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Behavioural Brain Research 167 (2006) 305–317
BEHAVIOURAL BRAIN RESEARCH
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Research report

Echolocation, vocal learning, auditory localization and the relative size of the avian auditory midbrain nucleus (MLd)

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Received 20 July 2005; received in revised form 12 September 2005; accepted 19 September 2005
Available online 26 October 2005

Abstract

The avian nucleus mesencephalicus lateralis, pars dorsalis (MLd) is an auditory midbrain nucleus that plays a significant role in a variety of acoustically mediated behaviours. We tested whether MLd is hypertrophied in species with auditory specializations: owls, the vocal learners and echolocaters. Using both conventional and phylogenetically corrected statistics, we find that the echolocating species have a marginally enlarged MLd, but it does not differ significantly from auditory generalists, such as pigeons, raptors and chickens. Similarly, all of the vocal learners tend to have relatively small MLds. Finally, MLd is significantly larger in owls compared to all other birds regardless of how the size of MLd is scaled. This enlargement is far more marked in asymmetrically eared owls than symmetrically eared owls. Variation in MLd size therefore appears to be correlated with some auditory specializations, but not others. Whether an auditory specialist possesses a hypertrophied MLd appears to be depend upon their hearing range and sensitivity as well as the ability to resolve small azimuthal and elevational angles when determining the location of a sound. As a result, the only group to possess a significantly large MLd consistently across our analyses is the owls. Unlike other birds surveyed, owls have a battery of peripheral and other central auditory system specializations that correlate well with their hearing abilities. The lack of differences among the generalists, vocal learners and echolocaters therefore reflects an overall similarity in hearing abilities, despite the specific life history requirements of each specialization and species. This correlation between the size of a neural structure and the sensitivity of a perceptual domain parallels a similar pattern in mammals.

Keywords: Inferior colliculus; Prey capture; Echolocating; Parrot; Songbird; Hummingbird; Owls

1. Introduction

The evolution of sensory specializations is often correlated with an increase in size of the neural region(s) that mediate the specialization. Jerison [45] referred to this relationship as the 'principle of proper mass' whereby the size of a given neural structure is a reflection of the complexity of the behaviour that it subserves. Although there is considerable debate concerning how and why such a correlation exists [79], there are numerous examples of such correlations in vertebrates. For example, mammals with different somatosensory requirements can have dramatically different somatosensory representations, such as the expansion of the nose is the Star-nosed Mole (*Condylura cristata*) [11], the tail in Spider Monkeys (*Ateles* spp.) [67] and the forepaw in Raccoons (*Procyon lotor*) [68] This correlation between the size of a sensory region and behaviour is not restricted to the cortex or somatosensation, but is also present in visual [5], auditory [3,27] and gustatory systems [23]. Although there are numerous examples of this in mammals, systematic comparisons of behaviour and sensory regions are rare in birds [33]. Given that birds share many behavioural [55] and neural similarities [43,72] with mammals, it is likely that such correlations also exist in birds.

Abbreviations: IC, inferior colliculus; MLd, nucleus mesencephalicus lateralis, pars dorsalis; An, nucleus angularis; La, nucleus laminaris; MC, nucleus magnocellularis; SC, superior colliculus; SI, somatosensory cortex; TeO, tectum opticum

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doi:10.1016/j.bbr.2005.09.015

Audition is of critical importance to a wide range of behaviours in birds, such as prey capture, individual and species recognition, vocal learning and mate selection. As a result of the range of behaviours that rely upon acoustic cues, studies of avian audition have revealed marked species differences in hearing range and the ability to localize sounds and discriminate pitch, intensity and temporal differences (see review in [21]). From this and other evidence, it is clear that several groups have evolved unique auditory specializations that are not present in other birds: localization of prey using only acoustic cues, vocal learning and echolocation. The first of these, the location of prey using acoustic cues, has been well documented in owls. Asymmetrically eared owls, like the Barn Owl (*Tyto alba*), can accurately acoustically locate prey up to 7 m away in complete darkness [63]. The vocal learners are all species that learn some, or all, of their vocal repertoire and includes the songbirds, parrots and hummingbirds. Specialized forebrain nuclei and their projections to and from auditory and motor structures in the thalamus, midbrain and hindbrain mediate the learning and production of vocalizations in all three taxa [7,25,31,42,44,80]. Unlike the owls and vocal learners, the echolocating birds have received relatively little attention. The only species known to echolocate are the Oilbird (*Steatornis caripensis*) [28] and the Swiftlets (*Aerodramus* and *Collocalia* spp.) [58,66,69]. All of these species primarily echolocate only when navigating through roosting sites and caves and do not appear to use echolocation to capture prey.

One region that is likely to be integral to all forms of acoustic-mediated behaviours is the nucleus mesencephalicus lateralis, pars dorsalis (MLd). MLd receives input from the two parallel auditory pathways [10,47] and as such plays a role in the integration of auditory information. MLd is homologous to both the mammalian inferior colliculus (IC) and the torus semicircularis (TS) in non-avian reptiles and amphibians [9,47,51]. Rylander [73] reported that MLd is hypertrophied in songbirds and Cobb [13,14] reported a similar hypertrophy of MLd in the echolocating Oilbird and Black-nest Swiftlet (*Aerodramus maximus*), which parallels the hypertrophy of IC in echolocating bats (Fig. 1). Lastly, the most detailed studies of the anatomy and function of MLd are in the Barn Owl, in which MLd plays a critical role in the auditory localization of prey (see reviews in [50,52]). Several authors reported that MLd appears to be enlarged in the Barn Owl and other asymmetrically eared owls, such as Saw-whet (*Aegolius acadicus*) and eared (*Asio*) owls, compared to symmetrically eared owls and other birds [13,84]. Thus, there is ample evidence to support a significant role of MLd in vocal learning, echolocation and prey localization that might result in its hypertrophy. A systematic analysis of size variation in MLd has not, however, been performed across species to test this hypothesis. Here, we present a detailed analysis of size variation in MLd across 84 species including the echolocating Swiftlets and Oilbird, all three vocal learning taxa and several owl species using both conventional and phylogenetically based statistics. Based on previous reports [13,14,73], we expected MLd to be significantly larger in all three auditory specialists compared to other birds (i.e., auditory 'generalists').

