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ORIGINAL PAPER

The retinal projection to the nucleus lentiformis mesencephali in zebra finch (*Taeniopygia guttata*) and Anna's hummingbird (*Calypte anna*)

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Abstract

In birds, the nucleus of the basal optic root (nBOR) and the nucleus lentiformis mesencephali (LM) are retinal recipient nuclei involved in the analysis of optic flow and the generation of the optokinetic response. In both pigeons and chickens, retinal inputs to the nBOR arise from displaced ganglion cells (DGCs), which are found at the margin of the inner nuclear and inner plexiform layers. The LM receives afferents from retinal ganglion cells, but whether DGCs also project to LM is a matter of debate. Previous work in chickens had concluded that DGCs do not project to LM, but a recent study in pigeons found that both retinal ganglion cells and DGCs project to LM. These findings leave open the question of whether there are species differences with respect to the DGC projection to LM. In the present study, we made small injections of retrograde tracer into the LM in a zebra finch and an Anna's hummingbird. In both cases, retrogradely labeled retinal ganglion cells and DGCs were observed. These results suggest that a retinal input to the LM arising from DGCs is characteristic of most, if not all, birds.

Keywords Displaced ganglion cells · Optic flow · Optokinetic · Accessory optic system · Nucleus of the basal optic root

Abbreviations

DGC	Displaced ganglion cell
GCL	Ganglion cell layer
GLv	Lateral geniculate nucleus, pars ventralis
GT	Tectal grey
INL	Inner nuclear layer
IPL	Inner plexiform layer
LMm/l	Nucleus lentiformis mesencephali pars medialis/lateralis
nBOR	Nucleus of the basal optic root
nRT	Nucleus rotundus
ONL	Outer nuclear layer
OPL	Outer plexiform layer
RGC	Retinal ganglion cell
TeO	Optic tectum
TrO	Optic tract

Introduction

In all vertebrates, specialized visual pathways are involved in the analysis of optic flow, the motion that occurs across the entire retina during self-motion (Gibson 1954). These visual pathways include retinal recipient nuclei in the accessory optic system and pretectum (Simpson 1984; Gamlin 2006; Giolli et al. 2006). In birds these nuclei are the nucleus of the basal optic root (nBOR) of the accessory optic system (Brecha et al. 1980), and the pretectal nucleus lentiformis mesencephali (LM) (Gamlin and Cohen 1988). As in all vertebrates, in birds these pathways are involved in generating the optokinetic response to facilitate retinal image stabilization (Waespe and Henn 1987), without which both visual acuity and relative velocity discrimination are impaired (Westheimer and McKee 1975; Nakayama 1981). The visual response properties of neurons in LM and nBOR are very similar; in both nuclei, most neurons have large receptive fields in the contralateral visual field and exhibit direction-selectivity in response to largefield visual motion (Morgan and Frost 1981; Winterson and Brauth 1985).

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In birds, input to nBOR arises from "displaced ganglion cells" (DGCs) a specialized subset of retinal cells, which are found at the margin of the inner nuclear layer (INL) and inner plexiform layer (IPL) rather than the ganglion cell layer (Karten et al. 1977; Reiner et al. 1979; Fite et al. 1981). The identity of the retinal neurons that project to LM has been more difficult to discern. Two initial studies in chickens and pigeons reported that only retinal ganglion cells (RGCs) in the ganglion cell layer, but not DGCs, project to LM (Fite et al. 1981; Bodnarenko et al. 1988), while other authors later suggested that, at least in pigeons, DGCs may project to LM (see Woodson et al. 1995). In the case of Bodnarenko et al. (1988), the authors concluded, after examining retinal labeling resulting from large injections of retrograde tracer in the LM of chickens, that DGCs did not project to LM. In their study, RGCs were retrogradely labeled from all injections, but DGCs were labeled only after injections that spread into the optic tract. Because the LM is located about 2 mm lateral to the nBOR, it is unclear how the spread of an injection into the optic tract adjacent to the LM would label fibers of the basal optic root. Recently, Wylie et al. (2014), used small injections of neural tracers in LM to show that this nucleus receives projections from both DGCs and regular RGCs. This finding in pigeons suggests that the conclusions of the previous studies in chickens were erroneous, or there is a species difference with respect to the retinal projection to LM. Interestingly, Gaede et al. (2017), has recently shown that the response of cells in the LM to optic flow are different in the Anna's hummingbird (*Calypte anna*) when compared to pigeons and zebra finch (*Taeniopygia guttata*). Thus perhaps the retinal projection to LM could vary between different species of birds. Here we made small injections of retrograde tracers in the LM of Anna's hummingbird and zebra finch. We found that, as in pigeons, DGCs project to LM. Thus, projections from DGCs to LM have now been documented in four phylogenetically diverse species examined, suggesting a general pattern among birds.

