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The Optic Tectum of Birds: Mapping Our Way to Understanding Visual Processing

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Over the past few decades there has been a massive amount of research on the geniculo-striate visual system in primates. However, studies of the avian visual system have provided a rich source of data contributing to our understanding of visual processing. In this paper we review the connectivity and function of the optic tectum (homolog of the superior colliculus) in birds. We highlight the retinotopic projections that the optic tectum has with the isthmal nuclei, and the functional topographic projections that the optic tectum has with the nucleus rotundus and entopallium (homologs of the pulvinar and extrastriate cortex, respectively) where retinotopy has been sacrificed. This work has been critical in our understanding of basic visual processes including attention, parallel processing, and the binding problem.

Keywords: retinotopic maps, visual streams, nucleus rotundus, entopallium, isthmal nuclei

"A good map is both a useful tool and a magic carpet to faraway places" (Anonymous).

Visual Capabilities of Birds

Since the seminal studies of Hubel and Wiesel (1968), there has been an enormous amount of work on the visual system in mammals, particularly in primates, which are regarded as having a sophisticated visual system. However, an extensive amount of research into the avian visual system should not be overlooked. There are about 10,000 known species of birds, over three times the number of mammalian species, and it is therefore not surprising that birds present numerous visual specialisations that require sophisticated visual processing. For example, eagles and falcons have visual acuity that is double that of primates (Fox, Lehmkuhle, & Westendorf, 1976; Gaffney & Hodos, 2003; Reymond, 1985; Shlaer, 1972); owls and a few other birds have global stereopsis (Fox, Lehmkuhle, & Bush, 1977; Nieder & Wagner, 2001; J. D. Pettigrew, 1979; van der Willigen, Frost, & Wagner, 1998); the

peculiar oilbird (*Steatornis caripensis*), which spends much of it's life deep in caves in total darkness, has a retina comprised almost entirely of densely packed rods for scotopic vision (Martin, Rojas, Ramirez, & McNeil, 2004; Rojas, Ramirez, McNeil, Mitchell, & Marin, 2004); Budgerigars (*Melopsittacus undulatus*) have excellent colour discrimination (Goldsmith & Butler, 2005); and a wide range of species are capable of detecting ultraviolet (UV) wavelengths (Odeen & Hastad, 2003). Even the generic pigeon (*Columba livia*), although certainly not a visual specialist in any respect, displays an extensive array of visual abilities. This is not surprising given that they have more than 2.5 million retinal ganglion cells and only a fourfold decrease in the density of ganglion cells between the central fovea and the periphery (Binggeli & Paule, 1969). These abilities include: good detection of static and dynamic stimuli in noise (Kelly, Bischof, Wong-Wylie, & Spetch, 2001), detection of biological motion (Watanabe & Troje, 2006) and other complex motion (Frost, Wylie, & Wang, 1994; Sun & Frost, 1998), colour and UV vision (Palacios & Varela, 1992; Remy & Emmerton, 1989; Vos Hzn, Coemans, & Nuboer, 1994), and stereopsis (McFadden & Wild, 1986). The pigeon visual system, particularly the tectofugal system, has been studied extensively (see below). Although a lot of emphasis is placed on the exquisite topography in the primate visual system, such as the presence of up to 30 cortical maps (Chklovskii & Koulakov, 2004; Kaas, 2008), the multiple topographic projections within the pigeon visual system are equally impressive. Moreover, the division of function in the pigeon tectofugal system is reminiscent of the visual streams in the cortex of primates (Milner & Goodale, 2008). These aspects of the pigeon visual system are highlighted in this article.
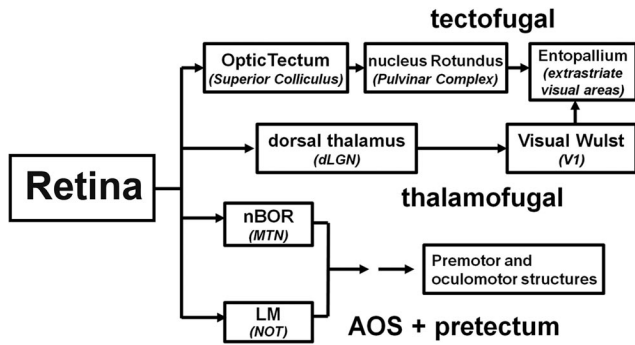
Visual Pathways in Birds

As in other vertebrates, there are three major visual pathways in birds, shown in Figure 1. The thalamofugal pathway proceeds from the retina to the principal optic nucleus of the thalamus

Figure 1. A reduced schematic, showing the three major visual pathways in birds. In parentheses, the equivalent mammalian structures are shown. AOS = accessory optic system; dLGN = dorsal lateral geniculate nucleus; LM = nucleus lentiformis mesencephali; MTN = medial terminal nucleus; nBOR = nucleus of the basal optic root; NOT = nucleus of the optic tract; V1 = primary visual cortex.

(OPT) to the visual Wulst. The OPT and Wulst, are the putative homologs of the lateral geniculate nucleus (LGN) and primary visual cortex (V1) in mammals, respectively (Butler & Hodos, 2005; Medina & Reiner, 2000; Reiner, Yamamoto, & Karten, 2005). The tectofugal pathway proceeds from the optic tectum (TeO), to the nucleus rotundus (nRt) of the thalamus, to the entopallium in the telencephalon (Benowitz & Karten, 1976). While the nRt and TeO are respectively homologous to the pulvinar complex and superior colliculus in mammals, the entopallium is likely equivalent to several areas of mammalian extrastriate cortex (Butler & Hodos, 2005; Karten & Shimizu, 1989; Mpodozis et al., 1996; Nguyen et al., 2004). The third visual pathway consists of nuclei in the Accessory Optic System (AOS) and pretectum, which are highly conserved in vertebrates (Butler & Hodos, 2005; Fite, 1985; Giolli, Blanks, & Lui, 2005; McKenna & Wallman, 1985; Simpson, 1984). The retinal-recipient nuclei in the AOS and pretectum project to numerous areas in the brain (Brecha, Karten, & Hunt, 1980; Gamlin & Cohen, 1988), but most studies have focused on projections to the cerebellum (Lau, Glover, Linkenhoker, & Wylie, 1998; Pakan & Wylie, 2006; Wylie, 2001). The AOS and pretectum are important for the analysis of optic flow and the generation of the optokinetic response to control posture and stabilising eye movements (Giolli et al., 2005; Simpson, 1984; Simpson, Leonard, & Soodak, 1988).

