Comparative Study of Visual Pathways in Owls (Aves: Strigiformes)

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Abstract

Although they are usually regarded as nocturnal, owls exhibit a wide range of activity patterns, from strictly nocturnal, to crepuscular or cathemeral, to diurnal. Several studies have shown that these differences in the activity pattern are reflected in differences in eye morphology and retinal organization. Despite the evidence that differences in activity pattern among owl species are reflected in the peripheral visual system, there has been no attempt to correlate these differences with changes in the visual regions in the brain. In this study, we compare the relative size of nuclei in the main visual pathways in nine species of owl that exhibit a wide range of activity patterns. We found marked differences in the relative size of all visual structures among the species studied, both in the tectofugal and the thalamofugal pathway, as well in other retinorecipient nuclei, including the nucleus lentiformis mesencephali, the nucleus of the basal optic root and the nucleus geniculatus lateralis, pars ventralis. We show that the barn owl *(Tyto alba)*, a species widely used in the study of the integration of visual and auditory processing, has reduced visual pathways compared to strigid owls. Our results also suggest there could be a trade-off between the relative size of visual pathways and auditory pathways, similar to that reported in mammals. Finally, our results show that although there is no relationship between activity pattern and the relative size of either the tectofugal or the thalamofugal pathway, there is a positive correlation between the relative size of both visual pathways and the relative number of cells in the retinal ganglion layer.

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Introduction

In birds, several studies have shown that differences in activity pattern are correlated with differences in the visual system. For example, compared to diurnal birds, nocturnal species tend to exhibit a number of adaptations that serve to enhance visual sensitivity, such as: a larger cornea relative to total eye size, high rod:cone photoreceptor ratios, relatively fewer retinal ganglion cells (RGCs) and a relatively smaller optic foramen [Tansley and Erichsen, 1985; Rojas de Azuaje et al., 1993; Hall and Ross, 2007; Hall et al., 2009; Iwaniuk et al., 2010a; Corfield et al., 2011]. Although within most avian orders activity pattern

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is fairly uniform (e.g. all members are diurnal), in a few orders species vary widely in activity pattern along the nocturnal-diurnal gradient. One order of specific interest in this respect is that of the owl: Strigiformes. Although owls are generally regarded as nocturnal birds, only about 30% of owl species are strictly nocturnal; the rest of the species exhibit a wide range of activity patterns, from crepuscular or cathemeral, to diurnal [Martin, 1986; Voous, 1988; del Hoyo et al., 1999; König and Weick, 2008]. Past studies have shown that these differences in activity pattern are associated with the organization of the visual system of these birds. Owl species with different activity patterns differ in their photoreceptor density, shape and depth of the fovea [Oehme, 1961], rod:cone ratios, critical flicker fusion frequency [see Lisney et al., 2011] and number and distribution of RGCs [Oehme, 1961; Bravo and Pettigrew, 1981]. Recently, a detailed study [Lisney et al., 2012] of the eyes and retinas of eight species of owl with different activity patterns showed that nocturnal owls have relatively larger corneal diameters than diurnal species. Further, it was shown by these authors that the topographic distribution of neurons in the RGC layer among owl species is related to both activity pattern and habitat preference. Species that live in open habitats and/or are more diurnal have well-defined, elongated visual streaks, while more nocturnal and/or forest-dwelling species have a poorly defined visual streak and exhibit a more radially symmetrical retinal topography pattern.

In recent years, several studies have shown that different demands on the visual system in birds are correlated with variation in the relative size of visual areas in the brain [Iwaniuk and Wylie, 2006, 2007; Iwaniuk et al., 2008, 2010b; Corfield et al., 2011]. However, despite the compelling evidence that differences in activity patterns among owl species are reflected in the organization of the eyes, there has been no attempt so far to correlate these differences with variation in the relative size of visual regions in the brain. Owls, like all vertebrates, have several visual pathways from the retina to the brain [Bravo and Pettigrew, 1981; Bagnoli et al., 1990]. One of the main visual pathways in birds is the tectofugal pathway, which is comprised of three main structures: optic tectum (TeO), nucleus rotundus (nRt) and entopallium (E). This pathway is involved in processing brightness, colour, pattern discrimination, simple motion and looming stimuli [Wang et al., 1993; Bischof and Watanabe, 1997; Sun and Frost, 1998; Husband and Shimizu, 2001; Nguyen et al., 2004]. A second pathway is the thalamofugal pathway, which includes the dorsal thalamus and the wulst (also known as the hyperpallium) [Reiner et al., 2004].

In owls, contralateral retinal projections reach the lateral part of the nucleus dorsolateralis anterios thalami (DLL) [Karten and Nauta, 1968; Karten, 1969], which in turn give rise to ipsilateral and contralateral projections to the visual wulst [Karten et al., 1973]. Several studies show that cells in the visual wulst of owls respond to binocular disparity which suggest that this structure is involved in stereopsis [e.g. Pettigrew and Konishi, 1976; Pettigrew, 1979; Wagner and Frost, 1994; Nieder and Wagner, 2001; Baron et al., 2007]. This is further supported by the presence of an enlarged wulst in owls and other bird species with large binocular fields [Iwaniuk et al., 2008]. There is also some evidence that the visual wulst is involved in the representation of illusory contours [Nieder and Wagner, 1999] and learning of visual discrimination tasks [Budzynski and Bingman, 2004]. Other retinorecipient nuclei in birds include the nucleus lentiformis mesencephali (LM) and the nucleus of the basal optic root (nBOR) [Karten et al., 1977; Fite et al., 1981; McKenna and Wallman, 1985; Gamlin and Cohen, 1988], which are involved in the generation of the optokinetic response [Frost et al., 1994], as well as the nucleus geniculatus lateralis, pars ventralis (GLv), the function of which remains largely unclear [but for some proposed functions see Maturana and Varela, 1982; Gamlin et al., 1984; Wakita et al., 1992; Vega-Zuniga et al., 2011].