Methods

Animals

Experimental subjects included one adult male zebra finch (*Taeniopygia guttata*; Eastern Bird Supplies, Quebec, Canada), and one adult male Anna's hummingbird (*Calypte anna*; caught on the University of British Columbia campus, February 2017).

Surgery and electrophysiological recording procedures

Each bird was anesthetized by intramuscular injection in the pectoral muscles with a ketamine/xylazine mixture (65 mg/kg ketamine/8 mg/kg xylazine). Supplemental doses were administered as required. Subcutaneous injections of 0.9% saline were given to maintain fluids. Once anesthetized, birds were placed in a custom-built stereotaxic frame (Herb Adams Engineering, Glendora, CA, USA) with ear bars and an adjustable beak bar suitable for both species. For the hummingbird, the ear bars were inserted into the external auditory meatus to firmly hold the skull so that the brain could be positioned in accordance with unpublished histological studies in the Anna's hummingbird. The LM coordinates were calculated using serial photomicrographs of fixed, Nissl-stained brain sections. For the zebra finch, the ear bars were pinned against the otic process of the quadrate bone, which lies in the anterior part of the opening to the external acoustic meatus. This allowed for positioning of the head in accordance with the stereotaxic atlas of the zebra finch brain (Konishi, unpublished). The head was pitched downward at an angle of 45° to the horizontal plane. Using these coordinates, sufficient bone and dura mater overlying the right telencephalon were removed to expose the surface of the brain and allow access to the LM with vertical penetrations.

To ensure placement in LM we recorded the activity of single units to moving largefield stimuli. Extracellular recordings were made using glass micropipettes filled with 2 M NaCl, with tip diameters of 4–5 µm, which were advanced through the brain using an electric microdrive (National Aperture Inc., Salem, NH, USA). Extracellular signals were amplified and filtered. Upon isolation of a unit in LM, the direction preference of the unit was qualitatively determined by moving a large (90° × 90°) handheld visual stimulus, consisting of black bars, wavy lines and dots on a white background, in the receptive field of the unit. With such stimuli LM units can be easily identified (Pakan et al. 2010). Once a responsive cell was isolated, the responses to a computer-generated largefield random dot patterns were recorded. Details can be found in Gaede et al. (2017). The stimulus measured 83° × 53°, and moved at 36°/s in eight directions 45° apart. Each sweep consisted of 5 s of motion, followed by a 5-s pause (see Fig. 1). Subsequently, the recording electrode was replaced with a micropipette (tip diameter 20–30 µm) containing a fluorescent biotinylated dextran; micro-ruby (red; 3000K molecular weight; Molecular Probes, Eugene, OR, USA). To ensure we were at the correct location, recordings were made of the visual responses with the dextran-containing micropipette prior to the injection. The dextran