There are differences with respect to the relative sises of visual nuclei that are correlated with species typical visual behaviours. For example, the sise of visual Wulst is correlated with the amount of binocular overlap and shows a massive hypertrophy in owls and other species (e.g., frogmouths and owlet-nightjars) that are thought to possess global stereopsis (Iwaniuk, Heesy, Hall, & Wylie, 2008; Iwaniuk & Wylie, 2006; Pettigrew, 1986; van der Willigen et al., 1998; Wagner & Frost, 1993). Hummingbirds show a massive hypertrophy of the pretectal nucleus lentiformis mesencephali, as the optokinetic response and the analysis of optic flow is critical to hovering (Iwaniuk & Wylie, 2007). However, generally speaking, the tectofugal pathway would be described as the major pathway in birds. With a glance at an avian brain, the massive optic tectum is hard to dismiss (Figure 2C): compared to other vertebrates

the tectum is quite large (Butler & Hodos, 2005), and the tectofugal pathway is generally regarded as the primary route of visual information to the telencephalon (Bischof & Watanabe, 1997; Shimizu & Karten, 1991). As a result of its sise and importance in many aspects of visual processing (see below), there have been numerous anatomical, immunohistochemical, developmental, and electrophysiological studies of the avian tectum (e.g., Khanbabaie, Mahani, & Wessel, 2007; Letelier et al., 2000; Luksch, 2003; Manns, Freund, Patzke, & Gunturkun, 2007; Metzger, Britto, & Toledo, 2006; Sebesteny, Davies, Zayats, Nemeth, & Tombol, 2002; Wang, Luksch, Brecha, & Karten, 2006).

The optic tectum is responsible for the generation of orienting movements to stimuli of interest. As stimuli of interest in the environment tend to be moving (e.g., prey, predators), it is not surprising that many tectal neurons respond to moving stimuli (Frost, Cavanagh, & Morgan, 1988; Frost & Nakayama, 1983; Frost, Wylie, & Wang, 1990). The tectum is a laminated structure with 15 layers (Figure 2A; Ramon y Cajal, 1911), and is retinotopically organised (Figure 2B), with the nasal-temporal dimension of the retina represented along the rostro-caudal axis of the contralateral optic tectum. The tectum has efferent and afferent connections with numerous parts of the brain, and the retinotopy is maintained in some of the connections, but not others (see below). We (Gutiérrez-Ibáñez, Pakan, & Wylie 2008) have been examining the connections of the tectum using fluorescent-tagged biotinylated dextran amines (miniruby: red, cat no. D-3312 or miniemerald: green, cat no. D-7178; 10,000 mol wt; 10% solution in 0.1 M phosphate buffer; Invitrogen, Carlsbad, CA), which are effective as bidirectional tracers. With injections of red and green tracers at adjacent points in the tectum (Figure 3A), we can examine the topography of the projections directly.

Topographic Projections of the Optic Tectum

Of the connections of the tectum where retinotopy is maintained, the isthmal nuclei have been studied in the most detail (Brecha, 1978; Güntürkün & Remy, 1990; Hellmann, Manns, & Gunturkun, 2001; Hunt & Kunzle, 1976; Wang, Major, & Karten, 2004; Wang et al., 2006; Tombol, Alpar, Eyre, & Nemeth, 2006). The isthmal nuclei include the magnocellular and parvocellular portions of nucleus isthmi (Imc, Ipc) and the nucleus semilunaris (SLu). The topographic projections in this system are impressive, and both Ipc and Slu possess reciprocal topographic efferent and afferent projections. From injections of red and green tracers in the tectum tight bands containing anterogradely labelled terminals and retrogradely labelled cells can be seen in coronal sections through the Ipc and SLu, (Figure 3A, B, C). Imc has a spatially topographic efferent projection from the tectum (Figure 3D, E). From tectal injections, there are retrogradely labelled cells in the Imc, however, this connection is not topographic (Figure 3F) and there are many cells that are double labelled. This is because Imc cells project widely throughout the tectum, with the exception of the area from where they receive projections. That is, whereas there are homotopic reciprocal connections reciprocal connections between the tectum and SLu and Ipc, and a homotopic projection from the tectum to Imc, the projection from Imc to the tectum is heterotopic.
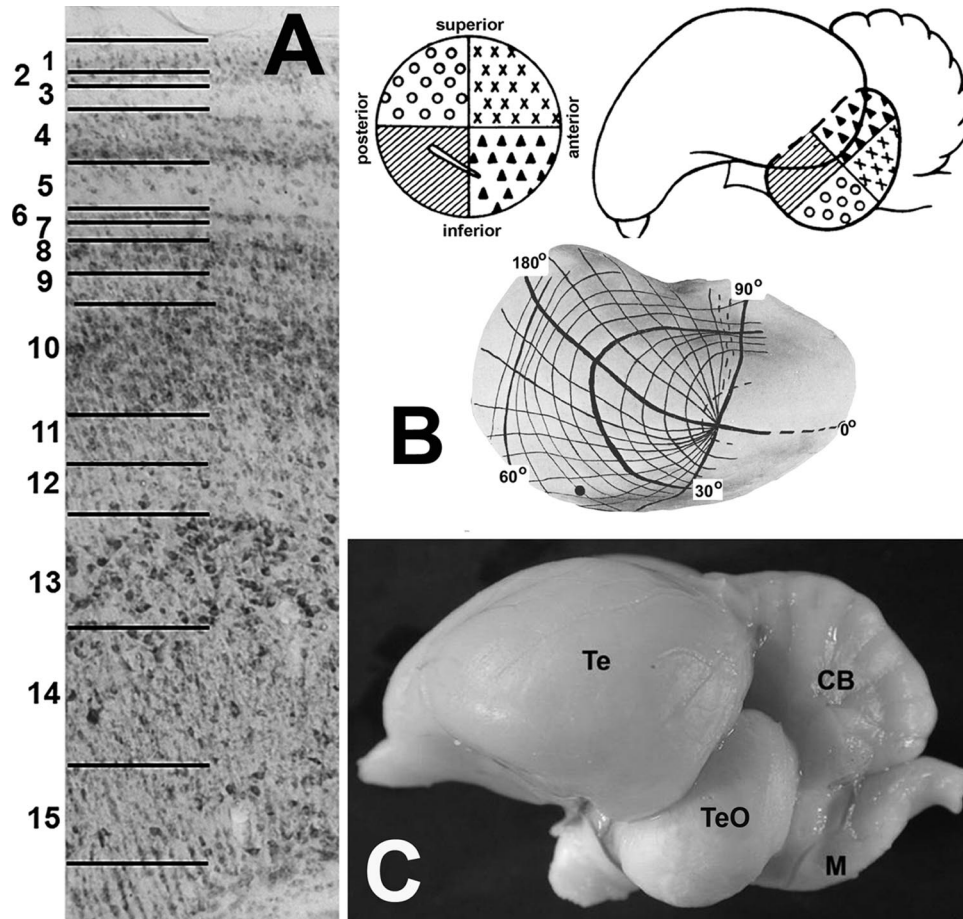
Figure 2. The optic tectum in birds. (A) is a photomicrograph through the optic tectum (TeO) showing the 15 layers according to Ramon y Cajal (1911). (B) illustrates the retinotopic map in the TeO. On the top, a lateral view of pigeon brain (right) shows the optic tectum, indicating the gross topography of the retina (left; from McGill, Powell, & Cowan, 1966). Below, a detailed map of the visual field projected on the tectum is shown (from Clarke & Whitteridge, 1976). (C) shows a lateral view of the pigeon brain, to indicate the impressive sise of TeO. CB = cerebellum; Te = telencephalon; M = medulla.

