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Comparisons of Visual Properties between Tectal and Thalamic Neurons with Overlapping Receptive Fields in the Pigeon

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Key Words

Directional selectivity · Luminance · Receptive field · Speed selectivity · Tectofugal pathway · Thalamofugal pathway · Birds

Abstract

The present study is the first attempt to make comparisons of the visual response properties between tectal and thalamic neurons with spatially overlapping receptive fields by using extracellular recording and computer mapping techniques. The results show that in neuronal pairs about 70% of thalamic cells have excitatory receptive field alone, whereas 85% of tectal cells possess an excitatory receptive field surrounded by an inhibitory receptive field. In 70% of pairs the tectal cells are selective for direction of motion different from that which the thalamic cells prefer. Most thalamic cells prefer high speeds (80–160°/s), whereas tectal cells prefer intermediate (40°/s) or low (10–20°/s) speeds. Photergic and scotergic cells exist in the thalamus but not in the tectum. These results provide evidence that tectal and thalamic cells extract different visual information from the same region of the visual field. The functional significance of these differences is discussed.

Introduction

In nonmammals such as birds, the tectofugal and thalamofugal pathways are two main parallel paths for visual information processing. The tectofugal pathway goes from the optic tectum to the ectostriatum via the nucleus rotundus [Karten and Revzin, 1966; Karten and Hodos, 1970; Bischof and Watanabe, 1997]. The thalamofugal pathway runs from the nucleus opticus principalis thalami (OPT), also designated as the nucleus geniculatus lateralis pars dorsalis, of the dorsolateral thalamus to the visual wulst [Karten et al., 1973; Güntürkün and Karten, 1991; Deng and Rogers, 1998; Shimizu and Bowers, 1999].

Lesions of the tectofugal pathway in birds resulted in severe impairments in a variety of visual capabilities (e.g., intensity, color and pattern discrimination), whereas those of the thalamofugal pathway only produced small effects on these capabilities [Hodos and Karten, 1966; Hodos, 1969, 1993; Jarvis, 1974]. These differences could be explained by the fact that most retinal ganglion cells project to the tectum and pigeons fixate the key with the red field of the retina that has only a small projection to OPT [Remy and Güntürkün, 1991]. The tectofugal pathway may process stimulus localization and identification [Bischof and Watanabe, 1997] as well as object motion

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[Frost et al., 1990; Wang and Frost, 1992; Wang et al., 1993; Sun and Frost, 1998; Frost and Sun, 2003], and the thalamofugal pathway probably participates in the perception of self-motion [Wylie et al., 1998] and sun-compass-guided homing in pigeons [Budzynski et al., 2002].

Though extensive electrophysiological studies in birds have been performed separately on the receptive field organization and visual responses of tectal [Jassik-Gerschenfeld and Guichard, 1972; Hughes and Pearlman, 1974; Frost and Di Franco, 1976; Frost and Nakayama, 1983; Frost et al., 1990; Schmidt et al., 1999; Gu et al., 2000; Sun et al., 2002] and OPT cells [Britto et al., 1975; Jassik-Gerschenfeld et al., 1976; Pateromichelakis, 1981], the physiological differences between both visual centers remain unclear. Particularly, comparisons are lacking between the visual properties of tectal cells and those of OPT cells, both of which receive information from the same region of the visual field. Therefore, we intended to compare the visual properties of tectal cells with those of OPT cells with overlapping RF by using extracellular recording and computer mapping techniques.

Materials and Methods

Thirty-two pigeons *(Columba livia)* having body weights of 360–420 g were used and all procedures followed the guidelines for laboratory studies established by the Society for Neuroscience. The experimental procedures were previously described [Yang et al., 2002]. Briefly, each pigeon was anesthetized with urethane and then placed in a stereotaxic apparatus. The left tectum and caudal forebrain were exposed and the dura mater excised. The right eye was kept open and the left eye covered. A screen was placed 24 cm away from the viewing eye. The horizontal meridian of the visual field was rotated by 38° (visual angle) to meet the pigeon's normal conditions [Erichsen et al., 1989].