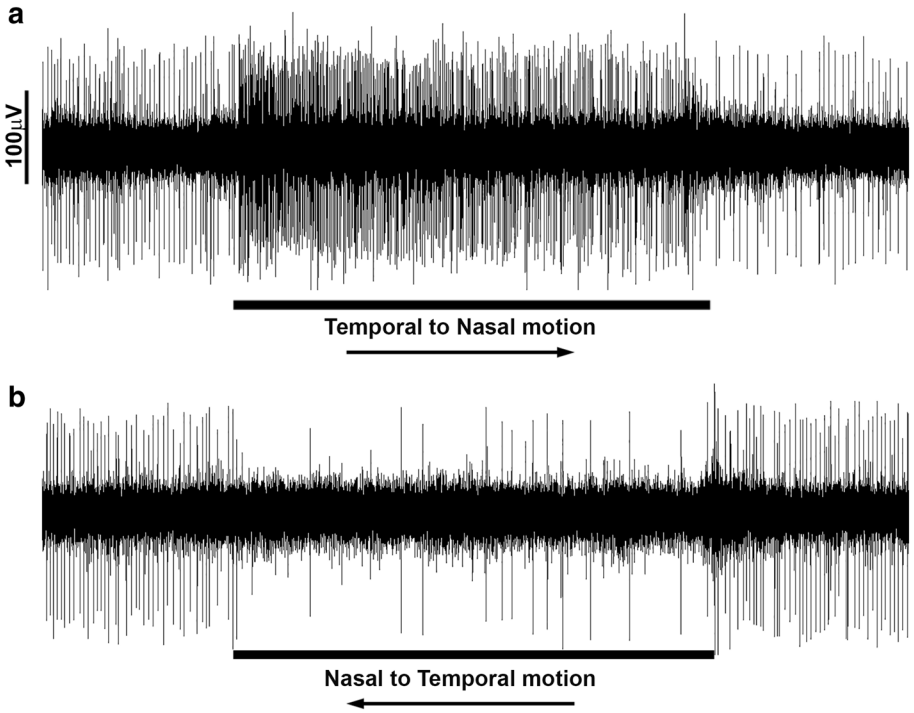

Fig. 1 Example of the response of LM neurons in the zebra finch to large field motion during 5 s (black bar) on the preferred (**a**) and anti-preferred directions (**b**)

was iontophoretically injected (+4 µA, 1 s on, 1 s off) for 15 min. At the end of the injection period, the electrode was left undisturbed for 5 min, and then withdrawn.

After the injections, the craniotomy was filled with bone wax, the wound was sutured with cyanoacrylate (Vetbond, 3M, USA), and the animals were given an i.m. injection of buprenorphine (0.012 mg/kg) as an analgesic. After a recovery period of 24 h (hummingbird) or 5 days (zebra finch) the animals were deeply anesthetized with a ketamine/xylazine mixture and immediately transcardially perfused with saline (0.9% NaCl) followed by 4% paraformaldehyde in 0.1 M phosphate buffer (pH 7.4). The brain and the left eye were extracted from the skull and immersed in paraformaldehyde for several days at 4 °C. The eye was hemisected along the limbus and the lens and vitreous were removed before the retina was dissected out of the overlying scleral eyecup. The brain and eye were then cryoprotected by placing them in 30% sucrose in 0.1 M PBS until they sank. Subsequently, they were embedded in gelatin and again cryoprotected in 30% sucrose in 0.1 M PBS overnight. Using a freezing stage microtome, the brain was sectioned in the coronal plane (40 µm thick) through the rostro-caudal extent of the injection sites and stored in individual wells containing PBS. The entire retina was also sectioned on the microtome, but in the horizontal plane (40 µm thick sections). These sections were mounted on gelatinized glass slides, dried, and stored at +4 °C. For those sections of the retina that were photographed, a blue nuclear stain was applied to visualize the retinal layers. A few drops of SlowFade Gold antifade reagent with DAPI (Invitrogen, Eugene, OR, USA) was applied and the slides were coverslipped.

Immunohistochemistry

The brain slices were immunoprocessed for calretinin (CR) to aid in the identification of the borders of LM, as in birds it helps to discern the borders between LMl, LMm and LPC (Wylie et al. 2014). Free floating brain sections were washed several times in 0.1 M PBS and blocked with 10% normal donkey serum (Jackson Immunoresearch Laboratories, West Grove, PA) and 0.4% Triton X-100 in PBS for 1 h at room temperature. Sections were then incubated for 48 h at 4 °C in PBS containing 2.5% normal donkey serum, 0.4% Triton X-100 and a rabbit polyclonal anti-CR antibody (1:2000; 7699/3H, Swant, Switzerland). Sections were then rinsed in PBS and incubated for 2 h at room temperature in PBS, 2.5% normal donkey serum, and 0.4% Triton X-100 containing Alexa Flour 488 (green) conjugated donkey anti-rabbit IgG (H + L) (1:200, Jackson Immunoresearch Laboratories). The tissue was finally rinsed in PBS and mounted onto gelatinized slides for viewing. Because we were interested in obtaining a precise delineation of the injection sites in LM, and addressing the possible encroachment of the injections into the optic tract and other structures, once images of the injections were obtained (see below), the slides containing the LM injections were subsequently stained with thionin and coverslipped with Permount.

Microscopy and image analysis

Sections were viewed with a compound light microscope (Leica DMRE) equipped with the appropriate fluorescence filters (rhodamine and FITC). Images were acquired using a Retiga EXi *FAST* Cooled mono 12-bit camera (Qimaging, Burnaby, BC, Canada) and analyzed with OPENLAB imaging software (Improvision, Lexington, MA, USA, RRID:rid_000096). Helicon Focus (Kyiv, Ukraine) was used to bring stacks of images into focus, and panoramas were stitched together with PTGui (Rotterdam, Netherlands). Adobe Photoshop was used to compensate for brightness and contrast.