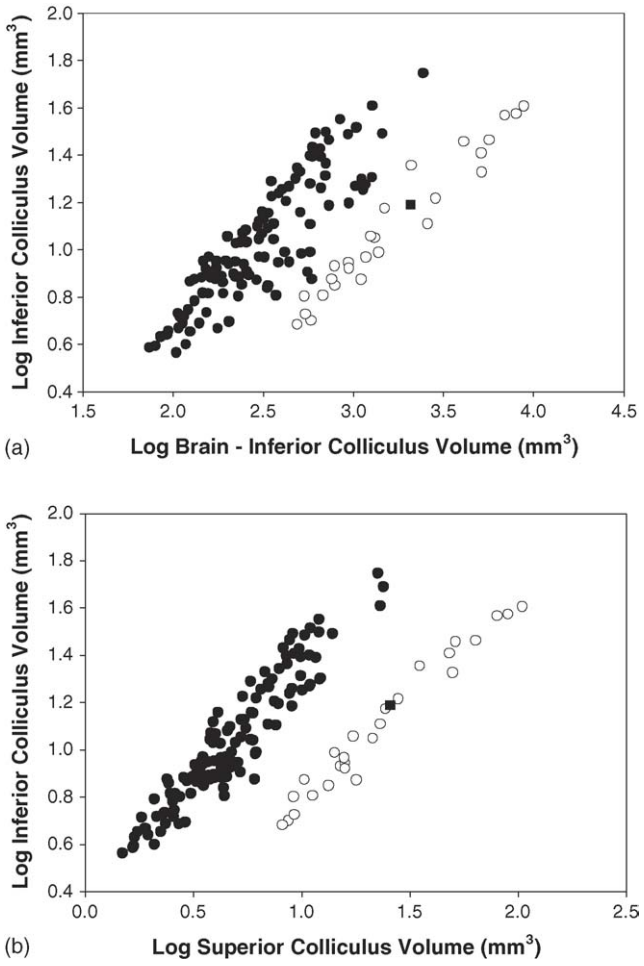

Fig. 1. Scatterplots of log-transformed inferior colliculus (IC) volume against (a) brain volume minus IC volume and (b) superior colliculus volume for echolocating (closed symbols) and non-echolocating (open circles) bats (data from [4]). It should be noted that all species of the suborder Megachiroptera are non-echolocating, with the exception of the Egyptian Fruit Bat (*Rousettus aegyptiacus*), which is indicated by the filled square.

2. Materials and methods

2.1. Specimens

We measured MLd and tectum opticum (TeO) in 72 specimens representing 54 species (Table 1). Representatives of all three auditory specializations were surveyed as well as representative species from other taxa in order to encompass as much interspecific variation in MLd size as possible. Two echolocating species were measured: Oilbird and Pygmy Swiftlet (*Collocalia troglodytes*) [66]. Closely related non-echolocating taxa were also measured. For the Oilbird, we measured several caprimulgiform species (Table 1), which are regarded by some as close relatives [8,17,56,77]. For the echolocating Swiftlet, we measured the closely related [65,66] and non-echolocating Glossy Swiftlet (*C. esculenta*) and the Common Swift (*Apus apus*), a swift that is not closely related to the Swiftlets and does not echolocate. Species from all three orders that exhibit vocal learning were also sampled: songbirds (11 spp.), parrots (15 spp.) and hummingbirds (5 spp.). Lastly, two asymmetrically eared owls, Barn Owl and Saw-whet Owl, and one symmetrically eared owl, the Southern Boobook Owl (*Ninox boobook*), were measured. Data for an additional 31 species were obtained from Boire [6] and Cobb [13], which included four vocal learners, one echolocating Swiftlet and several species classified as auditory generalists (see Table 1). For those species that were both measured and gleaned from the literature, the values presented are the means of the two data sets.

Table 1
A list of the 84 species surveyed, the auditory category they each belong to, brain, tectum opticum (TeO) and nucleus mesencephalicus lateralis, pars dorsalis (MLd) volumes (all in mm^3) and the ratio of MLd to TeO

Order	Species	*n*	Auditory category[a]	Brain volume	TeO volume	MLd volume	MLd:TeO	Source
Anseriformes								
Mallard	*Anas platyrhynchos*	2	G	6065	187.48	7.916	0.042	[6], This study
Plumed Whistling-duck	*Dendrocygna eytoni*	1	G	9421	164.81	7.850	0.047	This study
Apodiformss								
Black-nest Swiftlet	*Aerodramus maximus*	1	E	–	–	–	0.061	[13]
Common Swift	*Apusapus*	2	G	668	42.84	0.813	0.019	This study
Chimney Swift	*Chaetura pelagica*	2	G	343	30.47	0.668	0.033	[6,2]
Glossy Swiftlet	*Collocalia esculenta*	2	G	121	9.51	0.504	0.043	This study (FMNH, SEA132), [13]
Pygmy Swiftlet	*C. troglodytes*	2	E	139	9.71	0.543	0.056	This study (FMNH, SEA133, SEA134)
African Palm-swift	*Cypsiurus parvus*	1	G	300	–	–	0.052	[13]
Caprimulgiformes								
Feline Owlet-nightjar	*Aegotheles insignis*	1	G	1540	73.64	3.801	0.052	This study (BBM-NG 101365)
Indian Nightjar	*Caprimulgus asiaticus*	1	G	–	–	–	0.060	[13]
Nightjar	*Caprimulgus* sp.	1	G	734	58.81	2.319	0.039	[6]
Whip-poor-will	*Caprimulgus vociferus*	1	G	820	–	–	0.052	[2]
Spotted Nightjar	*Eurostopodus argus*	1	G	1013	60.97	3.515	0.058	This study
Common Poorwill	*Phalaenoptilus nuttallii*	1	G	–	–	–	0.057	[13]
Tawny Frogmouth	*Podargus strigoides*	2	G	5627	296.64	9.908	0.033	This study
Oilbird	*Steatornis caripensis*	2	E	3900	104.74	5.363	0.062	This study (USNM, 431365), [13]
Charadriiformes								
Least Sandpiper	*Calidris minutilla*	1	G	472	35.52	1.241	0.035	[6]
Killdeer	*Charadrius vociferus*	1	G	1073	100.92	1.817	0.018	[6]
Short-billed Dowitcher	*Limnodromus griseus*	2	G	1231	51.12	1.807	0.035	[6], this study
Common Tern	*Sterna hirundo*	1	G	1593	121.49	1.700	0.014	[6]
Masked Lapwing	*Vanellus miles*	1	G	2686	206.30	4.937	0.024	This study
Ciconiiformes								
Grey Heron	*Ardea cinerea*	1	G	8446	525.32	4.653	0.009	[6]
Cattle Egret	*Bubulcus ibis*	1	G	4025	213.76	2.068	0.010	This study
Columbiformes								
Pigeon	*Columba livia*	2	G	2189	143.85	4.296	0.030	This study, [6]
Ringneck Dove	*Streptopelia risoria*	1	G	1141	95.11	2.319	0.024	[6]
Coraciiformes								
Laughing Kookaburra	*Dacelo novaeguineae*	3	G	4027	333.48	5.116	0.015	This study
Falconiformes								
Brown Goshawk	*Accipiter fasciatus*	1	G	4875	236.92	3.792	0.016	This study
Brown Falcon	*Falco berigora*	1	G	6007	387.05	7.950	0.021	This study
Australian Hobby Falcon	*Falco longipennis*	1	G	3035	200.36	3.230	0.016	This study
Galliformes								
Chukar	*Alectoris chukar*	1	G	2500	147.76	5.453	0.037	[6]
Ruffed Grouse	*Bonasa umbellus*	2	G	3136	182.33	8.574	0.047	This study
Golden Pheasant	*Chrysolophus pictus*	1	G	3369	211.64	9.664	0.046	[6]
Northern Bobwhite	*Colinus virginianus*	1	G	1091	81.13	3.826	0.047	[6]
Common Quail	*Coturnix coturnix*	1	G	811	67.90	2.650	0.039	[6]
Chicken	*Gallus domesticus*	1	G	2993	201.23	7.595	0.038	[6]
Turkey	*Meleagns gallopavo*	1	G	6097	552.93	19.766	0.036	[6]
Helmeted Guineafowl	*Numida meleagris*	1	G	3951	233.86	10.239	0.044	[6]
Chaco Chachalaca	*Ortalis canicollis*	1	G	3374	203.67	6.436	0.032	[6]