Given the variation among activity patterns, eye morphology and retinal organization in owls, there are likely corresponding differences in the size of retinorecipient and other brain regions processing visual information. For example, several studies suggest that a transition from diurnality to nocturnality results in a reduction of the number of RGCs and a reduction of the tectofugal pathway [Kay and Kirk, 2000; Kirk and Kay, 2004; Hall et al., 2009; Iwaniuk et al., 2010b; Corfield et al., 2011]. Therefore, we would expect that nocturnal owl species have a relative smaller tectofugal pathway than more diurnal species. With respect to the thalamofugal pathway, Bravo and Pettigrew [1981] compared the amount of RGCs that project to the TeO and the thalamus between the burrowing owl *(Athene cunicularia)* and the barn owl *(Tyto alba)*. These authors found that while both species have a peak density of RGCs that project to the TeO of around 10,000 cells/mm^2, the peak density of RGCs that project to the thalamus is much smaller in the barn owl, around 4,000 cells/mm^2. These two species differ in activity pattern with the burrowing owl being diurnal while the barn owl is strictly nocturnal, but they also belong to the two different families within the order Strigiformes: Strigidae and Tytonidae, respectively [del

Hoyo et al., 1999; König and Weick, 2008]. On the basis of Bravo and Pettigrew's [1981] results, we expect differences in the relative size of the thalamofugal pathway, between diurnal and nocturnal species and/or between strigid and tytonid owls. Finally, we have recently shown that asymmetrically eared owls have enlarged auditory pathways when compared to symmetrically eared ones [Gutiérrez-Ibáñez et al., 2011]. Several studies in mammals [Eisenberg, 1981; Baron et al., 1996; Barton, 1998; Catania, 2005] have shown that trade-offs can occur between different sensory systems, and species that rely heavily on one sensory modality (with a corresponding enlargement of associated brain areas) have relatively smaller brain regions dedicated to other sensory modalities. If such a 'trade-off' exists in owls, we expect that asymmetrically eared owls will have relatively smaller visual pathways compared to symmetrically eared owls because of the presumably greater reliance on auditory rather than visual cues when foraging in asymmetrically eared species. Here, we test all of the predictions discussed above across nine owl species that vary in activity pattern.

Methods

We measured the relative volume of eight visual nuclei in 12 specimens representing nine species of owl and the tawny frogmouth *(Podargus strigoides)*, a caprimulgiform (see below). All specimens were provided to us dead by conservation authorities or wildlife veterinarians, or were donated by other researchers. In some cases the head without the eyes was provided to us. Owls are classified into two extant families: Tytonidae (barn and bay owls) and Strigidae ('typical' owls) [del Hoyo et al., 1999; König and Weick, 2008]. The barn owl is the most studied species with respect to the visual system [for review see Harmening and Wagner, 2011] and we include one individual in our analyses as a representative tytonid owl. Within the Strigidae, we examined eight species: the northern saw-whet owl *(Aegolius acadicus)*, the short-eared owl *(Asio flammeus)*, the snowy owl *(Bubo scandiacus)*, the great horned owl *(Bubo virginianus)*, the great grey owl *(Strix nebulosa)*, the barred owl *(Strix varia)*, the northern hawk owl *(Surnia ulula)* and the boobook owl *(Ninox boobook)*. This last species was not included in our previous work on the relative size of the auditory system [Gutiérrez-Ibáñez et al., 2011] or retinal organization of owls [Lisney et al., 2012] because we had no access to the eyes of this specimen and there was some tissue damage to the cochlear nuclei during processing of the brain. Finally, we included the tawny frogmouth *(P. strigoides)* for comparative purposes. This is a nocturnal bird with feeding habits and morphology similar to owls [Cleere, 1998; Higgins, 1999]. They have frontally oriented eyes with similar binocular overlap to owls [Wallman and Pettigrew, 1985] and the relative size of the brain, telencephalon and wulst are similar to that of owls [Iwaniuk and Hurd, 2005; Iwaniuk and Wylie, 2006; Iwaniuk et al., 2008].

For all specimens, the head was immersion-fixed in 4% paraformaldehyde in 0.1 M phosphate buffer. The brain was then extracted, weighed to the nearest milligram, cryoprotected in 30% sucrose in phosphate buffer, embedded in gelatine and sectioned in the coronal or sagittal plane on a freezing stage microtome at a thickness of 40 μm. Sections were collected in 0.1 M phosphate-buffered saline, mounted onto gelatinized slides, stained with thionine and coverslipped with Permount. The olfactory bulbs were intact in all the specimens we collected and sectioned. All brains were cut following bird brain atlases [e.g. Karten and Hodos, 1967; Puelles et al., 2007] in which the brainstem ends at the same rostrocaudal point as the cerebellum. In this manner, brain measurements were consistent among our specimens. Photomicrographs of every fourth section were taken throughout the rostrocaudal extent of each nucleus using a Retiga EXi *FAST* Cooled mono 12-bit camera (Qimaging, Burnaby, B.C., Canada) and OPENLAB Imaging system (Improvision, Lexington, Mass., USA) attached to a compound light microscope (Leica DMRE, Richmond Hill, Ont., Canada). Measurements of all the nuclei were directly from these photos with ImageJ (NIH, Bethesda, Md., USA; http://rsb.info.nih.gov/ij/) and volumes were calculated by multiplying the area in each section by the thickness of the section (40 μm) and the sampling interval. For those species represented by more than one specimen (table 1), the average of the measurements was taken as the species' given value. Brain volume for each specimen was calculated by dividing the mass of the brain by the density of brain tissue (1.036 g/mm^3) [Stephan, 1960] as in previous studies [Iwaniuk and Wylie, 2006; Iwaniuk et al., 2007, 2008, 2010b].

We measured the volume of all the nuclei comprising the two main visual pathways in birds (see Introduction), the tectofugal pathway (TeO, nRt and E) and the thalamofugal pathway (DLL and wulst). Additionally, we measured the relative size of three retinorecipient nuclei, LM, nBOR and GLv in order to assess whether differences in the relative size of visual areas between owl species apply to all retinorecipient areas or are independent for each pathway. We also tested for a correlation between the relative volume of all the visual nuclei measured in this study and the relative volume of auditory pathways for some of the same species, which were obtained from Gutiérrez-Ibáñez et al [2011]. The total relative volume of auditory pathways is the sum of the relative volume of the nucleus angularis, the nucleus magnocellularis, the nucleus laminaris, the posterior part of the dorsal lateral lemniscus, the anterior part of the dorsal lateral lemniscus, the ventral part of the lateral lemniscus, the superior olive, inferior colliculus and the nucleus ovoidalis.

Activity Pattern

We classified the nine different owl species measured in this study into three different activity pattern categories following the same classification used in our previous work with the same species (table 1) [for details see Lisney et al., 2012]. Briefly, species where classified as: (1) diurnal, meaning active during the day in photopic conditions, (2) crepuscular, meaning active during dawn and dusk periods and (3) nocturnal, meaning active during the night in scotopic conditions. Within the crepuscular category there is some variation as some species can be classified as crepuscular-nocturnal while others as crepuscular-diurnal [for details see Lisney et al., 2012]. It should also be noted that the short-eared owl is included in the crepuscular category even though it can be

Table 1. List of the owl species surveyed, sample sizes, volumes of the brain and all nuclei measured