Results

Figure 1 shows an example of the typical response of an LM neuron to largefield motion in the preferred (Fig. 1a) and anti-preferred direction (Fig. 1b). In this cell, from the zebra finch, temporal-to-nasal motion produces a clear increase in the firing rate, while nasal to temporal produces a clear decrease (see Gaede et al. 2017 for a more detailed description of the visual responses of LM neurons in zebra finches and Anna's Hummingbirds). Figure 2 shows photomicrographs of the LM injection site from the hummingbird and zebra finch cases. In a and c, the red injection sites are shown with calretinin immunoreactivity (green). In b and d, the same sections are shown, stained for thionine with the injection sites visualized on top. In both cases, the core of the injection was in a similar location, in the rostral and dorsal parts of LM. Moreover, in both cases the bulk of the injection was in the medial subnucleus (LMm) but included the lateral subnucleus (LMl) and there was a small amount of encroachment on the adjacent tectal grey (GT), which also receives projections from the retina (Gamlin and Cohen 1988). The injection in the hummingbird also labeled some fibers in the isthmo-optic tract which provides efferent feedback to the retina (Woodson et al. 1995). As the injection micropipette passed through the optic tract dorsal to LM, it is impossible to rule out leakage to the optic tract. Most importantly, in both cases the injection was distant to nBOR. In both species DGCs and RGCs were clearly labeled. Figure 3 shows photomicrographs of retrograde labeled DGCs and RGCs in the retina of the hummingbird and zebra finch. The DGS at the border of the IPL and INL were characteristically large and generally the axons of these cells could be seen leaving the cell body perpendicular to the layers of the retina, towards the ganglion cell layer. In both species, the cell body of DGCs was located mainly in