Table 1 (*Continued*)

Order	Species	*n*	Auditory category[a]	Brain volume	TeO volume	MLd volume	MLd:TeO	Source
Peafowl	*Pavo meleagris*	1	G	7355	284.95	15.141	0.053	[6]
Ring-necked Pheasant	*Phasianus colchicus*	1	G	2762	129.83	8.164	0.063	[6]
Gruiformes								
American Coot	*Fulica americana*	1	G	2719	127.65	5.454	0.043	This study
Passeriformes								
Brown Thornbill	*Acanthiza pusilla*	1	VL	434	34.81	0.515	0.015	This study
Eastern Spinebill	*Acanthorhynchus tenuirostris*	1	VL	489	29.46	0.822	0.028	This study
Blue-faced Honeyeater	*Entomyzon cyanotis*	1	VL	2227	96.99	3.391	0.035	This study
Eastern Yellow Robin	*Eopsaltria australis*	1	VL	839	39.40	1.758	0.045	This study
Australian Magpie	*Gymnorhina tibicen*	1	VL	4017	202.27	3.281	0.016	This study
White-plumed Honeyeater	*Lichenostomus perspicillatus*	1	VL	917	47.94	0.720	0.015	This study
Noisy Miner	*Manonna melanocephala*	1	VL	2279	88.50	1.592	0.018	This study
Superb Lyrebird	*Menura novaehollandiae*	1	VL	10163	384.66	4.107	0.011	This study
Spotted Paradalote	*Pardalotus punctatus*	1	VL	401	17.09	0.837	0.049	This study
Grey Currawong	*Strepera versicolor*	1	VL	5425	270.86	4.200	0.016	This study
Double-barred Finch	*Taenwpygia bichenovii*	1	VL	409	25.81	0.655	0.025	This study
Zebra Finch	*Taeniopygia guttata*	1	VL	328	20.90	0.711	0.034	[6]
Pelecaniformes								
Double-crested Cormorant	*Phalacrocorax auritus*	1	G	7323	187.24	5.291	0.028	[6]
Procellariiformes								
Short-tailed Shearwater	*Puffinus tenuirostris*	1	G	4658	235.01	2.864	0.012	This study
Psittaciformes								
Masked Lovebird	*Agapornis personata*	1	VL	2824	82.57	2.575	0.031	This study
Australian King Parrot	*Alisterus scapularis*	1	VL	5305	200.90	4.455	0.022	This study
Blue-fronted Amazon	*Amazona aestiva*	1	VL	7955	273.47	4.142	0.015	This study
Galah	*Cacatua roseicapilla*	1	VL	6547	217.52	3.305	0.015	This study
Yellow-tailed Black-cockatoo	*Calyptorhynchus funereus*	1	VL	16111	309.66	5.340	0.017	This study
Eclectus Parrot	*Eclectus roratus*	1	VL	5796	208.59	4.492	0.022	This study
Musk Lorikeet	*Glossopsitta concinna*	2	VL	3198	99.52	2.669	0.027	This study
Budgerigar	*Melopsittacus undulatus*	1	VL	1220	43.53	2.386	0.055	[6]
Bourke's Parrot	*Neopsephotus bourkii*	1	VL	1213	56.42	1.884	0.033	This study
Cockatiel	*Nymphicus hollandicus*	3	VL	2263	75.31	2.111	0.028	This study
Blue-headed Parrot	*Pionus menstruus*	1	VL	5283	184.61	3.555	0.019	[6]
Crimson Rosella	*Platycercus elegans*	1	VL	3683	154.94	3.935	0.025	This study
Eastern Rosella	*Platycercus eximius*	2	VL	3155	129.25	2.678	0.021	This study
Superb Parrot	*Polytelis swainsonii*	2	VL	3157	134.88	3.586	0.027	This study
Red-rumped Parrot	*Psephotus haematonotus*	2	VL	1940	73.47	1.689	0.023	This study
African Grey Parrot	*Psittacus erithacus*	1	VL	6405	155.14	4.357	0.028	This study
Rainbow Lorikeet	*Trichoglossus haematodus*	2	VL	3728	123.42	2.578	0.021	This study
Rheiformes								
Greater Rhea	*Rhea americana*	1	G	19228	953.28	38.190	0.040	[6]
Sphenisciformes								
Magellanic Penguin	*Spheniscus magellanicus*	1	G	16757	383.31	9.967	0.026	[6]
Strigiformes								
Saw-whet Owl	*Aegolius acadicus*	1	0	2343	64.49	14.227	0.221	This study
Southern Boobook Owl	*Ninox boobook*	2	0	5626	148.15	9.261	0.063	This study
Barn Owl	*Tyto alba*	1	0	7143	107.09	26.150	0.244	This study
Tinamiformes								
Red-winged Tinamou	*Rhynchotus rufescens*	1	G	3377	327.43	9.964	0.030	[6]
Trochiliformes								
Anna's Hummingbird	*Calypte anna*	1	VL	183	12.33	0.329	0.027	This study
Blue-tailed Emerald	*Chlorostilbon mellisugus*	1	VL	119	10.44	0.554	0.053	[6]
Green-fronted Lancebill	*Doryfera ludoviciae*	1	VL	139	9.49	0.224	0.024	This study (FMNH 320498)
Buff-tailed Sicklebill	*Eutoxeres condamini*	2	VL	257	20.46	0.474	0.023	This study (FMNH 315304, 315300)

Table 1 (*Continued*)

Order	Species	*n*	Auditory category[a]	Brain volume	TeO volume	MLd volume	MLd:TeO	Source
Rufous-breasted Hermit	*Glaucis hirsuta*	1	VL	123	12.96	0.296	0.023	This study (USNM 616825)
Green-backed Firecrown	*Sephanoides sephanoides*	2	VL	134	10.19	0.238	0.023	This study (FMNH 316786, 316784)

The sources of the material are as follows—BBM: Bernice Bishop Museum (Honolulu, HI), USNM: National Museum of Natural History (Washington, DC), FMNH:Field Museum of Natural History (Chicago, IL) and references as indicated. Where more than one source is referenced, the values represent the mean.

[a] Auditory categories are as follows—E: echolocaters, G: generalists, O: owls and VL: vocal learners.