Common name	Species	n	Activity pattern	Brain volume mm³	TeO mm³	nRt mm³	E mm³	DLL mm	Wulst mm³	GLv mm³	nBOR mm³	LM mm³
Barn owl	*T. alba*	1	Nocturnal	5,849.80	136.510	2.926	7.111	5.479	509.071	1.326	0.660	3.374
Saw-whet owl	*A. acadicus*	2	Nocturnal	2,999.93	68.542	2.618	6.769	6.884	783.317	2.313	0.737	2.748
Short-eared owl	*A. flammeus*	1	Crepuscular	6,221.04	99.163	3.860	12.583	8.345	795.418	1.593	0.779	3.138
Great grey owl	*S. nebulosa*	1	Crepuscular	13,433.39	161.304	6.250	26.655	16.421	1,880.845	3.921	1.431	5.537
Barred owl	*S. varia*	1	Nocturnal	12,727.12	166.642	7.248	24.206	13.908	2,036.382	3.719	1.562	5.783
Great horned owl	*B. virginianus*	3	Crepuscular	17,199.09	277.015	9.711	34.883	18.545	2,617.419	3.510	2.640	5.977
Snowy owl	*B. scandiacus*	3	Diurnal	17,345.97	286.041	12.158	58.802	26.475	3,561.186	2.540	1.830	8.369
Hawk owl	*S. ulula*	1	Diurnal	9,408.30	204.755	7.678	29.798	13.332	1,544.342	1.907	1.182	4.213
Boobook owl	*N. boobook*	1	Nocturnal	6,338.80	148.150	5.503	15.800	10.499	1,503.680	2.153	2.214	4.281
Tawny frogmouth	*P. strigoides*	1	Nocturnal	5,311	290.880	8.948	38.000	5.935	1,226.890	1.320	2.561	1.914

considered crepuscular-cathemeral because some reports suggest that this species is most active around dawn and dusk [Clark, 1975; Voous, 1988; Reynolds and Gorman, 1999; König and Weick, 2008] whereas others have reported that this owl is active at various times of the day and night [Clark, 1975; del Hoyo et al., 1999].

Borders of Visual Nuclei

The borders of the different nuclei were determined based on descriptions of the nuclei in the literature (see below) and several stereotaxic atlases [Karten and Hodos, 1967; Stokes et al., 1974; Matochik et al., 1991; Puelles et al., 2007] (www.bsos.umd.edu/psyc/Brauthlab/atlas.htm). Figure 1 shows examples of the visual nuclei in several owl species. Detailed descriptions of the borders of TeO, nRt, E, GLv, LM and nBOR can be found in previous works [Iwaniuk and Wylie, 2007; Iwaniuk et al., 2010b]. For the borders of the lateral part of the nucleus DLL, we measured the area distinguished by the presence of densely packed, darkly stained cells (fig. 1d). We chose this area because according to the results of Bagnoli et al. [1990], this corresponds to the retinorecipient part of DLL in owls. This is in contrast to the more lateral and dorsal part of DLL, which shows less densely packed and less darkly stained cells, and does not receive retinal projections (fig. 1d) [Bagnoli et al., 1999]. For the borders of the wulst we followed Iwaniuk et al. [2008], which include the hyperpallium apicale, the nucleus interstitialis hyperpallii apicalis and the hyperpallium densocellulare (fig. 1e). It must be noted that this includes both the visual portions of the wulst as well as the rostral most part of it, which is not visual but rather receives somatosensory information [Karten et al., 1978; Manger et al., 2002; Wild et al., 2008]. Figure 1e shows an example of the borders of the wulst in an owl.

RGC Distribution and Total Number

We also compared the relative size of the different visual pathways to both the topographic distribution and total number of neurons in the RGC layer for the different species of owls, using data from Lisney et al. [2012]. To the best of our knowledge, similar data have not been published for the tawny frogmouth or the boobook owl and we had no access to retinas of either of these species, so we were not able to include them in this part of our analysis. Retinal topography is related to activity pattern in owls, with more diurnal species having a well-defined, elongated visual

streak, while more nocturnal species have a poorly defined visual streak and a more radially symmetrical arrangement [Lisney et al., 2012]. The pattern can be quantified using a 'H:V ratio'; the ratio of the maximum horizontal (H) and vertical (V) extent of the area enclosed by an isodensity contour line [Stone and Keens, 1980; Fischer and Kirby, 1991]. In this sense, a perfectly circular distribution of RGCs would result in an H:V ratio of 1, whereas a visual streak results in an H:V ratio greater than 1. We also compared the relative size of visual pathways with the number of cells in the RGC layer reported by Lisney et al. [2012]. The RGC layer in the retina contains not only RGCs, but also displaced amacrine cells [Bravo and Pettigrew, 1981; Hayes, 1984; Chen and Naito, 1999], which account for about 50% of the cells in the ganglion cell layer in the barn owl [Wathey and Pettigrew, 1989]. In addition, a population of displaced RGCs resides in the amacrine cell layer in birds [Karten et al., 1977; Reiner et al., 1979; Fite et al., 1981]. As detailed in Lisney et al. [2012], we were unable to reliably distinguish amacrine from RGCs within the RGC layer, so the total number of cells in the RGC layer is an overestimate of RGC number. Because the number of cells in the brain correlates positively with the absolute size of the brain [reviewed in Herculano-Houzel, 2011] we divided the total number of cells in the RGC layer by the brain volume of each species as a way to account for the differences in cell numbers related to the size of each species.