Indeed, other cells in Imc also have heterotopic projections to the Ipc and SLu. This is summarised in Figure 3E (Wang et al., 2006).

The functions of some the connections within the isthmo-tectal circuitry have been revealed with electrophysiological experiments. Most tectal cells have a centre-surround organisation, and respond best to a spot moving through the excitatory centre, as a background simultaneously moves in the opposite direction in the surround (Frost & Nakayama, 1983; Frost et al., 1988, 1990). Pharmacological inactivation of the Imc and Ipc with injections of lidocaine respectively abolishes the excitatory centre and inhibitory surround of tectal cells (Wang, Wang, & Frost, 1995; Wang, Xiao, & Wang, 2000). Imc and Ipc neurons have receptive fields consisting of a central vertically oriented excitatory strip flanked by inhibitory regions (Wang & Frost, 1991). Li, Xiao, & Wang (2007) have shown how tectal afferents, with the classic centre-surround receptive fields, are combined to create orientation-selective cells in Imc, similar to how lateral geniculate afferents are combined in mammalian primary visual cortex. Pharmacological inactivation of adjacent sites in the tectum, resulted in deletions at adjacent sites of the excitatory receptive field of Imc neurons. Injections of biccuculine in the Imc abolished the inhibitory receptive fields of Imc neurons, suggesting that these are mediated by intranuclear inhibitory mechanisms.