Several specimens were loaned to us from the Field Museum of Natural History (Chicago, IL), National Museum of Natural History (Washington, DC) and the Bishop Museum (Honolulu, HI). All of the museum specimens were captured in the field, immersion fixed in 10% formalin for several days to several weeks and then stored in 70% ethanol for 3–45 years before we extracted the brains. Other fixed specimens were acquired from wildlife shelters, veterinary clinics and other labs. For all specimens, including the museum specimens, the brain was extracted, weighed to the nearest milligram and post-fixed in 4% paraformaldehyde in 0.1 M phosphate buffer (PB) for several days. The brains were then blocked in the sagittal plane, cryoprotected in 30% sucrose in PB, embedded in gelatin and sectioned in the coronal 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 thionin and coverslipped with Permount.

2.2. Measurements

Previous studies of MLd [14,73] compared the volume of MLd to the size of the optic lobe. The optic lobe in these studies is defined as the volume of the optic tectum and mesencephalon within those sections that the IC is located. The problem, however, is that this measure of the optic lobe is highly dependent upon the plane of section. For example, if the angle the sections are cut at is angled more rostro-ventrally in one specimen than another, the resulting measures of optic lobe volume will be markedly different. For this reason, we chose to scale the size of MLd against TeO. We chose TeO because studies in mammals have suggested that there is a trade-off between the size of the IC and the superior colliculus (SC) that reflects the degree of visual or auditory specialization (Fig. 1) and SC is homologous with the TeO [9]. Furthermore, Cobb [13] notes that TeO is a more meaningful measure because TeO is primarily visual whereas the optic lobe measurement encompasses parts of the mesencephalon that are unrelated to vision or hearing and provides a MLd:TeO ratio for eight species. Finally, the relative size of a given brain region can vary depending upon what is used as a scaling factor [18,38,64,79] and therefore the use of multiple scaling factors is recommended to assess how consistent the results are. We therefore compared the volume of MLd to both TeO and brain volume.

In accordance with previous studies [6] we defined TeO as the laminated portion of the optic lobe excluding the optic tract. The caudal and rostral poles of MLd were defined as those regions ventral to the third ventricle that had larger, darker and more densely packed cells than adjacent regions. The ventral and lateral borders were defined by the presence of a distinct lamina that forms a fibre bundle surrounding MLd [51] and the dorsal and lateral borders were defined by the tectal ventricle (Fig. 2). Although MLd can be subdivided into several subdivisions [51,85], the border between the central and external nuclei is faint [83] and we were unable to reliably distinguish the subdivisions in most of the specimens. Therefore, our measurements are restricted to the entire volume of MLd. For both TeO and MLd, our borders were similar to those used in previous allometric studies [6,13,14,73]. Whole brain volumes were measured by dividing the mass of each brain by the average density of fresh brain tissue [6,36,38,40].

Digital photographs were taken throughout the rostro-caudal extent of MLd and TeO for all specimens that we measured. Sampling intervals varied from every second to every fifth section depending on the size of the brain. Using this method, we measured 10–20 sections containing MLd and 30–40 sections containing TeO for each specimen. Measurements of each region were made using the NIH ImageJ freeware computer program. Volumes were calculated by multiplying the area by the sampling interval and section thickness. All of these procedures are similar to those used in previous studies [6,13,14,73].

2.3. Statistical analysis

All species were classified according to four categories: owls, vocal learners, echolocaters and auditory generalists (i.e., species without any known auditory specializations). We then calculated MLd:TeO ratios (Table 1) and performed ANOVAs on these four categories to determine if there was a difference among the auditory specialists and other birds. To further examine relative size variation in MLd, we first logio-transformed MLd, TeO and brain minus MLd volumes (hereafter referred to as brain volume). Analyses of covariance (ANCOVAs) with auditory specialization and the scaling variables as covariates of MLd volume were then used to test for significant differences among groups. We also used ANOVAs of residuals derived from least-squares linear regression lines of MLd against TeO and brain volumes to assess differences among groups and Tukey–Kramer post hoc tests for pair-wise comparisons. In addition, we tested for differences among those orders represented by three or more species using ANOVAs of the MLd residuals to assess whether some orders tended to have larger MLds than others.

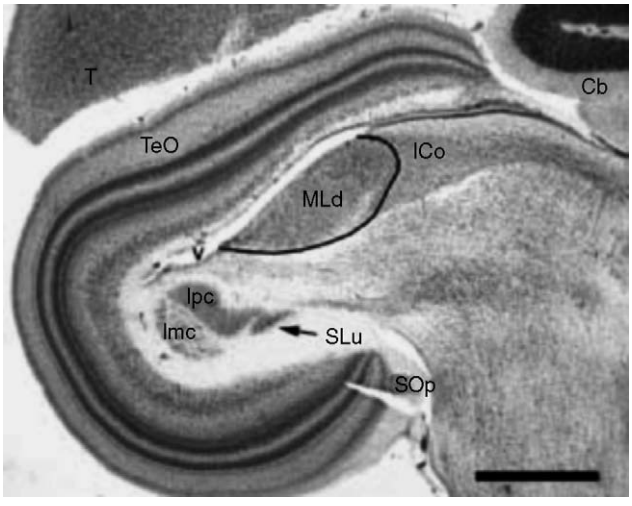

Fig. 2. A photomicrograph of the optic lobe of a songbird, the Spotted Pardalote (*Pardalotus punctatus*). The ventral and lateral borders of the nucleus mesencephalicus lateralis, pars dorsalis (MLd) are indicated by the solid line. Other structures shown are as follows: cerebellum (Cb), nucleus intercollicularis (ICo), nucleus isthmi, pars magnocellularis (Imc), nucleus isthmi, pars parvocellularis (Ipc), nucleus semiluminaris (SLu), stratum opticum (SOp), telencephalon (T), tectum opticum (TeO) and ventricle (V). Scale bar = 1 mm.

Because allometric analyses can be affected by phylogenetic relationships [32], we then repeated these analyses using phylogenetically based statistics. Phylogenetically corrected ANCOVAs and ANOVAs were performed using the PDAP software package (available from T. Garland). We performed these by simulating a null *F* distribution of traits along a phylogeny and using the critical values from this distribution as phylogenetically corrected critical *F*s as opposed to critical *F*s derived from conventional statistical tables [26]. This method has been used previously in comparative analyses of the brain and behaviour [36–38,64] and is less prone to type I error than conventional statistics when comparing data from many species [26]. To perform these analyses, a composite phylogeny was constructed using the inter-ordinal relationships in Sibley and Ahlquist [77] with resolution for some groups supplemented by additional references [1,2,12,48,66]. For each test, we constrained the simulation to biologically realistic values by setting the upper boundaries slightly higher and lower than that of the largest and smallest values respectively. The simulated *F* values were similar using both a gradual and a speciational model of evolutionary change, so we only report those of the gradual model.

3. Results

3.1. MLd:TeO ratio

The MLd:TeO ratio varied from 0.007 in the Grey Heron (*Ardea cinerea*) to 0.244 in the Barn Owl (Table 1). An ANOVA revealed a significant difference in MLd:TeO ratio among the auditory generalists and specialists (Table 2). Post hoc tests indicated that the owls have significantly larger MLd:TeO than any of the other groups and that the echolocaters have significantly larger ratios than the vocal learners (Fig. 3). Although the echolocating swifts (0.058) have a marginally higher ratio than the non-echolocating swifts (0.044), no significant difference was detected ($t_{(4)} = -1.80$, $p = 0.15$). The Oilbird, however, did have a significantly larger ratio than its putative relatives within the order Caprimulgiformes (single sample $t_{(7)} = 3.12$, $p = 0.02$). It should also be noted that there was substantial variability within the owls. Specifically, the asymmetrically eared Barn Owl and Saw-whet Owl have ratios three times that of the symmetrically eared Boobook Owl (Table 1).