Statistical Analyses

In many comparative studies dealing with relative size of brain structures, allometric effects are accounted for by comparing residuals from least-square linear regressions between the structures and body mass or brain volume [e.g. Iwaniuk et al., 2005, 2006; Iwaniuk and Wylie, 2007]. With a relatively small number of species, such comparisons become problematic because a single data point can have a huge influence on the slope and intercept of an allometric line. Instead, we have taken a qualitative approach by examining the relative size of each nucleus as a percentage of overall brain volume. Also, in recent years comparative analyses have used phylogenetically corrected statistics [e.g. Garland et al., 1992, 2005] to account for possible phylogenetic effects. The small number of species examined herein has low statistical power that would be even further reduced with such a correction. The low sample size of each of our activity pattern subgroups further constrains our statistical power, therefore making such phylogenetic corrections impractical. Instead, we compared the results of a hi-
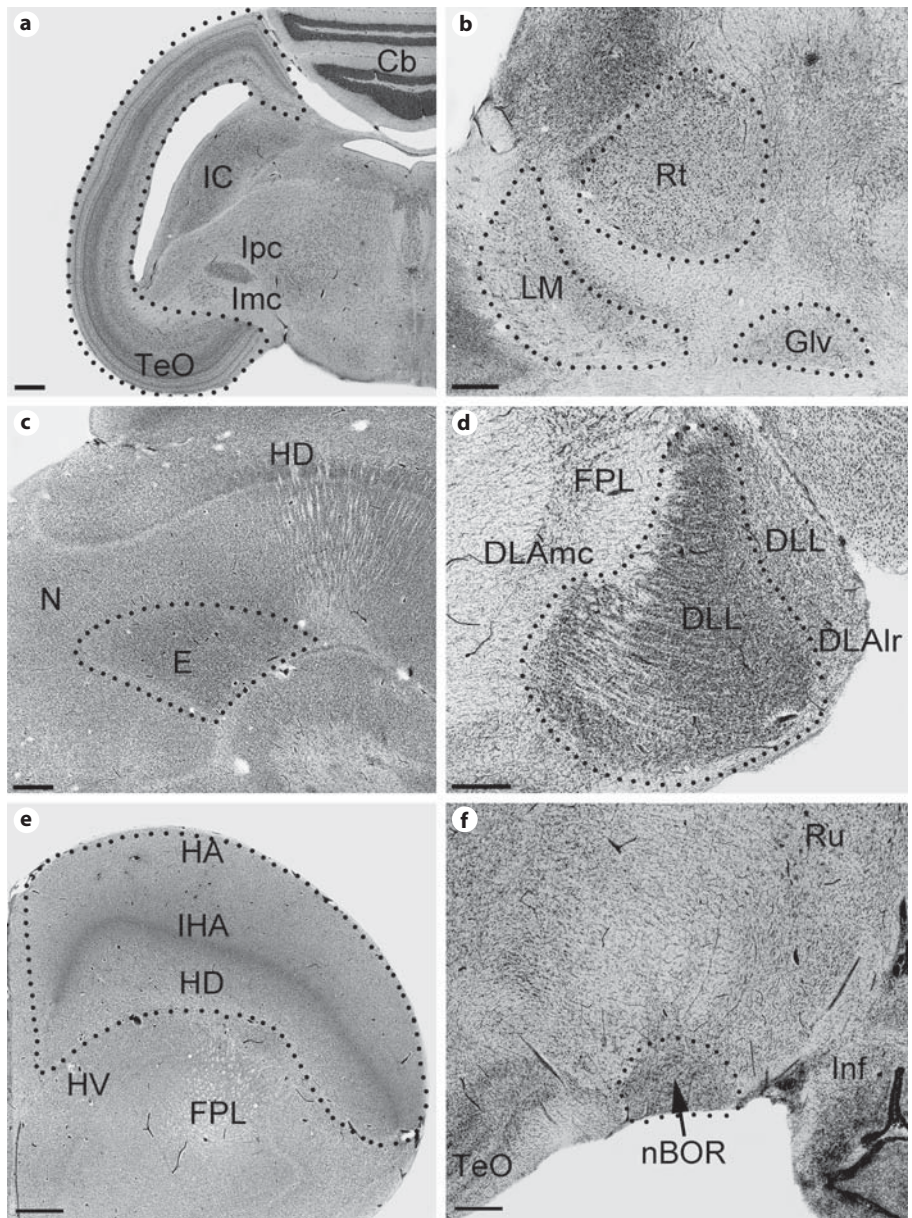
Fig. 1. Photomicrographs of coronal sections through the different components of the tectofugal pathway in owls. **a** The TeO of the northern hawk owl *(S. ulula)*. Scale bar = 800 μm. **b** The nRt of the great horned owl *(B. virginianus)*. Scale bar = 600 μm. **c** The E in the short-eared owl *(A. flammeus)*. Scale bar = 800 μm. **d** The dotted lines show the portion of the nucleus DLL measured (see Methods for details) in the northern hawk owl *(S. ulula)*. Scale bar = 400 μm. **e** The three components of the wulst, the hyperpallium apicale (HA), the nucleus interstitialis hyperpallii apicalis (IHA) and the hyperpallium densocellulare (HD) also in the northern hawk owl. **f** The borders of the nBOR in the snowy owl *(B. scandiacus)*. Scale bar = 600 μm. DLAmc = Nucleus dorsolateralis anterior, pars magnocellularis; DLAlr = nucleus dorsolateralis anterior, pars lateralis rostralis; FPL = fasciculus prosencephali lateralis; HV = hyperstriatum ventral; Ipc = parvocellular part of the nucleus isthmi; Imc = magnocellular part of the nucleus isthmi; IC = inferior colliculus; LM = nucleus lentiformis mesencephali; N = nidopallium; Ru = nucleus ruber; Inf = infundibulum.

erarchical cluster analysis to the most complete phylogenetic tree currently available for owls [Wink et al., 2008]. Using a similar approach to Iwaniuk and Hurd [2005], we performed a hierarchical cluster analysis of the proportional size of all auditory nuclei measured, with JMP (Version 7, SAS Institute Inc., Cary, N.C., USA). Although the dendrograms produced by hierarchical cluster analyses are based on similarities among species, comparing the dendrogram with a phylogeny of the species of interest can reveal whether interspecific differences have arisen largely through phylogenetic relatedness or independent evolution [Iwaniuk and Hurd, 2005; Gutiérrez-Ibáñez et al., 2011]. Here, we show the results generated using an average linkage method, but the dendrograms arising from other linkage methods (e.g. Ward's and UPGMA) shared the same topology.

Results

We found marked differences in the relative size of all visual brain structures among the species studied (fig. 2). In the thalamofugal pathway, the boobook and the northern saw-whet owls have the largest DLL relative volume (fig. 2a), more than twice the size of that of the barn owl, the species with the smallest relative volume. The situation is very similar regarding the wulst, which was largest in the boobook and the northern saw-whet owls and smallest in the barn owl (fig. 2b). In the case of the TeO the tawny frogmouth has the largest relative volume, al-

