birds. *Journal of Ornithology, 148,* S547–S562.

Martin, G. R., & Brooke, M. D. L. (1991). The eye of a procellariiform seabird, the Manx shearwater, *Puffinus puffinus*: Visual fields and optical structure. *Brain, Behavior and Evolution, 37,* 65–78.

Martin, G. R., & Coetzee, H. C. (2004). Visual Fields in Hornbills: Precision-Grasping and Sunshades. *Ibis, 146,* 18–26.

Martin, G. R., Jarrett, N., Tovey, P., & White, C. R. (2005). Visual fields in Flamingos: Chick-feeding versus filter-feeding. *Naturwissenschaften, 92,* 351–354.

Martin, G. R., Jarrett, N., & Williams, M. (2007). Visual fields in Blue Ducks and Pink-eared Ducks: Visual and tactile foraging. *Ibis, 149,* 112–120.

Martin, G. R., & Katzir, G. (1994a). Visual fields and eye movements in herons (Ardeidae). *Brain, Behavior and Evolution, 44,* 74–85. [PubMed]

Martin, G. R., & Katzir, G. (1994b). Visual fields in the stone curlew *Burhinus oedicnemus*. *Ibis, 136,* 448–453.

Martin, G. R., & Katzir, G. (1995). Visual fields in ostriches. *Nature, 374,* 19–20.

Martin, G. R., & Katzir, G. (1999). Visual field in Short-toed eagles *Circaetus gallicus* and the function of binocularity in birds. *Brain, Behavior and Evolution, 53,* 55–66. [PubMed]

Martin, G. R., McNeil, R., & Rojas, L. M. (2007). Vision and the foraging technique of skimmers (Rynchopidae). *Ibis, 149,* 750–759.

Martin, G. R., & Piersma, T. (2009). Vision and touch in relation to foraging and predator detection: Insightful contrasts between a plover and a sandpiper. *Proceedings of the Royal Society of London B: Biological Sciences, 276,* 437–445. [PubMed]

Martin, G. R., & Prince, P. A. (2001). Visual fields and foraging in Procellariiform seabirds: Sensory aspects of dietary segregation. *Brain, Behavior and Evolution, 57,* 33–38. [PubMed]

Martin, G. R., Rojas, L. M., Ramirez Figueroa, Y. M., & McNeil, R. (2004). Binocular vision and nocturnal activity in Oilbirds (*Steatornis caripensis*) and Pauraques (*Nyctidromus albicollis*): Caprimulgiformes. *Ornithologia Neotropical, 15,* 233–242.

Martin, G. R., Rojas, L. M., Ramirez, Y., & McNeil, R. (2004). The eyes of oilbirds (*Steatornis caripensis*): Pushing at the limits of sensitivity. *Naturwissenschaften, 91,* 26–29. [PubMed]

Martin, G. R., White, C. R., & Butler, P. J. (2008). Vision and the foraging technique of great cormorants *Phalacrocorax carbo*: Pursuit or flush-foraging?. *Ibis, 150,* 39–48. [PubMed] [Article]

Martin, G. R., Wilson, K. J., Wild, M. J., Parsons, S., Kubke, M. F., & Corfield, J. (2007). Kiwi forego vision in the guidance of their nocturnal activities. *PLoS One, 2,* e198. [PubMed] [Article]

Martin, G. R., & Young, S. R. (1983). The retinal binocular field of the pigeon (*Columba livia*): English racing homer. *Vision Research, 23,* 911–915. [PubMed]

Martin, G. R., & Young, S. R. (1984). The eye of the Humboldt Penguin, *Spheniscus humboldti*: Visual fields and schematic optics. *Proceedings of the Royal Society of London B: Biological Sciences, 223,* 197–222. [PubMed]

McFadden, S. A. (1994). Binocular depth perception. In M. N. O. Davies & P. R. Green (Eds.), *Perception and motor control in birds: An ecological approach* (pp. 54–73). Berlin: Springer-Verlag.

McKenna, O. C., & Wallman, J. (1985). Accessory optic system and pretectum of birds: Comparisons with those of other vertebrates. *Brain, Behavior and Evolution, 26,* 91–116. [PubMed]

Mench, J. A., & Andrew, R. J. (1986). Lateralization of a food search task in the domestic chick. *Behavioural and Neural Biology, 46,* 107–114. [PubMed]

Micheli, D., & Reperant, J. (1982). Thalmo-hyperstriatal projections in the pigeon (*Columba livia*) as demonstrated with retrograde double-labelling with fluorescent tracers. *Brain Research, 245,* 365–371.

Montgomerie, R., & Weatherhead, P. J. (1997). How do robins find worms? *Animal Behaviour, 54,* 143–151. [PubMed]

Norberg, R. A. (1978). Skull asymmetry, ear structure and function and auditory localization in Tengmalm's owl, *Aegolius funereus*. *Philosophical Transactions of the Royal Society of London B: Biological Sciences, 282B,* 325–410.

Pakan, J. M. P., & Wylie, D. R. W. (2006). Two optic flow pathways from the pretectal nucleus lentiformis mesencephali to the cerebellum in pigeons (*Columba livia*). *Journal of Comparative Neurology, 499,* 732–744. [PubMed]

Payne, R. S. (1971). Acoustic location of prey by barn owls. *Journal of Experimental Biology, 54,* 535–573. [PubMed] [Article]

Perisic, M., Mihailovic, J., & Cuenod, M. (1971). Electrophysiology of contralateral and ipsilateral projections to the Wulst of the pigeon (*Columba livia*). *International Journal of Neuroscience, 2,* 7–14. [PubMed]

Pettigrew, J. D. (1979). Binocular visual processing in the owl's telencephalon. *Proceedings of the Royal Society of London B: Biological Sciences, 204,* 435–454. [PubMed]

Pettigrew, J. D., & Konishi, M. (1976). Neurons selective for orientation and binocular disparity in the visual Wulst of the barn owl (*Tyto alba*). *Science, 193,* 675–677. [PubMed]

Rogers, L. J. (1991). Development of lateralization. In R. J. Andrew (Ed.), *Neural and behavioural plasticity: The use of the domestic chicken and a model* (pp. 503–535). Oxford: Oxford University Press.

Rogers, L. J. (2008). Development and function of lateralization in the avian brain. *Brain Research Bulletin, 76,* 235–244. [PubMed]

Schwab, I. R., & Hart, N. S. (2003). In the search for stereopsis. *British Journal of Ophthalmology, 87,* 1205.

Tucker, V. A. (2000). The deep fovea, sideways vision and spiral flight paths in raptors. *Journal of Experimental Biology, 203,* 3745–3754. [PubMed] [Article]

Tucker, V. A., Tucker, A. E., Akers, K., & Enderson, J. H. (2000). Curved flight paths and sideways vision in peregrine falcons (*Falco peregrinus*). *Journal of Experimental Biology, 203,* 3755–3763. [PubMed] [Article]

van der Willigen, R. F., Frost, B. F., & Wagner, H. (1998). Stereoscopic depth perception in the owl. *NeuroReport, 9,* 1233–1237. [PubMed]

Walls, G. L. (1942). *The vertebrate eye and its adaptive radiation*. Michigan: Cranbrook Institute of Science.

White, C. R., Day, N., Butler, P. J., & Martin, G. R. (2007). Vision and foraging in cormorants: More like herons than hawks? *PLoS One, 2,* e639. [PubMed] [Article]

Wilson, P. (1980). The organisation of the visual hyperstriatum in the domestic chick: Topology and topography of the visual projection. *Brain Research, 188,* 319–332. [PubMed]