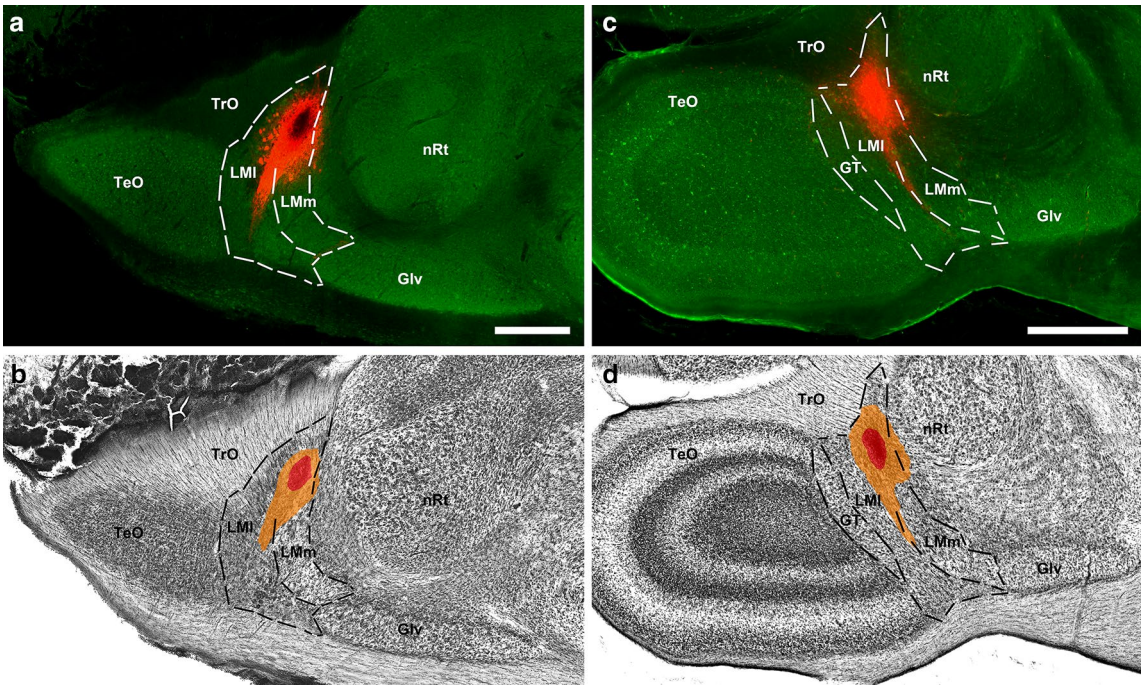

Fig. 2 Photomicrographs of injection sites. Injection in the nucleus lentiformis mesencephali (LM) in an Anna's hummingbird (*Calypte anna)*. **a** Red fluorescent injection site and immunolabeling against calretinin (green). In **b**, this injection is superimposed on the same section Nissl stained. Similarly, **c** red fluorescent injection in LM of the zebra finch (*Taeniopygia guttata*) and **d** the injection superimposed on the same section Nissl stained. Scale bars: 500 µm. *LMm/l* nucleus lentiformis mesencephali pars medialis/lateralis, *nRT* nucleus rotundus, *GLv* lateral geniculate nucleus, pars ventralis, *GT* tectal grey, *TeO* optic tectum, *TrO* optic tract

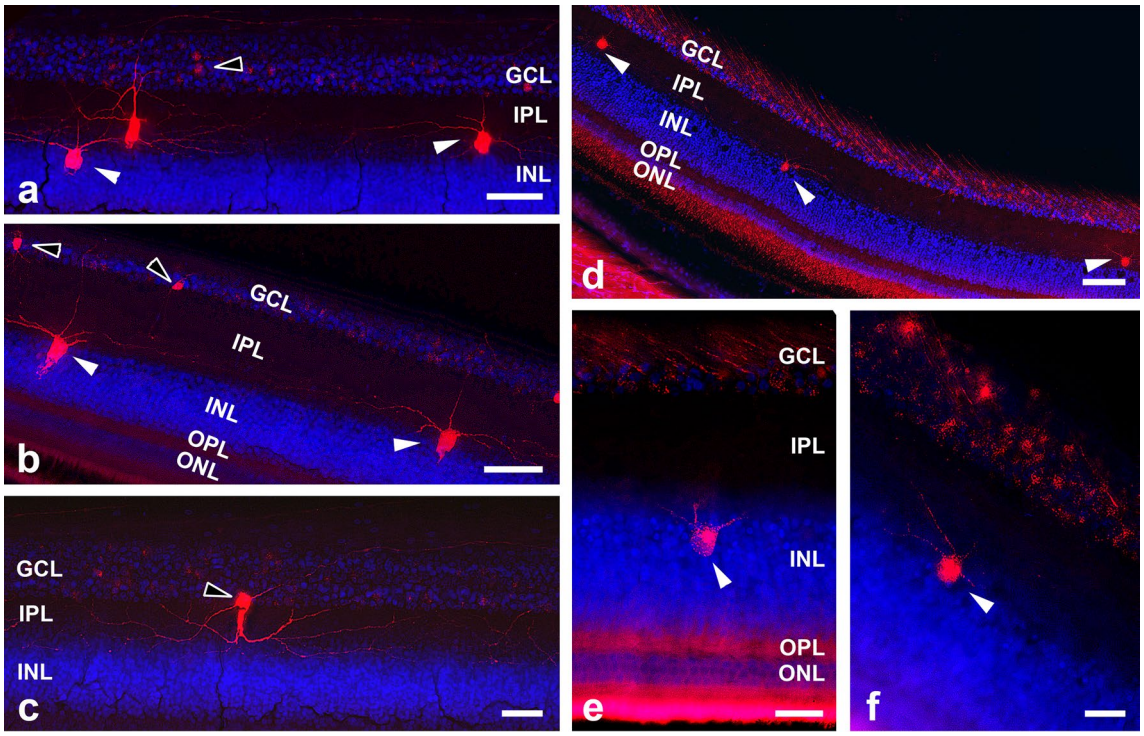

Fig. 3 Retrogradely labeled retinal ganglion cells (RGCs, black arrow heads) and displaced ganglion cells (DGCs, white arrow heads). A blue nuclear stain has been used to clearly visualize the layers of the retinae. Retrogradely labeled RGCs and DGCs from injections in the lentiformis mesencephali (LM) of a zebra finch (*Taeniopygia guttata*). Most of the RGCs were small (**a**), although some larger ones were seen (**b**). The largest labeled RGCs approached the size of the DGCs (**c**). Retrogradely labeled RGCs and DGCs from injections in LM of Anna's hummingbird (*Calypte anna*). **d** Lower magnification photomicrographs of three labeled DGCs and many RGCs. **e, f** High magnification photomicrographs of two other DGCs in the retina of the Anna's hummingbird. Scale bars: **a**–**c** 50 µm. **d** 75 µm. **e, f** 25 µm. *ONL* outer nuclear layer, *OPL* outer plexiform layer, *INL* inner nuclear layer, *IPL* inner plexiform layer, *GCL* ganglion cell layer