most twice that of the two closest owl species (the boobook and the northern saw-whet owl; fig. 2c), and more than four times larger than the owls with the smallest TeO, the great grey owl and the barn owl. The situation is similar for the Rt and E, the other components of the tectofugal pathway. The relative size of both of these structures is four to five times greater in the tawny frogmouth, compared to the owls (fig. 2d, e). Among owls, as with the TeO, the boobook and the northern saw-whet owls have the largest relative Rt volume (fig. 2d), but in the case of E, the owls with the largest relative volume are the snowy and northern hawk owls.
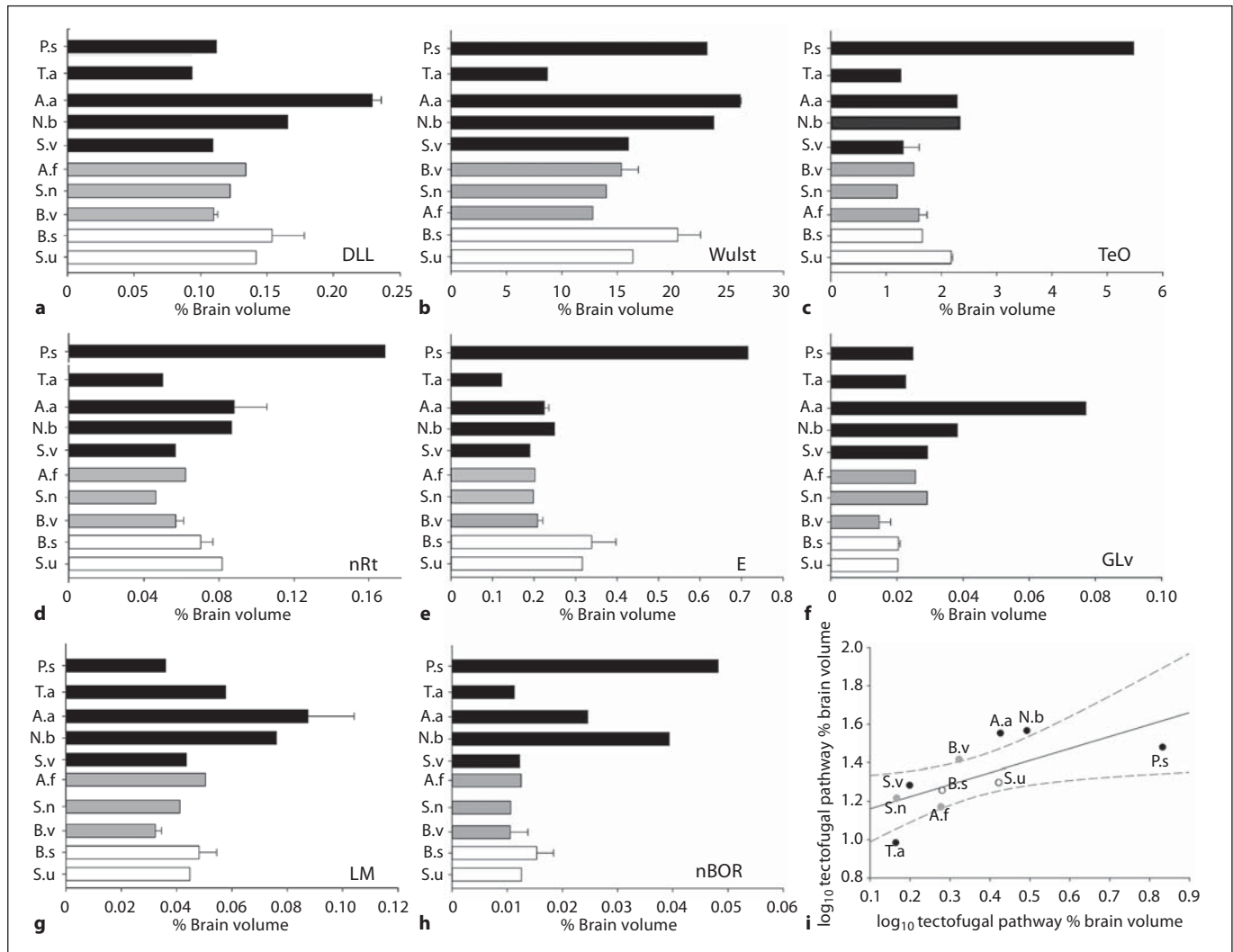

Fig. 2. Bar graphs showing the relative size of visual nuclei in the tawny frogmouth *(P. strigoides)* and nine species of owls expressed as a percentage of total brain volume. **a** Nucleus DLL. **b** Wulst. **c** TeO. **d** nRt. **e** E. Bar graphs also show the relative size of three additional retinorecipient nuclei in the same species: nucleus GLv (**f**), nucleus LM (**g**) and nBOR (**h**). The shading of the bars shows the activity pattern of each species: black = nocturnal, grey = crepuscular, white = diurnal. **i** A logarithmic scatter plot of the total volume of the thalamofugal pathway expressed as a percentage of total brain volume, plotted as a function of the total volume of the tectofugal pathway expressed as a percentage of total brain volume in the same species as above. The solid line indicates the least squares linear regression line for all species and the dotted lines are the 95% confidence interval around the regression line. The colour of the dot indicates the activity pattern of each species: black = nocturnal, grey = crepuscular, white = diurnal. T.a = Barn owl *(T. alba)*; A.a = northern saw-whet owl *(A. acadicus)*; A.f = short-eared owl *(A. flammeus)*; S.n = great grey owl *(S. nebulosa)*; S.v = barred owl *(S. varia)*; B.v = great horned owl *(B. virginianus)*; B.s = snowy owl *(B. scandiacus)*; S.u = northern hawk owl *(S. ulula)*; N.b = boobook owl *(N. boobook)*; P.s = tawny frogmouth *(P. strigoides)*.

We also found marked differences in the relative size of the other three visual nuclei we measured. In the case of GLv, the northern saw-whet owl has the largest relative volume, almost four times that of the great horned owl, the species with the smallest relative volume (fig. 2). For LM (fig. 2f) the boobook and northern saw-whet owls have the largest relative volumes, about twice that of other species. Finally, in the case of nBOR, the situation is more similar to the structures in the tectofugal pathway; the tawny frogmouth has the largest relative volume, followed by the boobook and northern saw-whet owls.

Figure 2i shows a scatterplot of the logarithm of the total relative volume of the tectofugal pathway (TeO + Rt + E) versus the total relative volume of the thalamofugal pathway (DLL + wulst) among the species studied. We found a significant positive correlation between the relative volume of these two pathways ($R^2 = 0.472$, $F_{1,8} = 7.148$, $p < 0.05$). This is also true when the tawny frogmouth is excluded ($R^2 = 0.619$, $F_{1,7} = 11.391$, $p < 0.05$). The barn owl appears as an outlier as it falls well below the confidence intervals with both the smallest tectofugal and thalamofugal pathways.

Visual Pathways and Neurons in the RGC Layer

We found no correlation between H:V ratio and the relative volume of any of the nuclei belonging to either the thalamofugal pathway or the tectofugal pathway (table 2), nor with the total volume of the thalamofugal pathway (table 2; fig. 3a) or the tectofugal pathway (table 2; fig. 3b).

We found a significant positive correlation between the relative volume of all the visual nuclei measured (tectofugal pathway + thalamofugal pathway + GLv + LM + nBOR) and the total number of RGC layer neurons, relative to brain volume ($R^2 = 0.523$, $F_{1,8} = 6.586$, $p < 0.05$; fig. 3c). Finally, figure 3d shows a scatterplot of the relative size of all the visual brain structures measured plotted against the total volume of all auditory nuclei measured in Gutiérrez-Ibáñez et al. [2011]. We found no correlation between the total volumes of the visual and auditory pathways ($R^2 = 0.0449$, $F_{1,7} = 0.282$, $p = 0.614$). In this comparison, the northern saw-whet owl appears as an outlier with both enlarged visual and auditory areas. When this owl is excluded, there is a significant, negative correlation between the total volume of all auditory and visual areas among the remaining species ($R^2 = 0.736$, $F_{1,6} = 13.960$, $p < 0.05$).