The excitatory receptive field (ERF) of an OPT cell was approximately plotted with a hand-held black square (2 × 2°) or precisely plotted with the computer in some cases [Fu et al., 1998; Yang et al., 2002]. Its inhibitory receptive field (IRF) was determined by lengthening a square stimulus (6 × 6°) up to 130° perpendicularly to its direction of motion [Frost et al., 1981; Schmidt et al., 1999; Wang et al., 2000a]. The cells' preferred direction was determined by motion at a speed of 20°/s randomly in eight directions spaced by 45°. The optimal speed was measured by motion in the preferred direction at speeds ranging from 10 to 160°/s. Then, 1–5 tectal cells were isolated whose ERF were all located within the OPT cells' ERF. Various parameters of these paired cells were measured to make comparisons between tectal and thalamic cells. Luxotonic responses of visual cells were examined at several luminance levels (1–60 lx) and maintained at each level for up to 30 min.

For extracellular recording, a micropipette (2–3 μm tip diameter) filled with 0.5 *M* sodium acetate and 2% pontamine-skyblue [Hellon, 1971] was stereotaxically advanced into the OPT [Karten and Hodos, 1967] or the tectum under visual control. Action potentials were amplified and fed into the computer for on-line or off-line analysis. The firing rate was averaged in three sweeps and the spontaneous firing rate was averaged in 10 s before visual stimulation. Some recording sites were marked with dye. Under deep anesthesia, the brain was removed and histologically processed for microscopic observation [Gu et al., 2000].

Results

A total of 42 thalamic cells and 51 tectal cells were isolated. Among them, 16 thalamic cells were paired with 41 tectal cells, ERF of each OPT cell covering ERF of one to five tectal cells because OPT cells usually had a much larger ERF than tectal cells. Other OPT cells and tectal cells could not be paired by ERF overlap and thus were omitted from further analysis. These paired OPT and tectal cells differed in their receptive field organization and size (fig. 1). Computer-mapped ERFs of OPT cells were 31 ± 23° (mean ± SD, n = 11) ranging from 10 to 85°, whereas those of tectal cells were 11 ± 5° (n = 25) ranging from 3 to 21°, generally increasing in size as the recording depth in the tectum was increased. Most OPT cells (69%) were characterized by an ERF alone and others (31%) by concentric ERF and IRF that was usually extended beyond the screen. In contrary, 85% of tectal cells possessed concentric ERF and IRF, and the IRF was 4.9 times larger than the ERF.

The distribution of computer-mapped ERFs of 14 OPT cells and 33 tectal cells in the visual field is shown in figure 2. It shows that ERFs of these OPT cells are mainly located in the lateral visual field, within 60° around the optic axis. Because the tectal cells examined in the present study are paired with the OPT cells, their ERFs are also located in the same region of the visual field.

The paired neurons were also different in their directional selectivity (fig. 3A, B). Among 28 cell pairs examined, 28.6% of the tectal cells preferred a direction opposite or orthogonal to that which the OPT cells preferred. Both tectal and OPT cells in 28.6% of the pairs had identical or no directionality. Either tectal or OPT cells in 42.8% of the pairs were selective for the direction of motion. Generally speaking, tectal cells preferred forward motion, whereas OPT cells preferred backward motion.

Paired OPT and tectal cells were selective for different speeds of motion (fig. 3C, D). In 62.1% of the pairs, OPT cells preferred high speeds (80–160°/s), whereas tectal cells preferred intermediate (40°/s) or low (10–20°/s) speeds. Both OPT and tectal cells in other pairs were selective for high (10.3%), intermediate (13.8%), or low (13.8%) speeds of motion.