the INL or the IPL. These two variances are shown for both species (zebra finch, Fig. 3a; hummingbird Fig. 3d). Figure 4 shows the distribution of labeled DGCs on the retina of the hummingbird (a) and the zebra finch (b). These were reconstructed by measuring the locations of all labeled DGCs from every second section through the retina. In both cases there is a concentration of labeled DGCs in the ventral half of the retina, but some differences between the two species exist. In the case of the hummingbird (Fig. 4a) although DGCs are concentrated in the ventral half, several can be found in more dorsal areas, particularly in the nasal part of the retina. In the case of the zebra finch (Fig. 4b), DGCs are

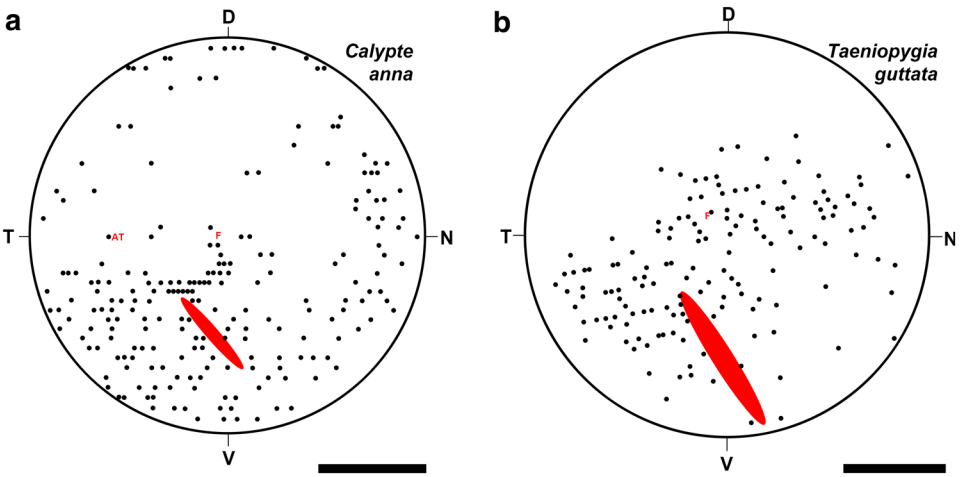

Fig. 4 Distributions of retrogradely labeled displaced ganglion cells (DGCs, black dots) for **a**, the Anna's hummingbird (*Calypte anna)* and **b**, the zebra finch (*Taeniopygia guttata*). These were reconstructed from horizontal sections through the retina, 80 µm apart. The red ellipsoid in the ventral retinal indicates the pecten (P). The red F indicates the position of the fovea and the red AT that of the area temporalis. *N* nasal; *T* temporal; *V* ventral; *D* dorsal. Scale bars: 2500 µm

found concentrated in the ventral part of the temporal retina but nearer to the midline in the nasal retina. Also, in contrast to the hummingbirds, no DGCs were found in the dorsal most part of the zebra finch retina.

Discussion

Here we show for the first time that, as in other birds (Wylie et al. 2014), in the Anna's hummingbird and the zebra finch, the LM receives projections from DGCs in addition to regular RGCs. The labeled DGCs are very similar in size and morphology to DGCs that project to the LM and nBOR in pigeons (Karten et al. 1977; Reiner et al. 1979; Wylie et al. 2014). In pigeons, using injections of different colors of retrograde tracer into LM and nBOR, Wylie et al. (2014) showed that DGCs that project to the LM likely constitute a different population to those which project to nBOR, because no double-labeled cells were observed. In this study, as we did not perform injections in nBOR, is not possible to say whether this is the case in the two species studied.