Lastly, we compared a dendrogram resulting from a hierarchical cluster analysis with a molecular phylogeny of the owl species we examined. Figure 4a depicts the phylogenetic relationships among the nine owl species used in this study [Wink et al., 2008] and figure 4b illustrates the similarity among the nine species based on a cluster analysis of the relative size of all visual brain

Table 2. Results of linear regressions between H:V ratio and the relative volume of TeO, nRt, E, DLL, wulst, total volume of the tectofugal pathway (TeO + Rt + E) and thalamofugal pathway (DLL + wulst)

Nuclei	R^2	$F_{1,8}$	p
GLv	0.0352	0.219	0.656
Wulst	0.252	2.698	0.139
TeO	0.0376	0.234	0.645
nRt	0.00246	0.0148	0.907
E	0.105	0.703	0.434
Tectofugal pathway	0.0793	0.517	0.499
Thalamofugal pathway	0.0000119	0.0000716	0.994

Table 3. RGC numbers, average density and amount of RGCs relative to brain volume for some of the owl species surveyed

Common name	Species	n	Total RGCs	Average RGC density, cells/mm²	RGCs number/brain volume, cells/mm³
Barn owl	*T. alba*	1	1,271,450	6,064	217.35
Saw-whet owl	*A. acadicus*	2	1,948,100	9,840	619.85
Short-eared owl	*A. flammeus*	1	2,451,200	9,682	394.02
Great grey owl	*S. nebulosa*	1	5,313,825	13,285	395.57
Barred owl	*S. varia*	1	6,915,200	12,105	543.34
Great horned owl	*B. virginianus*	3	6,858,000	7,410	398.74
Snowy owl	*B. scandiacus*	3	5,973,200	9,967	344.36
Hawk owl	*S. ulula*	1	5,920,425	13,855	629.28

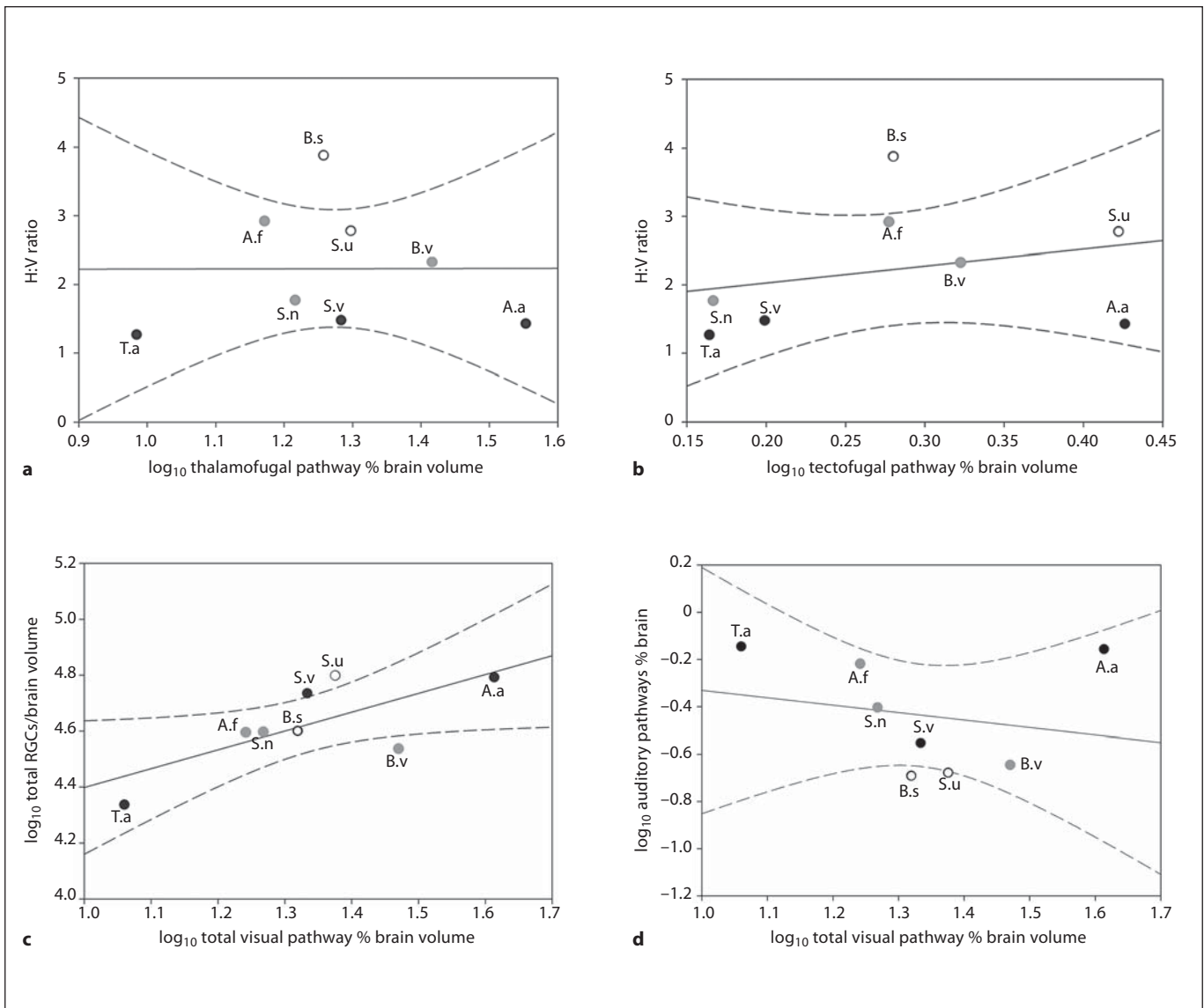RGC numbers and densities are from Lisney et al. [2012].

Fig. 3. Correlation between the relative volume of visual nuclei and retinal topography, RGC numbers and relative volume of auditory nuclei. **a** A scatter plot of H:V ratio plotted as a function of the logarithm of the total volume of the thalamofugal pathway expressed as a percentage of total brain volume for eight species of owl. **b** A scatter plot of H:V ratio plotted as a function of the logarithm of the total volume of the tectofugal pathway expressed as a percentage of total brain volume for eight species of owl. **c** A scatter plot of the logarithm of the total number of neurons in the retinal ganglion cell layer divided by the brain volume plotted as a function of the logarithm of the total volume of the visual pathway expressed as a percentage of total brain volume for the same eight species of owl. **d** A scatter plot of the logarithm of the total volume of the auditory nuclei expressed as a percentage of total brain (see Results) plotted as a function of the logarithm of the total volume of the visual pathway expressed as a percentage of total brain volume (see Results) for the same eight species of owl. The solid lines indicate the least squares linear regression line for all species and the dotted lines are the 95% confidence interval around the regression line. The colour of the dot indicates the activity pattern of each species: black = nocturnal, grey = crepuscular, white = diurnal. T.a = Barn owl *(T. alba)*; A.a = northern saw-whet owl *(A. acadicus)*; A.f = short-eared owl *(A. flammeus)*; S.n = great grey owl *(S. nebulosa)*; S.v = barred owl *(S. varia)*; B.v = great horned owl *(B. virginianus)*; B.s = snowy owl *(B. scandiacus)*; S.u = northern hawk owl *(S. ulula)*; N.b = boobook owl *(N. boobook)*; P.s = tawny frogmouth *(P. strigoides)*.