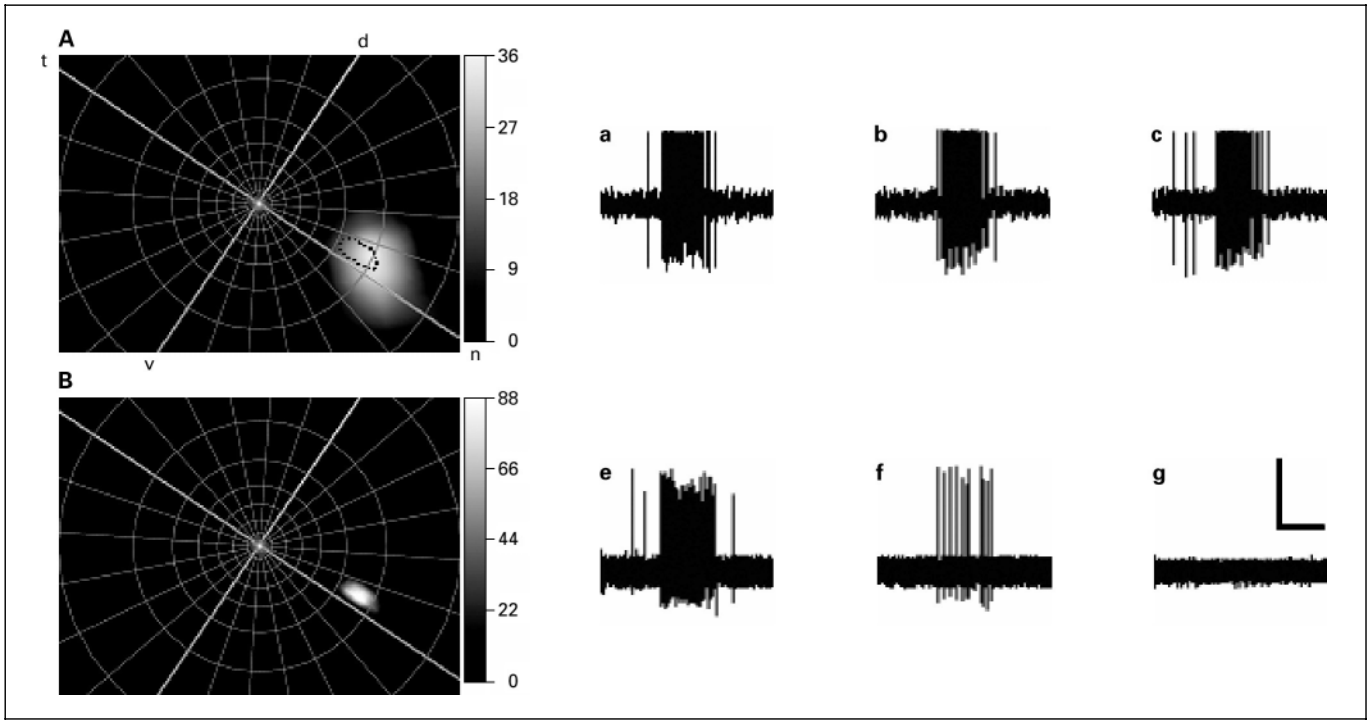

Fig. 1. Computer-mapped ERFs of paired OPT (**A**) and tectal (**B**) cells and their firing patterns. ERFs are delimited by equal firing rate as indicated by scales (spikes/s) on the right. Dotted ellipse in **A** shows ERF of cell **B**. Cell **A** was selective for motion at 160°/s in 315°, and cell **B** selective for 20°/s in 0 deg. Responses of cell **A** to motion of a rectangle of 6° wide and 6 (**a**), 24 (**b**) and 130 (**c**)° long show no IRF, and those of cell **B** to a rectangle of 3° wide and 3 (**e**), 12 (**f**) and 18 (**g**)° long show the existence of IRF. Letters d, t, v and n represent dorsal, temporal, ventral and nasal, respectively. Concentric circles are spaced by 10°. Scales: 200 μV, 0.5 s in **a–c**, and 140 μV, 1 s in **e–g**.