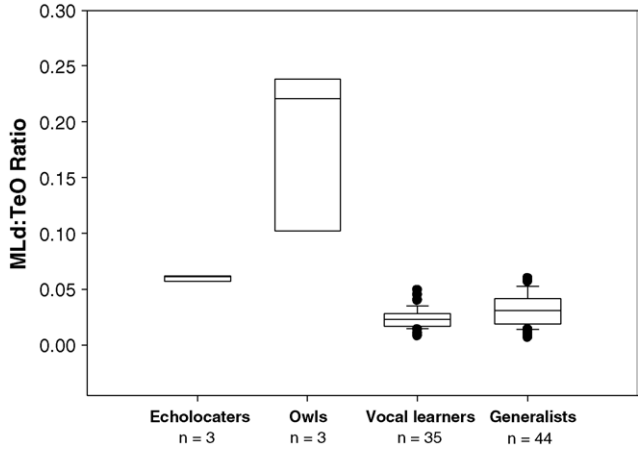

Fig. 3. Boxplots of the nucleus mesencephalic lateralis, pars dorsalis (MLd) to tectum opticum (TeO) ratio for the echolocaters, owls, vocal learners and auditory generalists. The boxes represent the 95% confidence interval for each category, the horizontal line is the median and the filled circles are outliers. Significant differences were present between the owls and all other groups and between the echolocaters and vocal learners.

A significant difference in MLd:TeO was also found among orders ($F_{(8,63)} = 21.43$, $p < 0.01$). Post hoc pair-wise comparisons revealed that owls have significantly larger ratios than all other orders and the caprimulgiforms (which includes the Oilbird) have significantly larger ratios than the parrots (Psittaciformes). The significant difference among orders did not, however, exceed the phylogeny-corrected critical *F* (26.89). Overall then, owls tend to have larger MLd:TeO ratios than other groups, but this difference is minimal when phylogeny is taken into account.

3.2. MLd and TeO

Comparing the size of MLd with TeO using an allometric approach yielded similar results to that of the MLd:TeO ratio. A scatterplot of MLd against TeO volume revealed that the two asymmetrically eared owls lie well above all of the other species sampled (Fig. 4a) and are, in fact, significant outliers. Although the Boobook Owl lies below the other two owls, it too has a larger MLd relative to TeO than the remaining species. An ANCOVA using auditory specializations and TeO volume as covariates of MLd volume did not yield a significant interaction

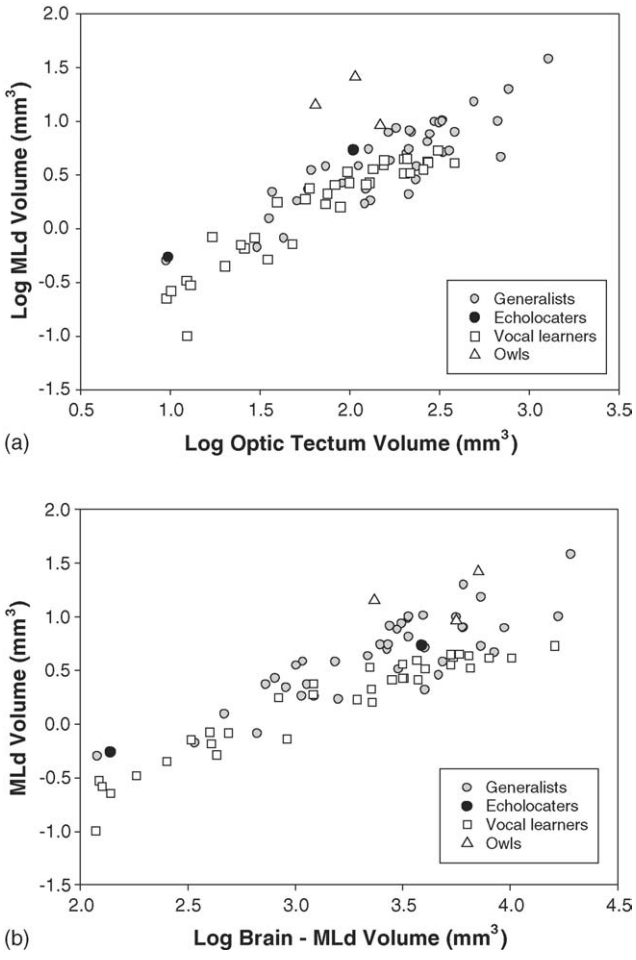

Fig. 4. A scatterplot of log-transformed nucleus mesencephalicus lateralis, pars dorsalis (MLd) against: (a) log-transformed tectum opticum (TeO) volume and (b) log-transformed brain volume minus MLd volume.

Table 2
The results of ANOVAs performed on relative nucleus mesencephalicus lateralis, pars dorsalis (MLd) volume using the scaling factors of: a ratio of MLd to tectum opticum (TeO) volume, residuals from a MLd volume and brain volume minus MLd volume regression and residuals from a MLd volume and TeO volume regression

Test	df	Calculated *F*	Critical *F*	Phylogeny-corrected critical *F*
MLd:TeO ratio	3, 81	**56.51**	2.72	9.76
MLd and TeO volume	3, 76	**20.34**	2.72	11.08
MLd and brain volume	3, 76	**13.75**	2.72	10.83

Critical *F*s were derived from conventional statistical tables whereas the phylogeny-corrected critical *F*s were calculated in PDANOVA (see text for details). Significant calculated *F*s are shown in bold.

term, but there was a significant effect of auditory specialization (Table 3). This remained significant even when the calculated *F* was compared to the phylogeny-corrected critical *F* (Table 3). Thus, there is a significant difference in the relative size of MLd amongst the auditory specialists and generalists regardless of whether phylogenetic relationships are accounted for or not. In fact, this multiple regression model accounted for more variation ($r^2 = 0.86$) than simply regressing MLd on TeO volume ($F_{(1,78)} = 235.54$, $p < 0.01$, $r^2 = 0.75$).

An ANOVA of residuals derived from a least-squares linear regression of MLd on TeO volume also found a significant difference among the three auditory specialists and the generalists (Table 4, Fig. 5a). Post hoc Tukey–Kramers revealed that relative to TeO, MLd is significantly larger in owls compared to all other groups and is significantly smaller in vocal learners compared to generalists. No significant difference was detected between the echolocating Swiftlet and the other swifts (single sample $t_{(2)} = -2.20$, $p = 0.16$) or between the Oilbird and the caprimulgiforms (single sample $t_{(4)} = -1.55$, $p = 0.20$).