On a grander scale, the focus of isthmo-tectal studies has examined this system's role in visual attention via a winner-take-all mechanism (Marin, Mpodozis, Sentis, Ossandon, & Letelier, 2005; Marin et al., 2007; Gruberg et al., 2006). How this might occur is inherent in the connectivity shown in Figure 3E. The retinal input to the tectum is to the superficial layers (Angaut & Reperant, 1976; Hunt & Webster, 1975; Remy & Gunturkun, 1991) and neurons in layer 10 project to SLu, Ipc, and Imc (Hunt & Kunzle, 1976; Wang et al., 2006). The reentrant signals from the SLu and Ipc are cholinergic and provide a positive feedback to the tectum. Concurrently, Imc neurons, which are GABAergic, project heterotopically to the tectum, SLu, and Ipc, effectively inhibiting activity throughout the tectum, except at the one locus (Wang et
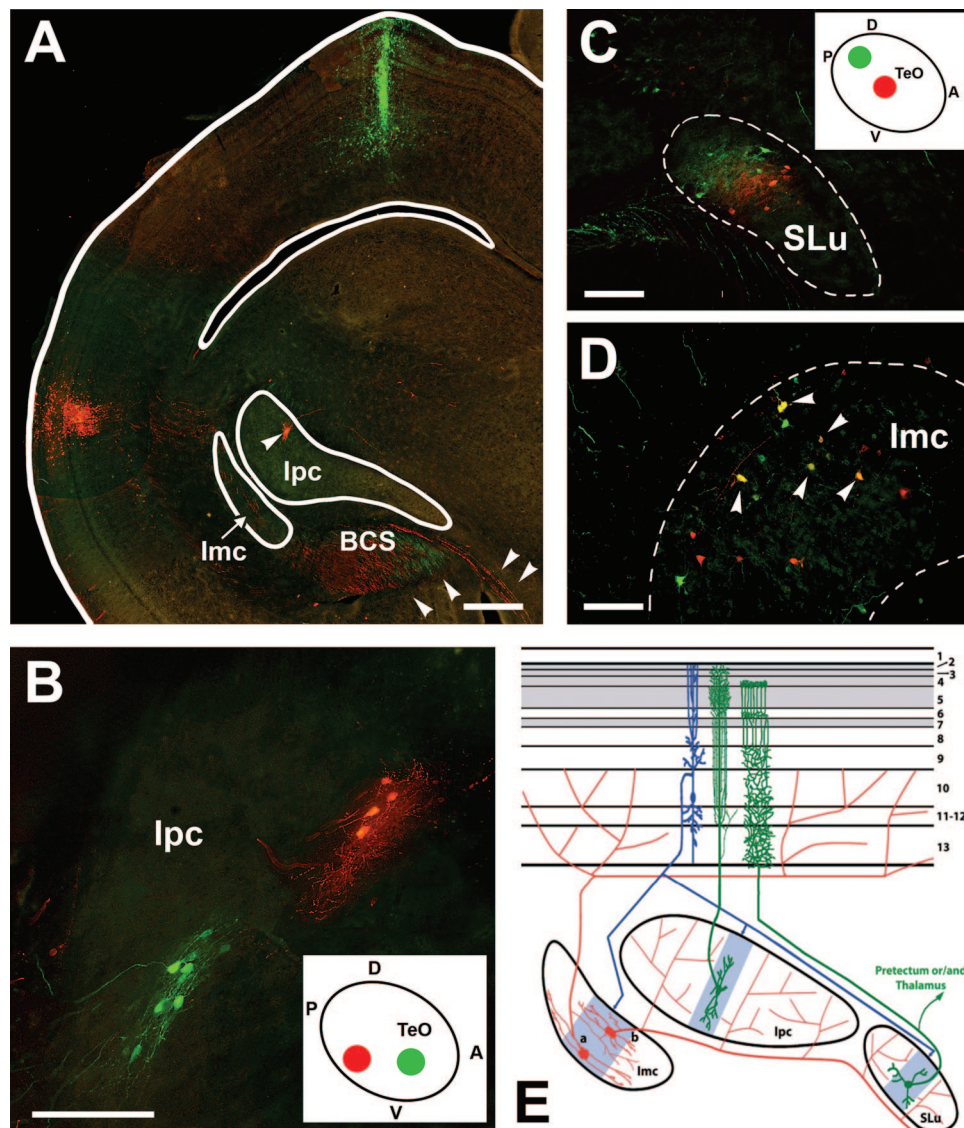
Figure 3. Connectivity of the isthmal nuclei with the tectum. (A) shows a coronal section through the tectum showing typical injections of fluorescent biotinylated dextran amines (BDA). A retrogradely labelled cell and anterogradely labelled terminals from the red injection can be seen in parvocellular nucleus isthmi (Ipc). The arrowheads in the lower right highlight fibres travelling along the brachium of the superior colliculus (BCS). (B) and (C) are photomicrographs showing retrogradely labelled cells set within tight clusters of fine terminals indicating the reciprocal connections of the tectum with the Ipc and nucleus semilunaris (SLu), respectively. The insets show the approximate locations of the injections of red and green fluorescent tracers in the optic tectum (TeO). (D) shows retrogradely labelled cells in the magnocellular division of nucleus isthmi (Imc) from the injections in the TeO as indicated in the inset for (C). This afferent projection is not topographic as Imc neurons project widely to TeO and there are several double labelled cells indicated in the photomicrograph (white arrows). (E) shows a schematic of the connectivity of the isthmal nuclei with the tectum (from Wang et al., 2006). See text for a detailed description. In all figures the photomicrographs are of coronal sections, the left side is lateral. A = anterior; P = posterior; D = dorsal; V = ventral. Scale bars: 600 µm in (A); 200 µm in (B–D).

al., 2004, 2006). Together, these excitatory and inhibitory mechanisms would augment activity associated with stimulation at a point in the visual field. The reentrant signals from Ipc and SLu are directed toward the dendrites of layer 13 cells (Wang et al., 2006), which are known as tectal ganglion cells (TGCs). It is interesting that the spatial topography is not maintained with the projections of TGCs (see below).

The tectum has other projections where the retinotopy is maintained (see Figure 4), although the functions of these projections have yet to be determined. There is a reciprocal projection with the ventral
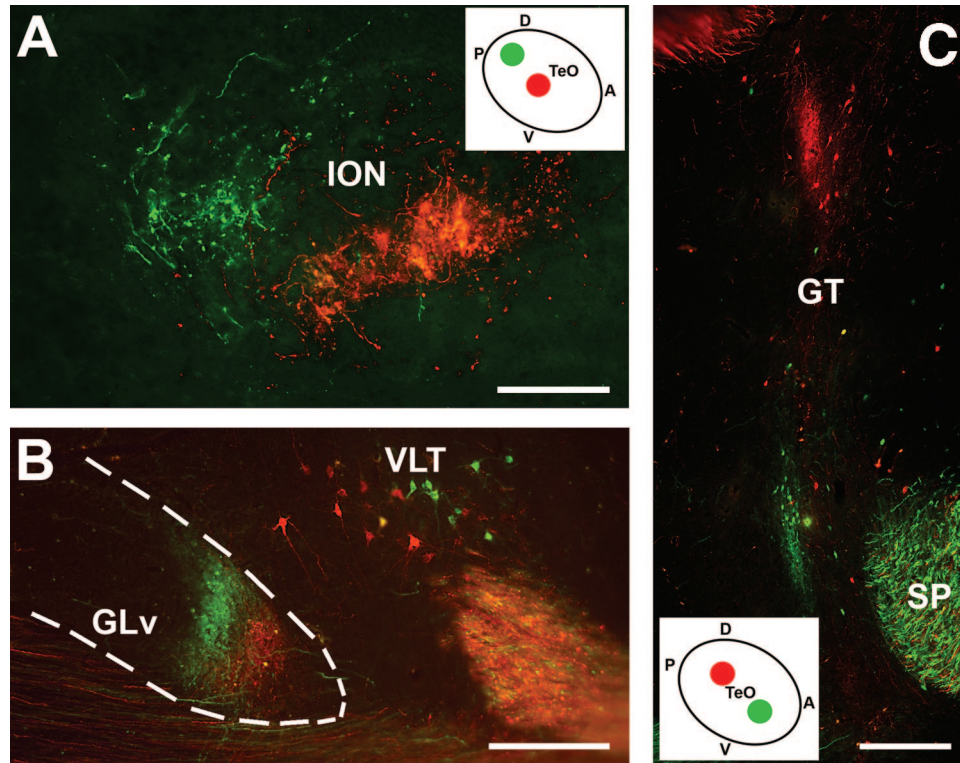
Figure 4. Nuclei having spatially topographic connections with the optic tectum (TeO). There are spatially topographic projections from the TeO to the isthmo-optic nucleus (ION; A), the ventral leaflet of the lateral geniculate nucleus (GLv; B) and the tectal grey (GT; C). There are also topographic afferent connections from the ventral lateral thalamus (VLT; B) and the GT (C). The inset in (C) showing a drawing of the injection sites in the TeO also applies to (B). A = anterior; P = posterior; D = dorsal; V = ventral; SP = nucleus subpretectalis. Scale bars: 600 μm in (A); 200 μm in (B, C).