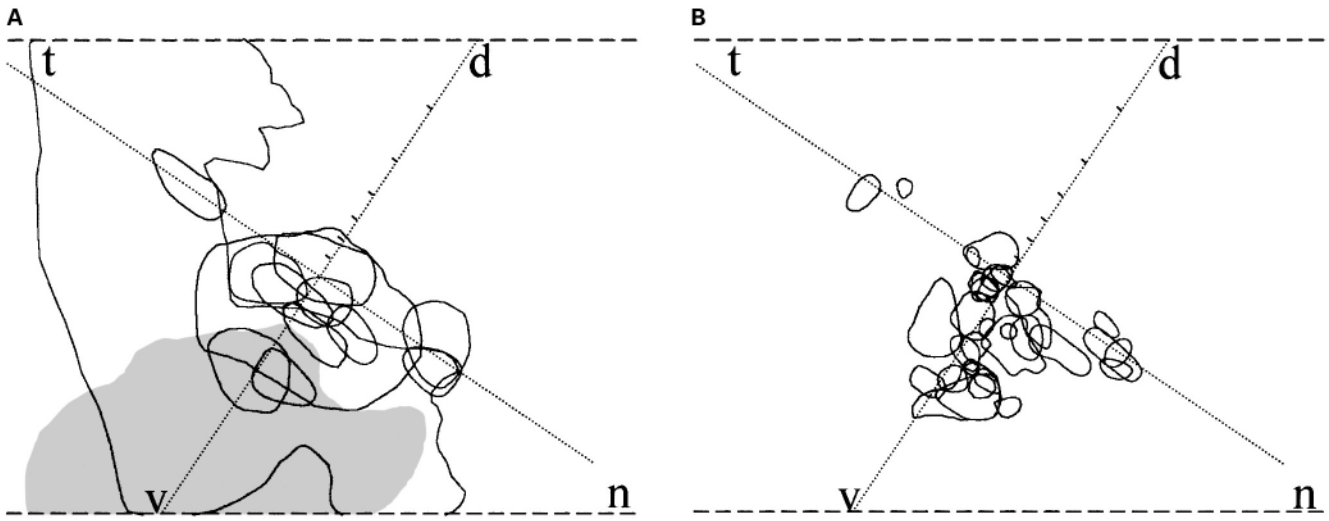

Fig. 2. Distribution of ERFs of paired OPT (**A**) and tectal (**B**) neurons in the visual field. These ERFs are mapped with a computer (see the Methods). The receptive field of a scotergic OPT neuron is partially shown in grey (**A**). Dashed horizontal lines represent the screen's top and bottom edges, indicating that the two largest receptive fields are truncated. The horizontal meridian of the visual field is rotated by 38° to meet the pigeon's normal conditions. Letters d, t, v and n represent dorsal, temporal, ventral and nasal, respectively. Scales represent 10°.