An ANOVA of the residuals also yielded a significant difference among orders ($F_{(8,58)} = 15.89$, $p < 0.01$). The pair-wise comparisons revealed that the owls have relatively larger MLd volumes than all other orders (Table 4). The order Caprimulgiformes also had significantly larger MLd residuals compared to the shorebirds, raptors and all vocal learners and the Galliformes had significantly larger MLd residuals than the hummingbirds. It should be noted, however, that the calculated *F* did not exceed the phylogeny-corrected critical *F* (34.08).

In summary, relative to TeO, MLd is significantly larger in owls than in other groups. MLd is not, however, relatively larger in echolocaters or either of the orders containing echolocating species (Apodiformes, Caprimulgiformes). MLd is also not significantly larger relative to TeO in the vocal learners.

3.3. MLd and brain volume

An examination of the allometric relationship between MLd and brain volume corroborated both analyses presented above. The asymmetrically eared Saw-whet and Barn Owls lie above all other species in a scatterplot of MLd against brain volume (Fig. 4b), although the difference between these owls and other birds is not as marked as the plot of MLd and TeO (Fig. 4a). An ANCOVA using brain volume and auditory specialization (owls, vocal learners and generalists) as covariates indicated no significant interaction term, but there was a significant effect of specialization (Table 3). Thus, there is a significant difference in relative MLd size amongst the auditory specialists and generalists. Furthermore, the r^2 for a regression model including auditory specialization was higher (0.86) than a regression of simply MLd against brain volume ($F_{(1,78)} = 248.72$, $p < 0.01$, $r^2 = 0.76$).

ANOVAs of the residuals from a least-squares linear regression line for all species also corroborated these findings (Table 2). A significant difference in relative MLd volume was found among the auditory specialists and generalists (Fig. 5b). Post hoc Tukey–Kramer tests revealed the owls have significantly larger MLd residuals than the generalists and vocal learners and vocal learners have significantly smaller MLd residuals than generalists. No significant difference in MLd residuals was detected between the echolocating Pygmy Swiftlet and the other swifts (single sample $t_{(2)} = -1.46$, $p = 0.28$). The Oilbird did, however, have a significantly larger MLd residual than the non-echolocating caprimulgiforms (single sample $t_{(4)} = -5.98$, $p = 0.03$).

When the residuals were grouped according to order, a significant difference was detected ($F_{(8,58)} = 19.27$, $p < 0.01$). Pair-wise comparisons (Table 4) revealed that owls have larger relative MLd volumes than all other orders, except for Galliformes and Caprimulgiformes. The Galliformes have significantly larger

Table 3
The results of ANCOVAs performed on relative nucleus mesencephalicus lateralis, pars dorsalis (MLd) volume using the scaling factors of: a ratio of MLd to tectum opticum (TeO) volume), MLd and brain volume minus MLd volume and MLd volume and TeO volume

Test	Effect	df	Calculated *F*	Critical *F*	Phylogeny-corrected critical *F*
TeO	Interaction	3, 72	1.46	2.73	9.98
	Main effect	3, 75	**20.30**	2.73	10.39
Brain	Interaction	3, 72	0.27	2.73	12.23
	Main effect	3, 75	**21.40**	2.73	11.14

Critical *F*s were derived from conventional statistical tables whereas the phylogeny-corrected critical *F*s were calculated in PDANOVA (see text for details). Significant calculated *F*s are shown in bold.

Table 4
The results of pair-wise comparisons made using post hoc Tukey–Kramer tests of residuals derived from least-squares linear regression lines of nucleus mesencephalicus lateralis, pars dorsalis (MLd) volume against both brain volume and tectum opticum (TeO) volume

	Apodiformes	Caprimulgiformes	Charadriiformes	Falconiformes	Galliformes	Passeriformes	Psittaciformes	Strigiformes	Trochiliformes
Apodiformes		-	-	-	-	-	-	+	-
Caprimulgiformes	-		+	+	-	+	+	+	+
Charadriiformes	-	-		-	-	-	-	+	-
Falconiformes	-	-	-		-	-	-	+	-
Galliformes	+	-	+	+		+	-	+	+
Passeriformes	-	+	-	-	+		-	+	-
Psittaciformes	-	+	-	-	+	-		+	-
Strigiformes	+	-	+	+	-	+	+		+
Trochiliformes	-	+	-	-	+	-	-	+	

Those shown above the shaded boxes are the results from the MLd/TeO residuals and those below the shaded boxes are from the MLd/brain residuals. For a list of the species within each order, refer to Table 1. Significant differences are indicated by a '+' whereas non-significant differences are indicated by a '–'.

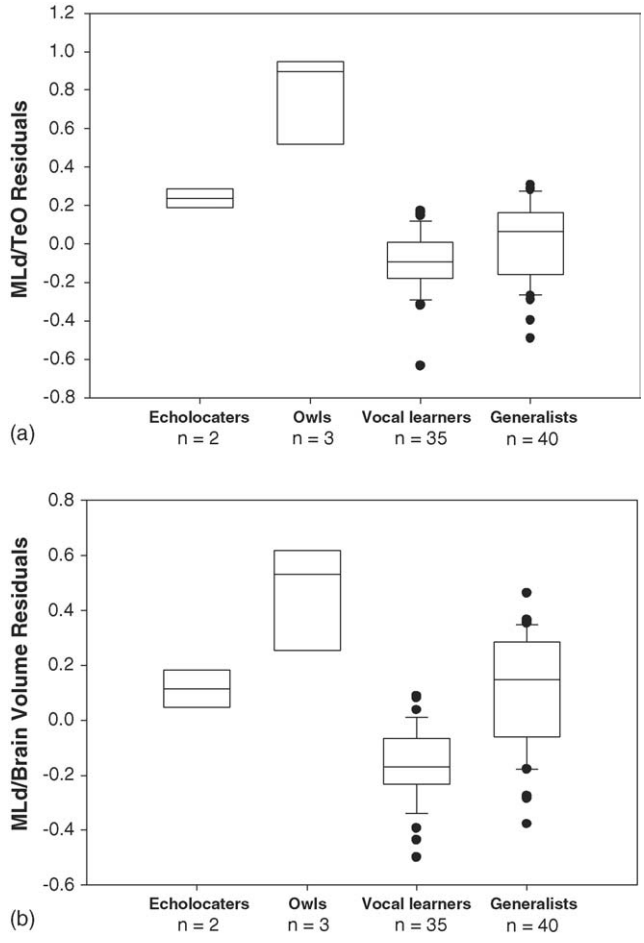

Fig. 5. Boxplots of residuals from least-squares linear regressions of log-transformed nucleus mesencephalicus lateralis, pars dorsalis MLd volume against (a) log-transformed tectum opticum (TeO) volume, and (b) log-transformed brain volume minus MLd volume grouped according to: echolocaters, owls, vocal learners and auditory generalists. The boxes represent the 95% confidence interval for each category, the horizontal line is the median and the filled circles are outliers.

MLd residuals than the swifts, shorebirds (Charadriiformes), raptors (Falconiformes) and all three orders of vocal learners and the Caprimulgiformes have significantly larger MLd residuals than all three vocal learners. As with the previous analysis of MLd and TeO, this difference among orders was not supported by a comparison of the calculated F with the phylogeny-corrected critical F (31.13).