lateral geniculate nucleus (GLv; Figure 4B), although the number of retrogradely labelled cells in GLv from tectal injections is always quite small (Brecha, 1978; Crossland & Uchwat, 1979; Hu, Naito, Chen, Ohmori, & Fukuta, 2004). This retinotopic map from the TeO is in register with a retinotopic projection from the retina (Crossland & Uchwat, 1979; Hu et al., 2004). The function of the GLv is not known, although it has been linked to both the optokinetic reflex and colour vision (Gioanni, Palacios, Sansonetti, & Varela, 1991; Hossokawa, Araki, Hamassaki-Britto, Wallman, & Britto, 1996). The tectum also has a reciprocal connection with the tectal grey (Figure 4C) and nucleus lentiformis mesencephali (LM not shown), which are adjacent parts of the pretectum (Hunt & Kunzle, 1976; Gamlin & Cohen, 1988; Hunt & Brecha, 1982). The function of the GT per se is not known, but the LM is critical for the optokinetic response (Gioanni, Rey, Villalobos, Richard, & Dalbera, 1983). The role of a spatially topographic connection with the tectum toward this behaviour is unknown. The tectum also has a clear topographic projection to the isthmo-optic nucleus (ION, Figure 4A) (Crossland & Hughes, 1978; Uchiyama & Watanabe, 1985). The ION provides a centrifugal projection to the retina and is thought to be involved in attention during feeding and the control of pecking (for review, see Repérant, Ward, Miceli, Rio, Medina, Kenigfest, et al., 2006). The ventromedial nucleus of the thalamus (VLT) receives nontopographic projection from the tectum, but has a loosely topographic projection to the deep layers of the tectum (Figure 4B) (Hunt & Kunzle, 1976; Brecha, 1978). The VLT is thought to play a role in coordinating bilateral visuomotor behaviour (Schulte, Diekamp, Manns, Schwarz, Valencia-Alfonso, Kirsch, et al., 2006).

Non-Topographic Projections of the Optic Tectum

One of the most extensively studied of the tectal efferent pathways is the projection to the nucleus rotundus (nRt), which is homologous to the pulvinar complex in mammals (Benowitz & Karten, 1976; Karten & Shimizu, 1989). Electrophysiological studies have shown that, although the nRt is not retinotopically organised, it has a clear functional topography. This is shown in Figure 5A, based on recordings of neurons in response to visual stimuli (Wang, Jiang, & Frost, 1993). Neurons in the dorsal-anterior nRt are responsive to colour or luminance, whereas the motion sensitive cells are found in the ventral, central and caudal nRt. Neurons in the dorsal-posterior region of rotundus are specialised for the detection of motion in depth ("looming"; Sun & Frost, 1997; Wang & Frost, 1992). Several studies have examined the tectal projection to the nRt. The input arises from the layer 13 TGCs, and retinotopy is absent in this projection (but see Hellmann & Gunturkun, 1999). Anterograde experiments show that the projections of individual TGCs project diffusely to nRt
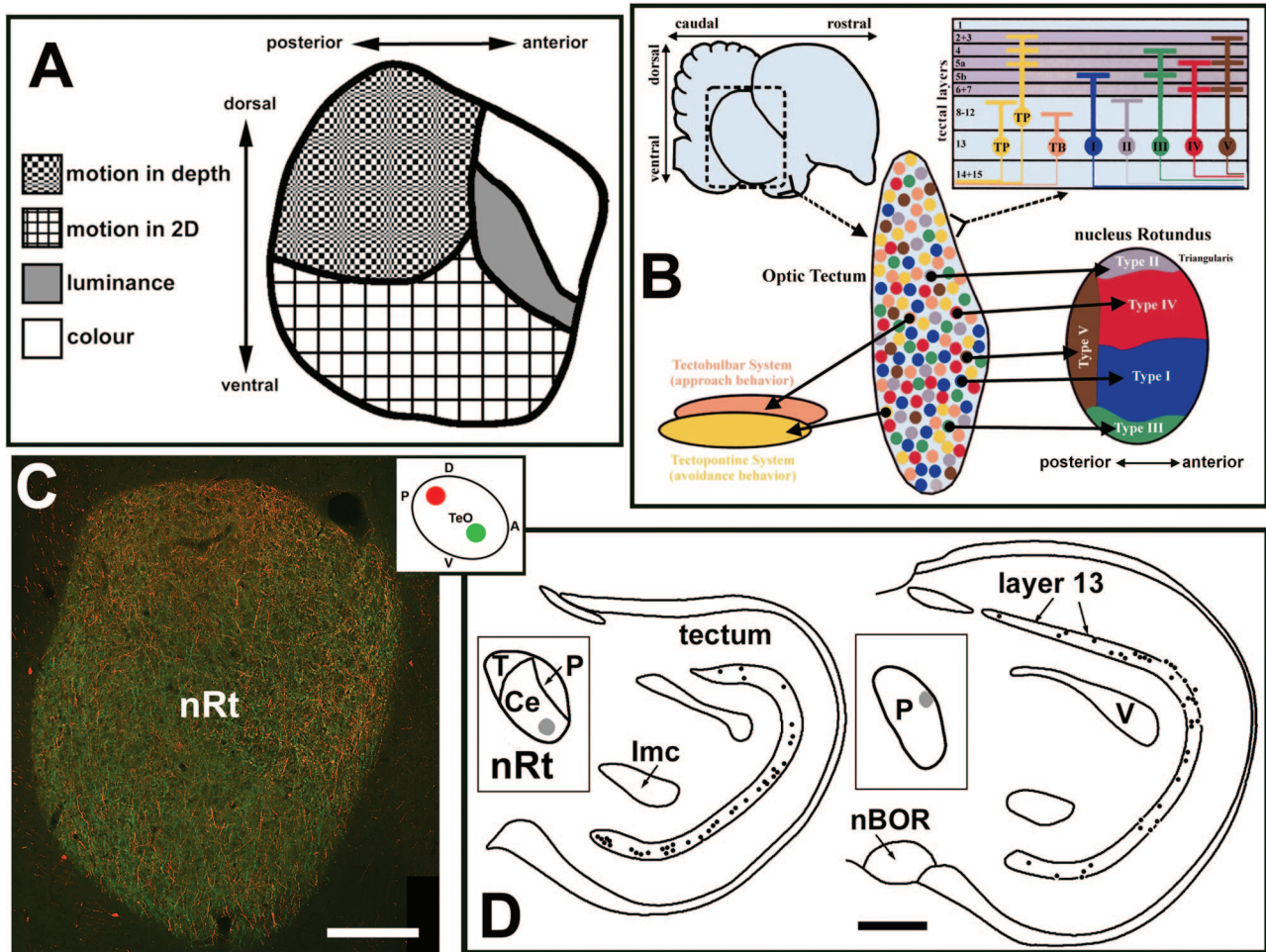
Figure 5. Functional topographic organisation of nucleus rotundus (nRT). **A** shows the topographical organisation of nRt with respect to processing of 3-D motion (looming), two-dimensional motion, colour, and luminance (from Wang, Jiang, & Frost, 1993). (B) shows the "tectal mosaic" proposed by Hellmann et al. (2004). Any point in layer 13 of the tectum consists of numerous cell types, each having a different arborization pattern in the superficial layers, and each projecting to different areas, either the subdivisions of nRt or to descending tectobulbar and tectopontine pathways. (C) shows anterograde labelling in nRt from localised injections of red and green fluorescent tracers in the tectum (TeO). Note that the labelling from both injections is very widespread. (D) shows retrograde labelling of layer 13 tectal ganglion cells from injections in the central (Ce) and posterior (P) regions of nRt. Note neurons are labelled throughout layer 13 from both injections (adapted from Marin, Letelier, Henny, Sentis, Farfan, Fredes, et al., 2003). nBOR = nucleus of the basal optic root; Imc = magnocellular nucleus isthmi. Scale bars; 300 μm in (C); 1 mm in (D).