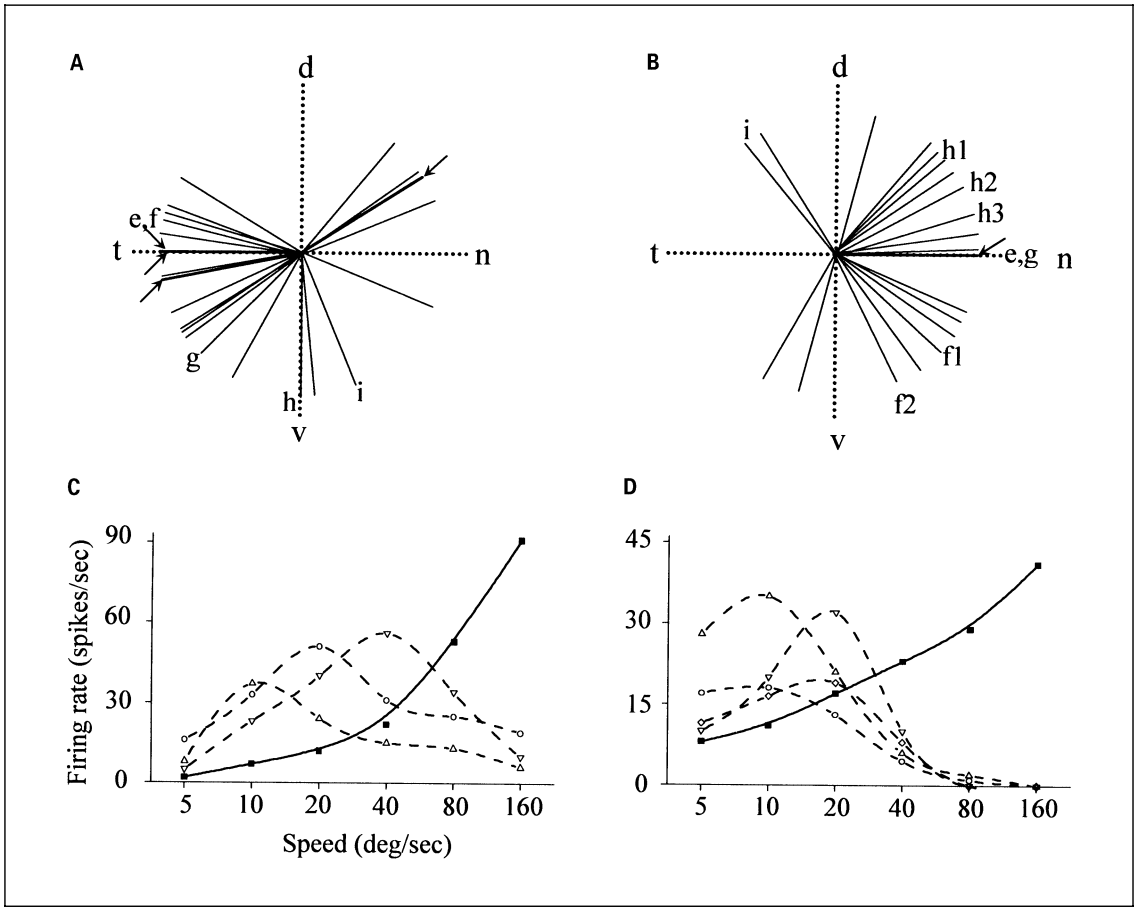

Fig. 3. Different selectivities between paired OPT and tectal cells for the direction (**A**, **B**) and speed (**C**, **D**) of visual motion. Distribution of directionalities is obtained by Gaussian fitting to the directional data collected in eight directions from 25 thalamic (**A**) and 24 tectal (**B**) cells. Oblique arrows point to two closely apposed lines. Identical letters e–i in **A** and **B** show five directional cells with one thalamic ERF overlapping one to three tectal ERFs. Speed tuning curves (**C**, **D**) show that two OPT cells (solid curves) prefer high speeds whereas paired three to four tectal cells (dashed curves) low speeds. Letters d, t, v and n represent dorsal, temporal, ventral and nasal, respectively.

Thalamic and tectal cells in pairs showed different responses to ambient luminance. Two OPT cells kept firing in the light but were silent in the dark, and their firing rates depended on light intensity. For example, when ambient luminance was increased from 1, 4 and 24 to 60 lx in steps, the firing rates of these photergic cells were increased from 0, 4.8, and 6.8 to 12.2 spikes/s, and from 0, 7.5 and 9.4 to 12.2 spikes/s, respectively. The third OPT cell behaved in just the opposite way (fig. 4). The firing rates of this scotergic cell were decreased from 10.2, 3.8 and 1.4 to 0.7 spikes/s when ambient luminance was changed as above. Their steady firing rates could be maintained for at least 30 min while luminance was kept at a constant level. The ERFs of these luxotonic cells were about 40 × 50, 30 × 40, and 60 × 90° in size, respectively (fig. 2). On the other hand, eight tectal cells paired with the three OPT cells did not elicit any luxotonic responses.

The recording sites of 12 thalamic cells were marked with dye within the OPT, including one in the nucleus lateralis anterior (LA), 8 in the nucleus dorsolateralis anterior thalami pars lateralis (DLL), and 3 in the nucleus dorsolateralis anterior thalami pars magnocellularis (DLAmc) according to the pigeon's brain atlas [Karten and Hodos, 1967]. The recording sites of 7 tectal cells were marked and their laminar distribution was one in each of layers 8, 11 and 12, and four in layer 13 in the tectum [see Luksch, 2003].