Bodnarenko et al. (1988) found DGCs after tracer injection in the LM of the chicken, but suggested that this was due to tracer leaking in to the adjacent optic tract. We have previously argued that this is unlikely (see "Introduction"; Wylie et al. 2014) and therefore it is very possible that DGCs also project to the LM in chickens. This, taken together with our results and the study in pigeons, suggests that this is a widespread characteristic among birds. It is unknown whether this is a characteristic in any other vertebrates, particularly non-avian reptiles. In frogs (*Rana pipiens*), ganglion cells that project to the LM reside in the ganglion cell layer (Montgomery et al. 1985), but DGCs project to nBOR (Montgomery et al. 1981). In non-avian reptiles, DGCs project to nBOR in chameleons (Bellintani-Guardia and Ott 2002) and turtles (Reiner 1981), but it is not known whether they also project to the homologue of the LM in these reptiles. Information regarding the nature of ganglion cells that project to the pretectum or the accessory optic system is not available in any crocodilian, the closest living relatives of birds. In mammals, the homologue of the LM, the nucleus of the optic tract (NOT), receives projections from two types of ganglion cells, but all of these cells reside in the ganglion cell layer (Fig. 5; Dhande et al. 2013). Interestingly, genetic labeling of a specific type of direction selective RGCs (DSGCs) in mice has shown that projections to the medial terminal nucleus (MTN), the mammalian homologue to nBOR, arise from one type of RGC, ON-DSGCs. At the same time, projections to NOT arise from two different types of RGCs, one the same as MTN-projecting cells, forward-preferring ON-DSGCs, and a second type, ON–OFF DSGCs (Dhande et al. 2013; Dhande and Huberman 2014). This suggests that DGCs in birds could be a homologue to

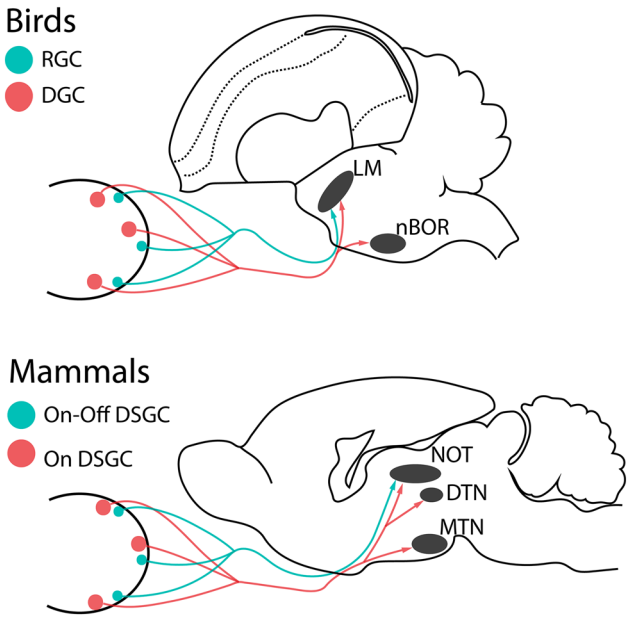

Fig. 5 Schematic comparing the retinal inputs to the accessory optic system (AOS) and the pretectum in birds and mammals. In birds, displaced ganglion cells (DGCs) project to the nucleus of the basal optic root (nBOR), part of the AOS, and to the pretectal nucleus lentiformis mesencephalic (LM). Additionally, LM receives projections from some regular retinal ganglion cells (RGCs). In mammals, the medial and dorsal terminal nucleus (MTN and DTN, respectively), which are part of the AOS, and the pretectal nucleus of the optic tract (NOT), receives projections from a specific type of direction selective RGCs (DSGCs). NOT additionally receives projections from a second type of retinal ganglions cells, ON–OFF DSGCs (Dhande et al. 2013)

ON-DRGCs, and RGCs that project to the LM homologue to ON–OFF DSGCs (Fig. 5).

Why some RGCs reside outside of the ganglion cell layer is unknown. In the case of DGCs that project to the accessory optic system and the pretectum in birds and reptiles, they have very particular morphologies and seem to belong to unique classes of RGCs (Karten et al. 1977; Reiner et al. 1979; Reiner 1981; Bellintani-Guardia and Ott 2002; Wylie et al. 2014). This in contrast to some rodents where DGCs have been found to project to the superior colliculus, the homologue of the optic tectum in birds, but this constitutes an heterogeneous group of ganglions cells, suggesting that their position in the retina is a developmental error (see Nadal-Nicolás et al. 2014). It is possible that the unique location of the cell bodies and dendrites of DGCs help to separate specific inputs to these neurons.

With respect to the topography of retinal projections to the LM, our results also seem to be in agreement with previous studies of the pigeon (Gamlin and Cohen 1988; Wylie et al. 2014).The LMl and LMm, each contain a full topographic map of the retina. Retinal inputs to LM arrive trough the border between the two subdivisions, which results in one map being the mirror image of the other (Wylie et al.