Based on this final analysis, it is clear that relative to brain volume, MLd is significantly larger in owls than in other birds. The Oilbird and its putative relatives, the caprimulgiforms, also have relatively large MLds, but only in comparison with the vocal learners. The other echolocaters, their relatives and all three groups of vocal learners do not, however, have relatively large MLds.

4. Discussion

Overall, our analyses show that compared to other birds, MLd is significantly larger in owls, but smaller in vocal learners. One of our analyses indicated that MLd is slightly larger in echolo-

caters compared to vocal learners and auditory generalists, but this was not corroborated by subsequent analyses. We therefore conclude that MLd is hypertrophied in owls, but not in vocal learners or echolocaters.

Although Cobb [13,14] and Rylander [73] reported that MLd was hypertrophied in both echolocaters and songbirds, there are several problems with their analyses (also see below). First, both authors used ratios to express the relative size of MLd. Ratios are problematic in allometric analyses because they are often correlated with the denominator and therefore do not reflect the true relative size of a structure [79]. Second, relatively few species were sampled in either study and therefore are unlikely to be representative of the variability in birds as a whole. For example, the relative size of MLd was not known for any of the vocal learning parrots and hummingbirds. Lastly, previous studies did not include any information on phylogenetic relatedness, which can have a significant effect on the analysis and interpretation of interspecific data [32]. Our analysis therefore represents a more comprehensive account of size variation in MLd among birds.

4.1. Vocal learning

Contrary to our prediction and the findings of Cobb [14] and Rylander [73], we found no evidence of MLd hypertrophy in songbirds, hummingbirds and parrots. In fact, vocal learners tend to have significantly smaller MLds relative to both brain and TeO volume than owls and auditory generalists. We contend that the reason for the discrepancy between our results and those of Cobb [14] and Rylander [73] is that their measurements were inaccurate. They calculated a ratio of MLd volume to that of the optic lobe, but only for those sections within which MLd was present. The danger of using such criteria is that the entire optic lobe was included. Furthermore, the area of their optic lobe measure is highly dependent upon the plane of section. As the plane of section moves from a coronal to a horizontal plane of section, the ratio increases because of the position of MLd within the optic lobe. Given that it is extremely difficult to obtain the same plane of section through all midbrain structures across species that vary in brain size and morphology, this is a highly unreliable measure. For this reason, we scaled MLd volume against our measures of the entire optic tectum and the entire brain volume.

The relatively small size of MLd in songbirds, parrots and hummingbirds might reflect their basic auditory abilities. Although songbirds can localize sounds well [59,60], their spatial resolution is not as fine as that of owls and some other birds (Table 5). The audiogram of songbirds is not any broader than that of auditory generalists, despite being shifted towards slightly higher frequencies [21]. In addition, songbirds do not have particularly sensitive hearing in so far as the minimum audibility thresholds are quite high [21, Table 5]. They share these same characteristics not only with parrots (Table 5) and hummingbirds [70], but also many auditory generalists, such as galliforms, ducks and raptors (Table 5). Given that vocal learners have generally unremarkable hearing compared to auditory generalists, it is perhaps not surprising that MLd tends to be of average to below average size in vocal learners, despite the findings of previous studies [14,73]. In fact, the tuning properties of MLd neurons are not different to that reported in auditory generalists [88,89], unlike those of owls [82,83]. Although MLd must play some role in vocal learning because of its connections with the rest of the auditory system [47,81], it does not appear to be specialized for this role. This could reflect the prominent role that forebrain nuclei play in vocal learning, perception and discrimination (see review in [42]). In fact, the relatively large forebrains of both parrots and songbirds appear to result from the enlargement of multimodal regions, such as the caudo-medial nidopallium and caudo-medial mesopallium [36,38,39,71], both of which are involved in the learning and perception of vocalizations [42]. Volumetric analyses have demonstrated that both parrots and songbirds have particularly large forebrains and small TeO for their brain size [36,38,39]. Thus, vocal learners appear to have hypertrophied forebrain regions involved in auditory integration rather than MLd.

4.2. Echolocation

Cobb [13] reported that MLd was enlarged in the echolocating Black-nest Swiftlet and Oilbird compared to three swifts and three nightjars, respectively. Our study partially supports his findings. Using the MLd:TeO ratio, we found a significant difference between echolocaters and vocal learners and a significant difference between echolocating and non-echolocating species within the Caprimulgiformes, but not in the swifts. Although the

Table 5
The auditory abilities of some of the taxa sampled (data from [20,48,52])

Group	Minimum absolute resolvable angle (°)	Higher frequency cutoff (kHz)	Auditory sensitivity at 500 Hz (dB)
Asymmetrically eared owls	1–6	12.5	<5
Symmetrically eared owl	7	7	<5
Songbirds	20–101	7–12	12–48
Budgerigar (*Melopsittacus undulatus*)	45–95	8	≈18
Oilbird (*S. caripensis*)	–	>8	≈35
Pigeon (*Columba livid*)	4–25	<6	23
Galliforms	≈100	6.5	32
Mallard (*Anas platyrhynchos*)	–	≈6.5	35
Raptors	2–14	7.5	25

The minimum absolute resolvable angle refers to the minimum angle difference that a bird can distinguish within a sound-attenuated room. The higher frequency cutoff is the frequency still detectable by the bird at 60 dB. The auditory sensitivity measure is the minimum dB detectable at a frequency of 500 Hz.

Oilbird did have a significantly larger MLd relative to brain volume than the caprimulgiforms, it should be noted that whether the Oilbird truly is a caprimulgiform or not is questionable [56]. From these mixed results and the fact that there were no significant differences detected between echolocating birds and auditory generalists, we conclude that echolocating birds may have slightly enlarged MLds compared to their relatives, but this enlargement does not differ in magnitude from that of other birds that do not echolocate. Therefore, unlike most bats, echolocating birds do not have a significantly enlarged MLd/IC, which likely reflects differences in the structure and function of echolocating vocalizations between bats and birds.

In both Oilbirds and Swiftlets, the echolocating calls are noisy broad-band clicks [15,22,24,53,66] and these calls are not used for the detection and capture of prey. Oilbirds feed primarily on fruit [19], which does not require echolocation to find, and Swiftlets likely use a combination of visual (e.g., motion parallax) and tactile (e.g., somatosensation by rictal bristles) to locate and capture insects in the air. The calls are primarily used when entering and exiting roosting sites within caves and likely function as an aid in navigating through dimly lit caves and around conspecifics [57]. This is further supported by experimental studies on the sensitivity and acuity of echolocation in both Oilbirds and Swiftlets. Swiftlets are able to successfully negotiate flight paths through large wooden dowels (6–10 mm), but their performance drops off significantly for thinner dowels [16,22,29,57,78]. Similarly, Oilbirds can avoid large objects in their flight path using echolocation, but not smaller objects [53].