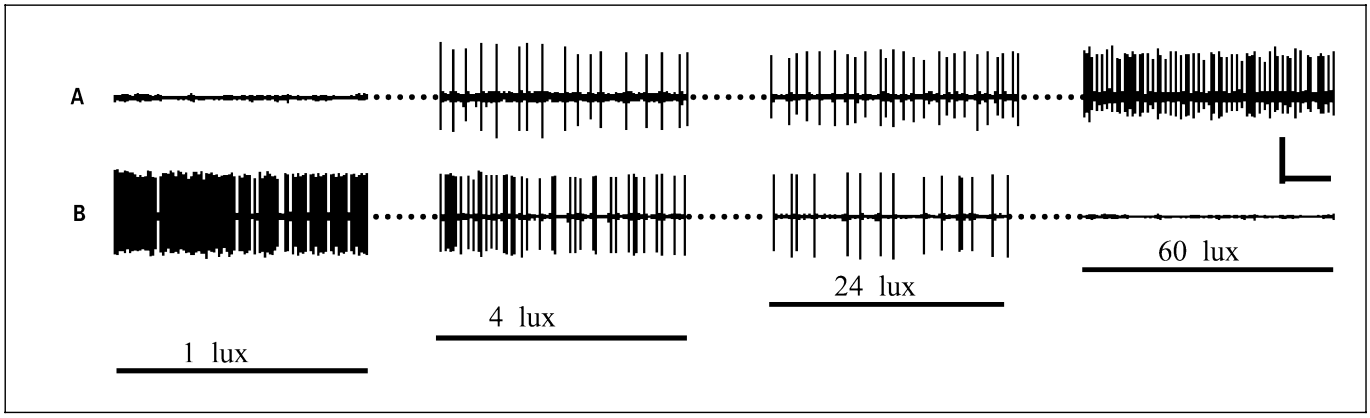

Fig. 4. Firing patterns of two luxotonic OPT cells (**A**, **B**) in response to stepwise changes in ambient luminance. Photergic cell **A** increased its firing rates as luminance was increased, whereas scotergic cell **B** behaved in the opposite way. Their steady firing rates were maintained for at least the 30 min tested while luminance was kept at a constant level. Bars beneath recording traces mark the duration of stimulation whose luminance levels are shown in lux. Scales: 150 μV in **A** and 200 μV in **B**, 1 s; interrupted lines represent duration of 45 s.

Discussion

The main finding of the present study is that OPT and tectal neurons with overlapping receptive fields in space extract different information from the same region of the visual field due to their differences in receptive field organization and selectivities for the direction and speed of stimulus motion, as well as responses to luminance. Most OPT cells are characterized by ERF without an inhibitory surround, whereas the majority of tectal cells paired with the OPT cells possess a concentrically organized ERF and IRF. It appears that ERFs of OPT cells are organized similarly to those of visual cells in the ventral tectum [Gu et al., 2000]. Generally speaking, ERFs in OPT cells are larger in dimensions than those of tectal cells. This difference might, if it is not exclusive, stem from differential inputs from the retina, i.e., large and medium ganglion cells project to OPT, whereas small retinal cells project to the tectum [Remy and Güntürkün, 1991]. This is the case with retinal projections to the tectum and thalamus in reptiles and mammals [Rapaport and Wilson, 1983; Martinez-Marcos et al., 2002].

The receptive fields of the OPT cells examined are mainly located in the lateral visual field in agreement with the finding that OPT receives retinal projections predominantly from the yellow field of the retina. Although the pattern of retinal afferents is quite different between the tectal and thalamic centers [Remy and Güntürkün, 1991], it is conceivable that ERFs of tectal cells paired with the OPT cells are also located in the same region of the visual field due to their overlapping receptive fields.

Paired tectal and OPT cells also differ in their directional selectivity in most cases. Most tectal cells prefer forward motion [Frost and Di Franco, 1976], whereas OPT cells prefer backward motion. It is evident that directional retinal cells project to both visual centers and not only to the tectum as suggested by Jassik-Gerschenfeld et al. [1976]. By comparison, OPT cells prefer high speeds, whereas tectal cells prefer intermediate and low speeds. This difference might be explained in part by the fact that there exist at least five groups of optic fibers in terms of impulse conduction speed, which all project to the tectum but only the four fastest groups project to the OPT [Mpodozis et al., 1995]. It seems that OPT cells might detect large or fast-moving targets, whereas tectal cells detect small or slow-moving ones within the same area of the visual field. These appear to support the notion that the tectofugal pathway is responsible for stimulus localization and identification [Bischof and Watanabe, 1997] and that the thalamofugal pathway might be involved in perception of self-motion or in distinguishing object-motion from self-motion. Further evidence is that the OPT receives input from the nucleus of the basal optic root and the pretectal nucleus lentiformis mesencephali, both of which detect optic flow induced by self-motion [Wylie et al., 1998], and that both nuclei could modulate visual responses of OPT neurons [Peng Cao, Yan Yang and Shu-Rong Wang, in preparation]. However, this modulation

might also exist in the tectofugal pathway as the nucleus of the basal optic root projects to the nucleus rotundus and exerts excitatory and inhibitory effects on rotundal cells [Wang et al., 2000b; Diekamp et al., 2001].