(Figure 5C). Likewise, with retrograde studies, small injections of tracer into any region in nRt results in diffuse labelling throughout layer 13 (Figure 5D). Thusly, nRt neurons are sampling large parts of the visual field for the processing of stimulus properties, rather than location (Hellmann & Gunturkun, 1999; Hellmann, Gunturkun, & Manns, 2004; Karten, Cox, & Mpodozis, 1997; Marin et al., 2003). It would be incorrect, however, to conclude that the tectal-rotundal projection is nontopographic. Injections of retrograde tracer at adjacent sites in nRt, however close together, results in few double-labelled TGCs (Marin et al., 2003). Most important, different regions of nRt label different classes of TGCs. Hellmann et al. (2004) described five types of TGCs that project to nRt that can be distinguished morphologically. Type II and type IV cells project to the nucleus triangularis and dorsal anterior regions of nRt and are thusly likely involved in the processing of colour and luminance. The Type I and III neurons project to the ventral half of nRt, the same region where neurons respond to two-dimensional motion. Type V neurons project to the caudal nRt, corresponding roughly with the region specialised for looming stimuli. Shown in Figure 5B, Hellmann et al. (2004) proposed the tectal mosaic for a comprehensive description of the various functional projections of the tectum. The tectum consists of functionally distinct TGCs in layer 13, arranged within the retinotopic map, but with independent projections subserving different functions. That is, each point in the tectum, which represents a point in visual space, gives rise to several functional pathways. In this light, the tecto-rotundal

projection effectively transforms a retinotopy into a functional topography.