In contrast to birds, the echolocation system of most bats is far more sensitive. Similar experiments to those conducted on Swiftlets have shown that bats are able to detect dowels/wires as thin as 0.06 mm [61]. In addition, most bat species do not use broad-band echolocating calls; instead, bats produce calls of a constant frequency (cf), frequency sweeps (fm) and a combination of constant frequency and frequency modulation (cf–fm) [61]. One notable exception to this is echolocating in fruit bats of the genus *Rousettus*, which employ broad-band clicks [35] when entering and exiting cave roosts and not for prey capture. *Rousettus* bats are therefore comparable to both the Swiftlets and the Oilbird in terms of the structure and function of their echolocating calls. These fruit bats also cannot resolve azimuthal angles as accurately as other echolocating bats [34], lack the spectral acuity of other echolocating bats [30] and do not have an enlarged IC (Fig. 1). Currently we do not have information on minimum resolvable angles of echolocating birds, which would provide further insight into how comparable echolocating birds are with *Rousettus*.

It must also be emphasized that our mixed results do not indicate that there are no neural specializations for echolocation in birds. Given the broad-band structure of both Swiftlet [15,22,24,66] and Oilbird calls [53], they may rely upon interaural timing differences (ITDs) more than interaural intensity differences (IIDs) to navigate. In birds, both ITDs and IID s are processed by MLd, but only after they are received by the cochlear nuclei, nucleus laminaris (La) and nucleus magnocellularis (MC) (see review in [52]). The Oilbird does have significantly larger La and MC than most other birds, the exceptions being the asymmetrically eared owls [54,86] and a similar hypertrophy of homologous cochlear nuclei also occurs in echolocating bats, but not in non-echolocating bats [3]. It is therefore likely that the echolocating Swiftlets also possess relatively large La and MC, which would enable them to respond quickly to ITDs in echoing calls without necessarily requiring a large MLd.

4.3. Auditory localization

Of all the species sampled, the owls were the only group to have a significantly larger MLd, regardless of the statistical method used. As predicted, this likely reflects the use of acoustic cues to locate prey. Owls can resolve smaller azimuthal angles than other birds [49, Table 5], possess a detailed map of auditory space in MLd [82] and have the broadest and most sensitive hearing of any group of birds [21], Table 5. In addition, all owls possess specializations in the peripheral auditory system, such as unique malleus morphology [75], a long cochlea [74,76] and a relatively large tympanic membrane [74,75]. Given the precision of sound localization in owls [63] and this assortment of auditory specializations, it is not surprising that MLd is significantly enlarged. This therefore represents a third case of central nervous system structure hypertrophy in owls, the other two being the Wulst [39,84] and the cochlear nuclei La and MC [54,86].

Not all owls share the same precision and unique adaptations of the Barn and Saw-whet Owls and this appears to relate to the hypertrophy of both MLd and the cochlear nuclei. Asymmetrically eared owls, such as the Barn Owl, Saw-whet Owl, Great Grey Owl (*Strix nebulosa*) and Long-eared Owl (*Asio otus*), not only have asymmetrical ear openings [62], but also the longest cochleae, basilar membranes and papillae [74]. Behaviourally, all of these species can hunt in complete darkness [63] and can discern angular differences at a fine level (Table 5). Neurons within MLd of these species encode for both azimuth and elevation [82,87]. In contrast, the symmetrically eared owls, such as the Boobook Owl, Screech Owl (*Otus asio*), Burrowing Owl (*Athene cunicularia*) and Great-horned Owl (*Bubo virginianus*), do not have markedly asymmetrical ears [62]. Although a detailed description of their inner ear anatomy is wanting, the symmetrically eared owls only have moderately enlarged cochleae [74]. These species also tend to be more diurnal in their habits, are unable to capture prey in complete darkness [63] and cannot resolve azimuthal angles as finely as the asymmetrically eared owls (Table 5). Electrophysiological studies in the Burrowing Owl and Great-horned Owl also failed to find neurons that were tuned to elevation [81,82]. In this study, we also found that the hypertrophy of MLd was far less in the Boobook Owl than it was in the Barn and Saw-whet Owls relative to both TeO and brain volume. Comparisons of cochlear nuclei found similar variation; all of the symmetrically eared owls had smaller nuclei than the asymmetrically eared owls [54,86]. Thus, it appears that the symmetrically eared owls do not share the same spectrum of peripheral and central specializations for auditory localization as the asymmetrically eared owls.

The difference between asymmetrically and symmetrically eared owls highlights the importance of MLd function in its

hypertrophy. In owls, IIDs and ITDs are combined to construct a map of auditory space within MLd [50,82,83]. As discussed above, the asymmetrically eared owls appear to use a more precise and detailed auditory map and therefore require a relatively large MLd. In other birds, such as vocal learners, auditory integration appears to take place in the forebrain rather than MLd. Thus, there may be a functional difference in the computations that MLd is performing among different taxa that underlies the variation in relative size. Further research into MLd tuning and function is, however, required amongst a range of avian species to support this hypothesis.

5. Conclusions

Despite the fact that two of our predictions were not supported by the data, the results do provide a better understanding of the function of MLd is acoustically mediated behaviours. Specifically, it appears that specialized tuning and hypertrophy of MLd is only present in asymmetrically eared owls and this is directly correlated with their ability to precisely locate prey using only acoustic cues. In doing so, our study supports a broader pattern observed in the evolution of behaviour and sensory systems in mammals and other vertebrates; the enlargement of a sensory region is correlated with the sensitivity of that sensory modality. As mentioned previously, Jerison [45] first suggested that the enlargement of brain regions is correlated with behavioural complexity and several studies have supported this principle. However, this is not always the case. For instance, the large representation of the forepaw in the primary somatosensory cortex (SI) of Raccoons was once considered to be indicative of their digital dexterity [68]. Thus, an expansion of the forepaw representation is correlated with an increase in the complexity of motor output such that Raccoons should be capable of similar digit movements as primates. A behavioural analysis of forepaw use in Raccoons [41], however, found that they are not as dexterous as many other species with smaller forepaw representations in SI, such as Rats (*Rattus norvegicus*). The Raccoon does have acute tactile discrimination abilities [46], but their motor output is not that dissimilar from many other mammals. Thus, the forepaw representation in Raccoons appears to reflect their ability to detect subtle tactile differences and not dexterity. This is the most likely functional outcome of the principle of proper mass [45]; the enlargement of a sensory region is correlated with sensitivity and not necessarily with any additional motor capacity and our analysis of MLd variation in birds supports this. The systematic sampling of sensory systems across birds will therefore provide significant insight into the correlated evolution of the brain and behaviour.

Acknowledgements

We wish to thank the curatorial staff of the Bishop Museum, Field Museum of Natural History and National Museum of Natural History for loaning us specimens, Healesville Sanctuary and David Madill for collecting many specimens on our behalf and Doug Altshuler, Barrie Frost and Gerard Gory for sending us heads of *Calypte anna*, *Aegolius acadicus* and *Apus apus*, respectively, and two anonymous reviewers for their helpful comments on a previous version of this manuscript. This research was funded by fellowships and grants from the Alberta Ingenuity Fund and the Natural Sciences and Engineering Research Council of Canada (NSERC) to AM, an NSF CAREER award to DHC and grants from NSERC and the Canada Research Chairs Program to DRWW.

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