Furthermore, some OPT cells, but not tectal cells, could keep firing steadily as long as ambient luminance is kept at a constant value and its rate changes as luminance is changed. These photergic and scotergic cells [Kayama et al., 1979] have also been reported in diurnal and nocturnal reptiles, respectively [Wang et al., 1983]. It suggests that this luxotonic activity could be relevant to estimating ambient luminance [Kayama et al., 1979]. It is interesting to note that intrinsically photosensitive retinal ganglion cells synchronizing circadian rhythms with the solar day also project to the lateral geniculate nucleus, which is homologous to the OPT in nonmammals, and these cells respond to a step increase in illumination [Berson, 2003].

Acknowledgements

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References

Berson DM (2003) Strange vision: Ganglion cells as circadian photoreceptors. Trends Neurosci 26: 314–320.

Bischof HJ, Watanabe S (1997) On the structure and function of the tectofugal visual pathway in laterally eyed birds. Eur J Morphol 35:246–254.

Britto LRG, Brunelli M, Francesconi W, Magni F (1975) Visual response pattern of thalamic neurons in the pigeon. Brain Res 97:337–343.

Budzynski CA, Gagliardo A, Ioalé P, Bingman VP (2002) Participation of the homing pigeon thalamofugal visual pathway in sun-compass associative learning. Eur J Neurosci 15:197–210.

Deng C, Rogers LJ (1998) Bilaterally projecting neurons in the two visual pathways of chicks. Brain Res 794:281–290.

Diekamp B, Hellmann B, Troje NF, Wang SR, Güntürkün O (2001) Electrophysiological and anatomical evidence for a direct projection from the nucleus of the basal optic root to the nucleus rotundus in pigeons. Neurosci Lett 305:103–106.

Erichsen JT, Hodos W, Evinger C, Bessette BB, Phillips SJ (1989) Head orientation in pigeon: Postral, locomotor and visual determinants. Brain Behav Evol 33:268–278.

Frost BJ, Di Franco DE (1976) Motion characteristics of single units in the pigeon optic tectum. Vis Res 16:1229–1234.

Frost BJ, Nakayama K (1983) Single visual neurons code opposing motion independent of direction. Science 220:744–745.

Frost BJ, Sun HJ (2003) The biological bases of time-to-collision computation. In: Time-to-Contact, Advances in Psychology series (Hecht H, Savelsbergh GJP, eds), pp13–38. Amsterdam: Elsevier.

Frost BJ, Scilley PL, Wong SCP (1981) Moving background patterns reveal double-opponency of directionally specific pigeon tectal neurons. Exp Brain Res 43:173–185.

Frost BJ, Wylie DR, Wang YC (1990) The processing of object and self-motion in the tectofugal and accessory optic pathways of birds. Vis Res 30:1677–1688.

Fu YX, Gao HF, Guo MW, Wang SR (1998) Receptive field properties of visual neurons in the avian nucleus lentiformis mesencephali. Exp Brain Res 118:279–285.

Gu Y, Wang Y, Wang SR (2000) Regional variation in receptive field properties of tectal cells in pigeons. Brain Behav Evol 55:221–228.

Güntürkün O, Karten HJ (1991) An immunocytochemical analysis of the lateral geniculate complex in the pigeon *(Columba livia)*. J Comp Neurol 314:721–749.

Hellon RF (1971) The marking of electrode tip positions in nervous tissue. J Physiol 214:12.

Hodos W (1969) Color discrimination deficits after lesions of the nucleus rotundus in pigeons. Brain Behav Evol 2:185–200.

Hodos W (1993) The visual capabilities of birds. In: Vision, Brain, and Behavior in Birds (Zeigler HP, Bischof HJ, eds), pp 63–76. Cambridge MA: MIT Press.

Hodos W, Karten HJ (1966) Brightness and pattern discrimination deficits in the pigeon after lesions of nucleus rotundus. Exp Brain Res 2: 151–167.

Hughes CP, Pearlman AL (1974) Single unit receptive fields and the cellular layers of the pigeon optic tectum. Brain Res 80:365–377.

Jarvis CD (1974) Visual discrimination and spatial location deficits after lesions of the tectofugal pathway in pigeons. Brain Behav Evol 9:195–228.

Jassik-Gerschenfeld D, Guichard J (1972) Visual receptive fields of single cells in the pigeon's optic tectum. Brain Res 40:303–317.

Jassik-Gerschenfeld D, Teulon J, Ropert N (1976) Visual receptive field types in the nucleus dorsolateralis anterior of the pigeon's thalamus. Brain Res 108:295–306.