The tectum also has other efferent and afferent connections with several nuclei where the retinotopy is not maintained. These include parts of the dorsal thalamus (Figure 6B), the nucleus pretectalis (PT; Figure 6D), nucleus subpretectalis (SP; Figure 6D), the pontine nuclei (Figure 6C), and the archistriatum (Figure 6A; Brecha, 1978; Dubbeldam, den Boer-Visser, & Bout, 1997; Gamlin, Reiner, Keyser, Brecha, & Karten, 1996; Hunt & Brecha, 1982; Hunt & Kunzle, 1976; Manns et al., 2007; Mpodozis et al., 1996; Reiner, Brecha, & Karten, 1982; Theiss, Hellmann, & Gunturkun, 2003; Zeier & Karten, 1971). These nuclei are involved in various visuomotor behaviours.
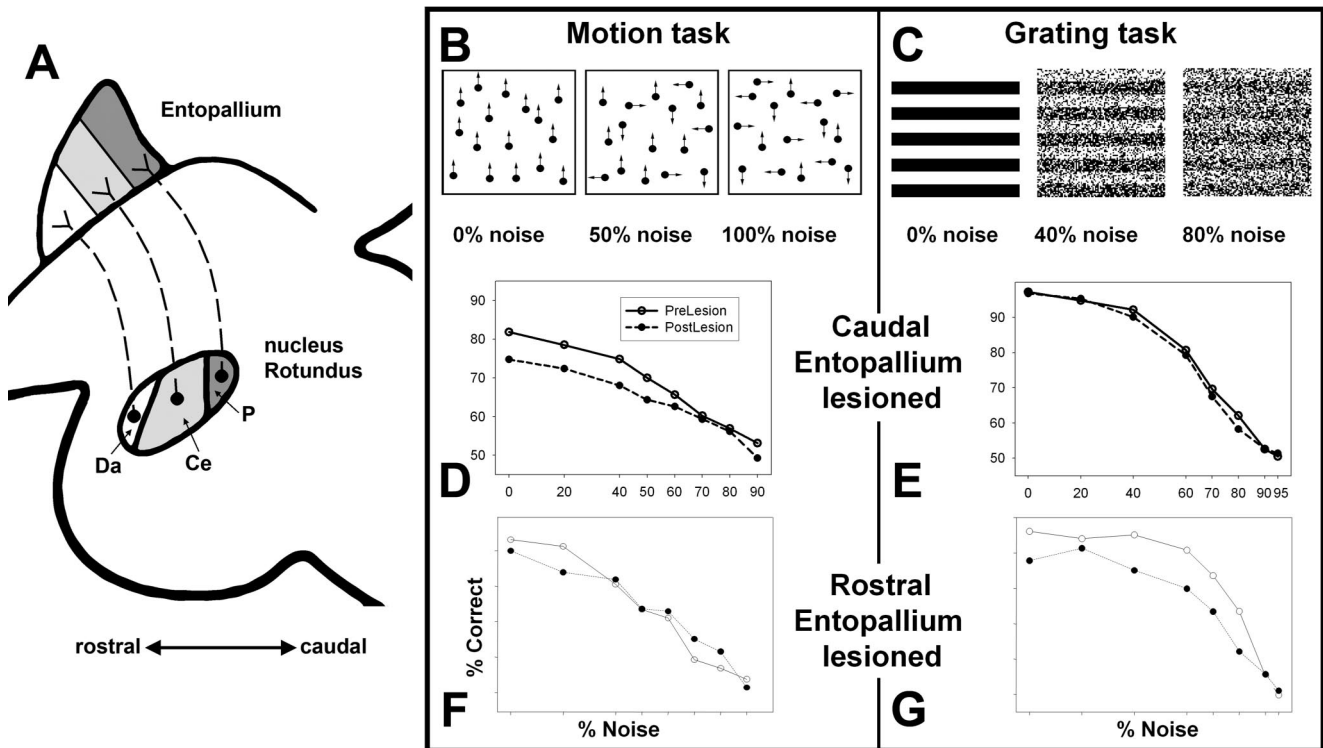
Topographic Connections from the Nucleus Rotundus to the Entopallium

The nRt projects topographically to the entopallium in the telencephalon, an area traditionally regarded as homologous with extrastriate visual cortex of mammals (Karten & Shimizu, 1989): the caudal nRt projects to the caudal parts of entopallium, and the rostral nRt projects to rostral entopallium (Figure 7A; Laverghetta &
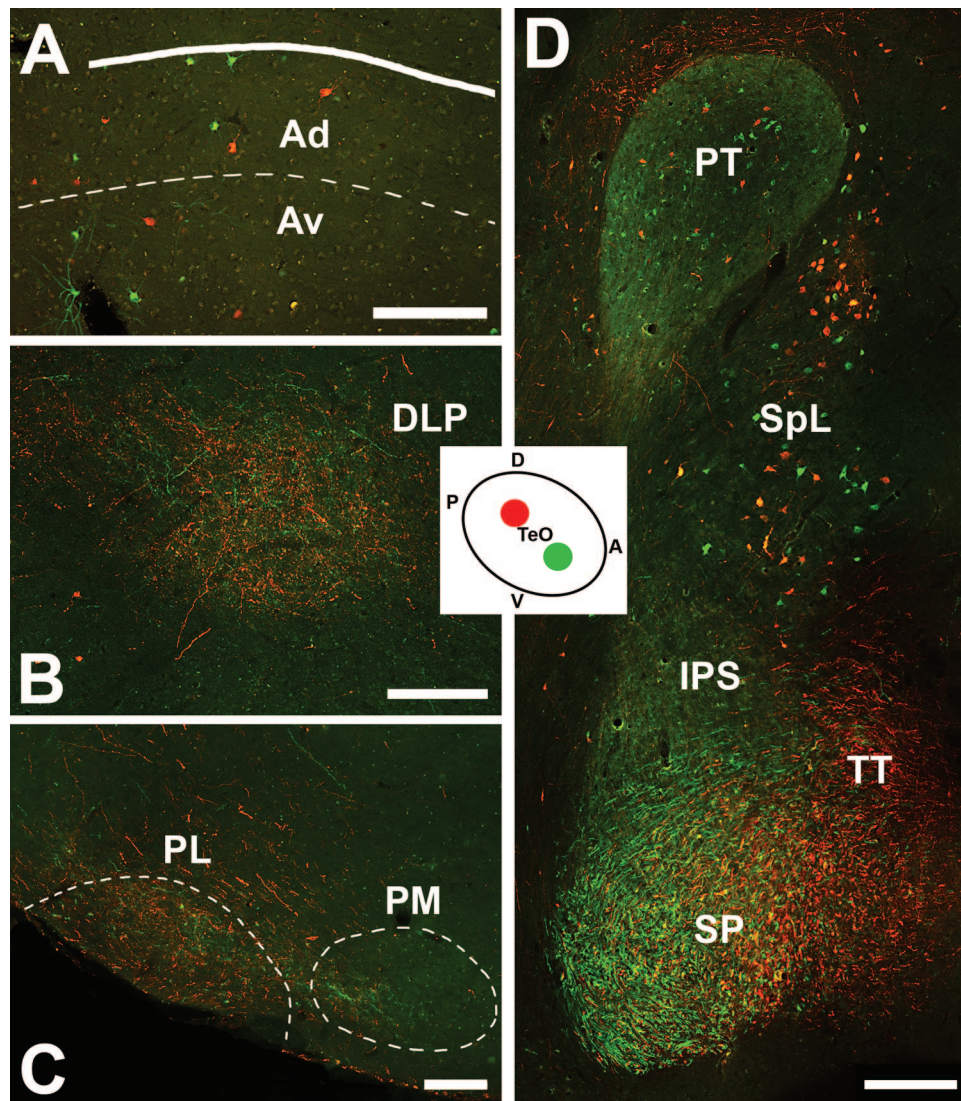
Figure 6. Nuclei having nontopographic connections with the optic tectum (TeO). From the injections shown in the central drawing, retrogradely labelled cells are shown in the dorsal and ventral divisions of the arcopallium (Ad, Av; A), the pretectal nucleus (PT; D) and lateral spiriform nucleus (SpL; D) and anterogradely labelled terminals are shown in the posterior nucleus of the dorso-lateral thalamus (DLP; B) the medial and lateral pontine nuclei (PM, PL; C) and the subpretectal nucleus (SP; D). Numerous fibres can also be seen coursing through the SP and tecto-thalamic tract (TT) en route to nucleus rotundus (D). IPS = nucleus interstitial pretecto-subpretectalis. A = anterior; P = posterior; D = dorsal; V = ventral. Scale bars: 200 μm in (A, B); 300 μm in (C, D).