Fig. 4. Comparison of owls phylogeny and cluster analysis of the relative volume of all visual brain structures. **a** Phylogenetic relationships among the nine species used in this study based on Wink et al. [2009]. **b** The similarity between species based on a cluster analysis of the relative size of all visual brain structures. The coloured squares indicate the activity pattern of each species: black = nocturnal, grey = crepuscular, white = diurnal.
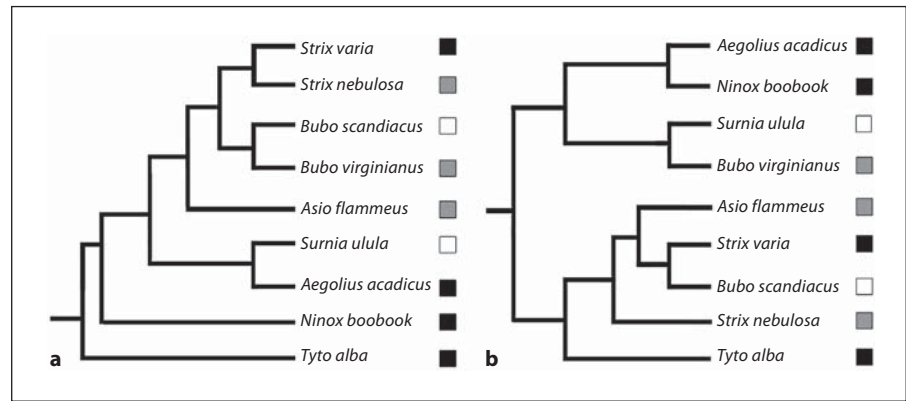
structures. This dendrogram has two main clusters and it is clear that the species are not separated by their activity pattern. In one cluster, the northern saw-whet owl and the boobook owl, both nocturnal species, are grouped with the northern hawk owl, a diurnal species, and the great horned owl, a crepuscular species. In the other cluster, the nocturnal barn owl appears as the root branch to a group that includes three crepuscular species and one diurnal, the snowy owl (fig. 4b). The dendrogram also does not resemble the phylogenetic relationships among species and therefore the relative size of the entire visual system does not reflect activity pattern or phylogeny.

Discussion

Overall, our study shows that there are clear differences in the relative size of the visual pathways among owl species. This is one of the few studies to evaluate relationships between retinal topography and RGC layer neuron numbers and the relative size of the brain visual pathways in any vertebrate. Previously, Kaskan et al. [2005] found that in mammals there is no correlation between rod:cone ratios and the relative size of cortical visual areas. Also, Collin and Pettigrew [1988a, b] suggested that in reef teleosts RGC topography is related to the relative size of the TeO.

Thalamofugal Pathway
On the basis of gross anatomy, Stingelin [1958] reported that the barn owl visual wulst appears much smaller than the wulst of strigid owls, mostly in that it does not extend completely to the lateral edge of the telencephalon. In agreement with this, Bravo and Pettigrew [1981] found

that the peak density of RGCs projecting to the TeO was similar between the barn owl and the burrowing owl, but the peak density of RGCs projecting to the thalamofugal pathway was four times larger in the burrowing owl. Our findings that the barn owl has both the smallest DLL (fig. 2a) and wulst (fig. 2b) of all species sampled confirms the suggestion that the thalamofugal pathway is smaller in the barn owl compared to strigid owls.

In both mammals [Barton, 2004] and birds [Iwaniuk et al., 2008], the relative size of the thalamofugal pathway is positively correlated with the size of the binocular visual field. Therefore, one may expect that because of the reduced thalamofugal pathway in the barn owl, there may also be differences in binocular overlap between the barn owl and other owl species, but this does not appear to be the case. The barn owl has neither less binocular overlap nor less convergent orbits than other owls [Iwaniuk et al., 2008]. We found that the barn owl also has a relatively small tectofugal pathway and, in fact, there is a positive correlation between the relative size of the thalamofugal and tectofugal pathway in all species (fig. 2f). This indicates that the barn owl does not have a specific reduction of the thalamofugal pathway, but an overall reduction of the visual pathways, which is most likely related to the relatively low number of RGCs in this species (see below; table 3). Why the barn owl is so different from strigid owls is not clear. The ecology and hunting behaviour of barn owls does not differ greatly from many strigid owls [König and Weick, 2008]. Tytonid owls do differ in several morphological aspects from strigid owls, such as the shape of the sternum and feet morphology [König and Weick, 2008], and several lines of evidence indicate a split between the two families dating back to the Neogene (23 mya) [Brown and Mindell, 2009], so these neuroanatomical differences could reflect aspects of this ancient diver-

gence. Given these apparent differences between strigid and tytonid owls, future studies should address whether the barn owl is typical of all tytonids and whether there are differences in the retinal and brain morphology between *Tyto* and *Phodilus*, the two genera within the Tytonidae.

Our results confirm previous findings [Iwaniuk et al., 2006, 2008] that the tawny frogmouth has a relative wulst volume similar to that of owls (fig. 2b), and also show that this is true for DLL, which relays information from the retina to the visual wulst [Karten et al., 1973; Bagnoli et al., 1990]. We also found that the relative size of the tectofugal pathway is much larger in the tawny frogmouth than in any owls (fig. 2c–e). Because the tawny frogmouth has feeding habits and morphology very similar to owls [Cleere, 1998; Higgins, 1999], we expected this species to be closer to owls with respect to the relative size of the tectofugal pathway. While some studies have placed caprimulgiformes and the frogmouth as closely related to owls [Sibley and Ahlquist, 1990], several other studies place them as more closely related to hummingbirds and swifts [Cracraft et al., 2004; Davis, 2008; Hacket et al., 2008] and thus the common habits of owls and the frogmouths probably evolved independently and the difference in the relative size of the tectofugal pathway could reflect different evolutionary histories.

Auditory-Visual Trade-Off?