Karten HJ, Hodos W (1967) A Stereotaxic Atlas of the Brain of the Pigeon *(Columba livia)*. Baltimore MD: Johns Hopkins Press.

Karten HJ, Hodos W (1970) Telencephalic projections of the nucleus rotundus in the pigeon *(Columba livia)*. J Comp Neurol 140:35–52.

Karten HJ, Revzin AM (1966) The afferent connections of the nucleus rotundus in the pigeon. Brain Res 2:368–377.

Karten HJ, Revzin AM (1966) The afferent connections of the nucleus rotundus in the pigeon. Brain Res 2:368–377.

Karten HJ, Hodos W, Nauta WJ, Revzin AM (1973) Neural connections of the 'visual wulst' of the avian telencephalon. Experimental studies in the pigeon *(Columba livia)* and owl *(Speotyto cunicularia)*. J Comp Neurol 150: 253–278.

Kayama Y, Riso R, Bartlett JR, Doty RW (1979) Luxotonic responses of units in macaque striate cortex. J Neurophysiol 42:1495–1517.

Luksch H (2003) Cytoarchitecture of the avian optic tectum: neuronal substrate for cellular computation. Rev Neurosci 14:85–106.

Martinez-Marcos A, Lanuza E, Martinez-Garcia F (2002) Retinal ganglion cells projecting to the optic tectum and visual thalamus of lizards. Vis Neurosci 19:575–581.

Mpodozis J, Letelier JC, Concha ML, Maturana H (1995) Conduction speed groups in the retinotectal and retino-thalamic visual pathways of the pigeon *(Columbia livia)*. Int J Neurosci 81: 123–136.

Pateromichelakis S (1981) Response properties of visual units in the anterior dorsolateral thalamus of the chick *(Gallus domesticus)*. Experientia 37:279–280.

Rapaport DH, Wilson PD (1983) Retinal ganglion cell size groups projecting to the superior colliculus and the dorsal lateral geniculate nucleus in the North American opossum. J Comp Neurol 213:74–85.

Remy M, Güntürkün O (1991) Retinal afferents to the tectum opticum and the nucleus opticus principalis thalami in the pigeon. J Comp Neurol 305:57–70.

Schmidt A, Engelage J, Bischof HJ (1999) Single cell responses from the optic tectum of the zebra finch (*Taeniopygia guttata castanotis* Gould). J Comp Physiol A 185:69–79.

Shimizu T, Bowers AN (1999) Visual circuits of the avian telencephalon: Evolutionary implications. Behav Brain Res 98:183–191.
Sun HJ, Frost BJ (1998) Computation of different optical variables of looming objects in pigeon nucleus rotundus neurons. Nat Neurosci 1: 296–303.
Sun HJ, Zhao J, Southall TL, Xu B (2002) Contextual influences on the directional responses of tectal cells in pigeons. Vis Neurosci 19:133–144.
Wang SR, Yan K, Wang YT, Jiang SY, Wang XS (1983) Neuroanatomy and electrophysiology of the lacertilian nucleus isthmi. Brain Res 275: 355–360.
Wang Y, Xiao J, Wang SR (2000a) Excitatory and inhibitory receptive fields of tectal cells are differentially modified by magnocellular and parvocellular divisions of the pigeon nucleus isthmi. J Comp Physiol A 186:505–511.
Wang Y, Gu Y, Wang SR (2000b) Modulatory effects of the nucleus of the basal optic root on rotundal neurons in pigeons. Brain Behav Evol 56:287–292.
Wang YC, Frost BJ (1992) 'Time to collision' is signaled by neurons in the nucleus rotundus of pigeon. Nature 356:236–238.
Wang YC, Jiang SY, Frost BJ (1993) Visual processing in pigeon nucleus rotundus: Luminance, color, motion, and looming subdivisions. Vis Neurosci 10:21–30.
Wylie DR, Glover RG, Lau KL (1998) Projections from the accessory optic system and pretectum to the dorsolateral thalamus in the pigeon *(Columbia livia)*: A study using both anterograde and retrograde tracers. J Comp Neurol 391: 456–469.
Yang J, Li X, Wang SR (2002) Receptive field organization and response properties of visual neurons in the pigeon nucleus semilunaris. Neurosci Lett 331:179–182.