Figure 7. Visual streams in the rotundal-entopallial projection. A shows the topographic projection from the nucleus rotundus to the entopallium (adapted from Laverghetta & Shimizu, 2003). Da, Ce, and P refer to the dorso-anterior, central and posterior subdivisions of the nucleus rotundus. (B–G) shows data from Nguyen et al. (2004) emphasising that there is a dissociation of motion and spatial vision in the entopallium. B and C respectively show the stimuli used to test motion and spatial vision: unidirectional motion of random dots in dynamic noise versus square wave gratings embedded in static noise. For both types of stimuli, the amount of noise can be varied from 0% to 100%. In (D–G), the effects of lesions to the caudal (D, E) and rostral entopallium (F, G) on performance on the motion (D, F) and spatial tasks (E, G) are shown. See text for details.

Shimizu, 2003; Miceli & Reperant, 1985; Nixdorf & Bischof, 1982). Thusly, one would expect a functional topography in the entopallium. Generally speaking, because the caudal nRt is involved in motion processing, the caudal entopallium should be involved in processing visual motion. Likewise, as the rostral nRt is involved in processing colour and luminance, the rostral entopallium should be involved in spatial vision of some sort. We (Nguyen et al., 2004) examined the effects of lesions to the entopallium on motion and spatial perception using the stimuli shown in Figure 7B and C. The motion stimuli were composed of moving dots in which the proportion of dots moving in the same direction could be varied from 0% (i.e., 100% dynamic noise) to 100% (all dots moving in the same direction). The spatial task was similar in that it involved the detection of horizontal or vertical bars imbedded in static noise, where the amount of noise could be varied. Lesions to the caudal entopallium resulted in impairments on the motion task (Figure 7D), whereas lesions to the rostral entopallium resulted in impairments on the spatial task (Figure 7G). Thusly, within the tectal-rotundal-entopallial pathway, there are subpathways specialised for processing visual motion and spatial vision (i.e., form and colour). Such a functional segregation of visual processing is reminiscent of what occurs in the dorsal and ventral streams of mammalian visual cortex (Milner & Goodale, 2008).

Concluding Thoughts

In this article, we have focused on a description of the topographic maps in the tectofugal visual pathway in birds. Although much work remains for a comprehensive description of tectal connectivity a great deal of study on tecto-isthmal connections and the tecto-rotundo-entopallial pathways has deepened our understanding of topographic maps in visual processing. The tecto-isthmal pathways involve an integral network of spatially topographic connections and speak to the selective attention when the visual system is faced with a deluge of stimuli, and the concept of a "winner-take-all process" in directing orienting movements to a particular location in the visual field (Marin et al., 2005; Marin et al., 2007; Wang et al., 2006; Wang et al., 2004). The tecto-rotundo-entopallial pathway involves a functional topography, concerned with stimulus attributes (motion, colour, form), but sacrificing localisation information (Hellmann et al., 2004; Marin et al., 2003; Wang, Luksch, Brecha, & Karten, 2005). It must be emphasised that the spatially topographic and functional topographic systems are very much interconnected. Indeed, the reentrant signals from Ipc and SLu target the dendrites of layer 13 TGCs that project to the nucleus rotundus (Wang et al., 2006).

Even at this point there seems to be a functional division as the Ipc targets dendrites of Type I TGCs (Wang et al., 2006), which innervate the ventral and posterior parts of nRT and are involved in motion processing (Luksch, Cox, & Karten, 1998; Luksch, Karten, Kleinfeld, & Wessel, 2001), whereas the SLu targets the dendrites of Type II TGCs, which innervate the dorsal part of nRT (Hellmann et al., 2004) and might be involved in colour processing (Wang et al., 1995). Wang et al. (2006) have suggested that Ipc and SLu serve, at least in part, to address the "binding" problem by temporally coordinating spatially coincident visual information (e.g., colour and motion of an object) that is processed in different parts of the tecto-rotundal-entopallial pathway.

Résumé

Au cours des dernières décennies, un nombre important de travaux ont été menés sur le système visuel géniculo-strié des primates. Cependant, les études du système visuel aviaire ont fourni une riche source de données contribuant à notre compréhension du traitement visuel. Dans cet article, nous effectuons une revue de la connectivité et de la fonction du tectum optique (homologue du colliculus supérieur) chez les oiseaux. Nous soulignons les projections rétinotopiques entre le tectum optique et les noyaux isthmiques, ainsi que les projections topographiques fonctionnelles entre le tectum optique et le noyau rotundus et l'entopallium (homologues du pulvinar et du cortex extrastrié, respectivement), où la rétinotopie a été sacrifiée. Ces travaux ont été cruciaux pour notre compréhension des processus visuels fondamentaux, incluant l'attention, le traitement parallèle et le problème du liage.

Mots-clés : cartes rétinotopiques, voies visuelles, noyau rotundus, entopallium, noyaux isthmiques

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