Although our results show no significant correlation between the relative size of visual and auditory pathways when all owl species are included, there is a significant negative correlation between these two sensory pathways when the northern saw-whet owl is excluded (see Results; fig. 3d). Why the northern saw-whet owl escapes this trend of a trade-off between the relative size of auditory and visual regions is unclear. The northern saw-whet owl is peculiar among the asymmetrically eared species with enlarged auditory pathways because it is both strictly nocturnal and hunts mostly in woodlands. Other asymmetrically eared, nocturnal species (e.g. barn and short-eared owls) hunt primarily in open habitats [del Hoyo et al., 1999; König and Weick, 2008]. The northern saw-whet owl therefore hunts in an especially dim habitat that is full of obstacles and thus might require more visually guided prey capture and navigation than other asymmetrically eared species. Although this life history is not unique amongst all owls, the saw-whet owl was the only species that had all of these traits in our analyses. This possible trade-off between sensory modalities

should be taken with caution as the inclusion of more species in the analysis, especially other nocturnal asymmetrically eared species that hunt primarily in woodlands (e.g. the mottled owl, *Ciccaba virgata*, and the boreal owl, *Aegolius funereus*) [Norberg, 1977; König and Weick, 2008] may show that the northern saw-whet owl is not an exception and that there is no significant relationship between the relative sizes of the auditory and visual pathways.

Despite the caveats in this analysis, similar sensory system trade-offs have been reported in mammals. For example, Baron et al. [1996] found that there is a trade-off between the relative sizes of auditory and visual structures in the mesencephalon in bats, and Eisenberg [1981] also suggested that a similar trade-off between visual and auditory pathways may occur in tenrecs, which use echolocation and have small eyes. In owls, the possible trade-off between the visual and auditory pathways is likely driven by the increased capability of asymmetrically eared owls to use auditory cues to locate prey. Species like the barn owl and the northern saw-whet owl can locate sounds within 2°, and some asymmetrically eared species can hunt in complete darkness [Payne, 1971; Konishi, 1973]. An improved ability to locate prey using auditory cues could loosen the selective pressure on maintaining a well-developed visual system for visually-guided prey capture and thus result in the reduction of the relative amount of RGCs and relative size of the visual pathways.

Activity Pattern

In birds, and vertebrates in general, one of the adaptations of the visual system to scotopic environments is to increase retinal summation, i.e. an increase in the amount of photoreceptors that converge onto one RGC [Warrant, 2004; Hall and Ross, 2007]. One consequence of this is a reduction in the number RGCs [Kay and Kirk, 2000, 2004; Hall et al., 2009]. In birds, there is evidence that this, in turn, results in a reduction of the tectofugal pathway [Martin et al., 2007; Iwaniuk et al., 2010b; Corfield et al., 2011]. Surprisingly, our results show that in owls there is no correlation between the relative size of the tectofugal pathway and activity pattern. First, we found no correlation between the relative size of the tectofugal (or the thalamofugal) pathway and H:V ratio (fig. 3a, b), which are correlated with activity pattern in owls [Lisney et al., 2012]. Second, in our cluster analysis (fig. 4b), species do not appear to be grouped by activity pattern, indicating that the relative size of visual pathways is not similar among species with similar activity

patterns. Also, in the boobook owl, a nocturnal species for which we did not have an H:V ratio, the size of the tectofugal pathway is relatively large compared to other owls (fig. 2c–e), further indicating that nocturnal owls do not have a reduced tectofugal pathway. Instead, our results show that the relative sizes of the visual pathways are correlated with the relative number of RGC layer neurons (fig. 3c), which, in turn, appears to be independent of activity pattern in the species examined. This is well exemplified by the northern saw-whet and barn owls. Both of these species are strictly nocturnal, but the northern saw-whet owl has almost three times as many neurons in the RGC layer, relative to brain size, as the barn owl (table 3). Previously, Hall et al. [2009] had found that there is no difference in the relative size of the optic foramen between diurnal and nocturnal owls, which also suggests that the number of RGCs is not correlated with activity pattern in owls. Thus, in owls, activity patterns are associated with differences in eye morphology [Lisney et al., 2012], rod:cone ratios and retinal topography [Oehme, 1961; Bravo and Pettigrew, 1981; Lisney et al., 2011, 2012], but not in the number of RGCs and the relative size of visual pathways. This is similar to what Kaskan et al. [2005] found in mammals where the relative size of cortical visual areas between diurnal and nocturnal species is not different despite a great variation in rod:cone ratios. One explanation for this lack of correlation between activity pattern and the relative size of visual pathways is that the amount of variation in the peripheral visual system related to changes in the activity pattern is enough to accommodate the changes in light available for vision resulting from a nocturnal to diurnal transition (or vice versa) and therefore changes in the number of RGCs or the relative size of visual pathways are not necessary. Alternatively, it is possible that the number of RGCs, and hence the relative size of visual pathways, is constrained by evolutionary history. Regardless of whether they are diurnal or nocturnal, all owls have relatively large eyes [Brooke et al., 1999], convergent orbits and a broad binocular visual field [Martin, 1986; Iwaniuk et al., 2008] and a relatively small optic foramen [Hall et al., 2009] when compared to other birds. All these characteristics strongly suggest that owls are descended from a nocturnal ancestor and more diurnal activity patterns have evolved independently several times. This would be similar to what has been proposed in the evolution of the visual system of mammals, where a nocturnal 'bottleneck' seems to define several of the characteristics of the mammalian visual system, even in diurnal species [Heesy and Hall, 2010].

Conclusion

Our results show that there is little correlation between the relative size of visual pathways and activity pattern in owls, despite the fact that several characteristics of the peripheral visual system (e.g. eye shape and RGC distribution, see Introduction) do vary with the activity pattern of each species. Instead, our results strongly suggest that the relative size of all visual structures in the brain is related to the number of cells in the RGC layer relative to brain size. Interestingly, the relative sizes of the main visual pathways (tectofugal and thalamofugal) covary, even though they have different functions. This is similar to what we found in our study of the relative size of the auditory pathways of owls [Gutiérrez-Ibáñez et al., 2011] where the relative size of two distinct auditory pathways, the intensity and time-delay pathways, are highly correlated. This is likely related to the hearing range of each species and therefore to the amount of sensory cells in the periphery [Gutiérrez-Ibáñez et al., 2011]. Further, several other studies in vertebrates suggest that the number of sensory cells is the main driver of the relative size of sensory areas [e.g. Roth et al., 1992; Kotrschal et al., 1998]. Together, these points emphasize the need for future research in sensory ecology to study variation at *all* levels within a given sensory pathway.

Finally, we still need to consider why there is so much variation in the relative number of cells in the RGC layer (and therefore visual pathways) among owls. As stated before (see Discussion) a combination of both phylogenetic history and particular aspects of the ecology of each species may help to explain these differences. Part of the difficulty in interpreting our findings derives from a limited sampling of owl species. Even though this is the most extensive study of its kind in owls, several other groups are missing. For example, the study of other nocturnal and diurnal species of small owls in the tribe Surniinae [Wink et al., 2008] could help to clarify the uniqueness of the visual system of the northern saw-wet owl.

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