2014). In pigeons, the inputs to the more dorsal parts of LM arise from cells in more ventral retinal areas whereas inputs to the ventral parts of LM arise from more dorsal retina areas. In agreement with this, in our injections in the LM of the hummingbirds and zebra finch were located in the dorsal part of LM (Fig. 2) and DGCs were found concentrated in the ventral parts of the retina (Fig. 4). This is at odds with results in chickens where two studies have found that the ventral retina projects to more rostral portions of LM while the dorsal retina projects to more caudal parts of LM (Bodnarenko et al. 1988; Ehrlich et al. 1989). Whether these are truly species differences or methodological differences, is not known.

Inputs to individual LM neurons

In pigeons, DGCs provide the majority of inputs to nBOR, and therefore it has been assumed that each nBOR neuron receives input from an array of DGCs (Fite et al. 1981). In the avian LM the situation is undoubtedly different to that in nBOR and there are at least two possibilities: (a) some LM neurons receive input exclusively from RGCs, whereas others receive input exclusively from DGCs; and/or (b) individual LM neurons receive input from several RGCs and fewer DGCs. Recording studies of the pigeon LM have shown that there are different response types, which could be expected if the LM contains neurons with differing types of retinal input. Whereas most LM neurons are direction-selective, a small percentage (< 3%) are omni-directional, responding equally well to motion in all directions (Wylie and Crowder 2000). Also, most neurons (about 50%) respond best to temporal-to-nasal (T–N) motion, whereas neurons preferring upward, downward and nasal-to-temporal (N–T) motion are equally represented (Wylie and Frost 1996; Wylie and Crowder 2000). Finally, differences in spatiotemporal tuning of different LM neurons have also been noted (Wylie and Crowder 2000; Crowder et al. 2003). Close to two-thirds of LM neurons have been found to be "fast" neurons, preferring drifting gratings of high temporal frequencies (TFs) and low spatial frequencies (SFs) (speed = TF/SF), while the remaining third are "slow" neurons, responding best to drifting gratings of low TFs and high SFs. Most nBOR neurons are classified as "slow" neurons (Crowder et al. 2003). Based on this, Wylie et al. (2014) speculated that the DGCs project to the neurons in the nBOR and LM that prefer "slow" largefield motion. Perhaps the "fast" LM neurons receive input from RGCs.

Recently, Gaede et al. (2017) found differences in the response properties of LM neurons between hummingbirds and those of zebra finches and pigeons. Specifically, in hummingbirds there was no bias towards neurons preferring N–T motion, and secondly, in hummingbirds most neurons preferred much faster velocities. Because of this we speculated that we might find differences with regard to the retinal inputs to LM between hummingbirds and zebra finches. We found that this is not the case, and therefore the difference in visual response properties of LM neurons between hummingbirds and other birds must arise from other factors. One possibility is that inputs other than those from the retina may have an influence on the response properties of LM neurons. In mammals, the visual response properties of neurons in the accessory optic system and NOT has been shown to be determined not only by retinal inputs, but also by non-retinal afferents from visual cortices (Grasse and Cynader 1990; Hoffmann et al. 2002). As there are inputs from the visual wulst to the LM in birds (Miceli et al. 1979; Rio et al. 1983; Crowder et al. 2004; Wylie et al. 2005), perhaps the differences in the responses of LM neurons in hummingbirds compared to other birds is a result of these telencephalic inputs.

Future research should aim to understand if, as in birds, two types of ganglion cells project to the regions homologous to the avian LM in non-avian reptiles, and whether their characteristics are similar to those of mammals. This in turn would aid our understanding of, and help to reveal how conserved the organization of image stabilizing neuronal circuits are among vertebrates.

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Author contributions All authors had full access to all the data in the study and take responsibility for the integrity of the data and the accuracy of the data analysis. Study concept and design: CG-I, AHG, DLA, DRW. Acquisition of data CG-I, AHG, MRD, DRW. Analysis and interpretation of data: CG-I, AHG, MRD, DLA, DRW. Drafting of the article: CG-I. Critical revision of the article for important intellectual content: CG-I, AHG, DLA, DRW. Obtained funding: DLA, DRW. Study supervision: DLA, DRW.

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Compliance with ethical standards

Conflict of interest The authors have no conflict of interest.

Ethical approval All experimental procedures were approved by the University of British Columbia Animal Care Committee in accordance with the guidelines set out by the Canadian Council on Animal Care.

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