

Centrifugal innervation modulates visual activity of tectal cells in pigeons

JIAN-LI LI, QUAN XIAO, YU-XI FU, AND SHU-RONG WANG

Laboratory for Visual Information Processing, Institute of Biophysics, Academia Sinica, 15 Datun Road, Beijing 100101, China

(RECEIVED April 16, 1997; ACCEPTED October 7, 1997)

Abstract

Centrifugal modulation of visual responsiveness of tectal cells by the isthmo-optic nucleus (ION) through the retina was studied in homing pigeons. Visual activity evoked by computer-generated stimuli was reduced by an average of 59% in tectal cells whose receptive fields (RFs) either overlapped with, or were close to, those of isthmo-optic cells whose activity was blocked by the injection of lidocaine through micropipettes. Activity usually recovered to 87% of pre-drug controls in 8–17 min (average 12.3 min) after stopping lidocaine injections. Those tectal cells whose RFs were far from those of ION cells did not show clear-cut changes in their visual responsiveness to isthmo-optic lidocaine application. The spatial relationship between receptive fields of tectal and isthmo-optic cells, saline controls, as well as the specificity, reproducibility and reversibility of effects of ION-injected lidocaine on tectal activity, show that this chemical action is pharmacological, not toxicological. Neuronal circuitry underlying centrifugal modulation of tectal activity by isthmo-optic cells is discussed.

Keywords: Centrifugal innervation, Modulation, Optic tectum, Isthmo-optic nucleus, Lidocaine, Pigeon

Introduction

Extensive studies have shown the existence of centrifugal innervation of the retina in all classes of vertebrates and obvious interspecies differences in the location, number of subnuclei, and density of neurons of the centrifugal nuclei, which are mainly located in the midbrain and the diencephalon (review, see Uchiyama, 1989; Malz & Meyer, 1994). An example of the most extensively studied centrifugal or retinopetal structure is the isthmo-optic nucleus (ION) in ground-feeding birds such as pigeons and chickens. This nucleus and its surrounding region, the ectopic isthmo-optic nucleus (EN), are located in the caudal region of the midbrain, just dorsomedial to the optic tectum (OT). They project efferents to the contralateral retina, and additionally, EN also issues minor projection to the ipsilateral retina (Hayes & Webster, 1981; Weidner et al., 1987; Wolf-Oberhollenzer, 1987; Woodson et al., 1995). These centrifugal fibers terminate in either “convergent” or “divergent” modes (Maturana & Frenk, 1965; Fritzsche et al., 1990; Woodson et al., 1995) on amacrine cells and displaced ganglion cells (Maturana & Frenk, 1965; Cowan, 1970; Nickla et al., 1994; Woodson et al., 1995; Uchiyama et al., 1995). All these displaced ganglion cells project axons to the accessory optic system, including the nucleus of the basal optic root (nBOR) and the nucleus lentiformis mesencephali (nLM) (Nickla et al., 1994; Woodson et al., 1995).

Immunocytochemical studies have shown that centrifugal or retinopetal neurons in birds contain nitric oxide (Morgan et al., 1994), but are not immunostained for γ -aminobutyric acid (GABA) (Miceli et al., 1995). It has been suggested that this pathway may exert excitatory action on amacrine cells and/or displaced ganglion cells, which may use excitatory amino acids as transmitters (Uchiyama et al., 1995).

Electrophysiological properties of the receptive fields (RFs) of isthmo-optic neurons have been described by several authors (Holden & Powell, 1972; Miles, 1972*a*), showing that most neurons recorded from the nucleus discharge to onset and offset of a light spot in their RF centers, and are sensitive to target movement. A large number of cells habituate to repetitively presented visual stimulation. It has been reported that lesions of centrifugal pathway produce controversial deficits in both visual acuity and pattern discrimination (Shortess & Klose, 1977; Knipling, 1978; Hahmann & Güntürkün, 1992). However, there is evidence that lesions of the ION, but not of its surrounding region, are correlated with a post-lesion deficit in the grain-grit discrimination of pigeons, indicating a functional difference between the isthmo-optic nucleus and the ectopic isthmo-optic nucleus (Hahmann & Güntürkün, 1992).

Several attempts have been made to reveal the effects of electrical stimulation of the centrifugal pathway on electrophysiological properties of retinal ganglion cells. Stimulating the isthmo-optic tract (IOT) in chicks enhances ganglion cell visual responses to light flashed on and off, probably resulting from disinhibition of the RF inhibitory periphery, or facilitation of the excitatory central region of the receptive field (Miles, 1972*b*). This enhancement of visual responses, but not the suppression of the RF inhibitory

Reprint requests to: Shu-Rong Wang, Institute of Biophysics, Academia Sinica, 15 Datun Road, Beijing 100101, People's Republic of China.

surround, was confirmed by a later study in the quail showing that ION stimulation enhances visual responses of retinal ganglion cells to sine-wave gratings without affecting their spatial properties (Uchiyama & Barlow, 1994). The visual enhancement or facilitation could be explained by the finding that centrifugal inputs excite amacrine cells, which in turn activate retinal ganglion cells (Marchiafava, 1976; Uchiyama et al., 1995; Clarke et al., 1996). On the other hand, controversial results have been obtained regarding influence of centrifugal blockage on visual responses of retinal ganglion cells. Reversible cooling of the isthmo-optic tract does not produce obvious effects on visual responses of ganglion cells (Miles, 1972c), while cooling the isthmo-optic nucleus decreases their responsiveness to visual stimuli (Pearlman & Hughes, 1976).

To clarify this discrepancy and investigate the centrifugal modulation of tectal cells, we used the anesthetic lidocaine to reversibly block the isthmo-optic nucleus in pigeons. The results show strong influence of the centrifugal pathway on visual activity of tectal cells.

Methods and materials

The experiments were carried out on adult homing pigeons (*Columba livia*) of both sexes, weighing 350–460 g. The pigeon was anesthetized with urethane (20%, 1.0 ml/100 g body weight) and then placed on a stereotaxic apparatus. Body temperature was maintained at 41°C using a heating pad. The optic tectum and the cerebellum on the left side were surgically exposed, and the dura mater overlaying the tectum and the cerebellum were removed. The brain was protected from drying with liquid paraffin. The nictitating membrane of the right eye was cut, the eye kept open, and the left eye covered with an occluder.

Action potentials of tectal cells were extracellularly recorded with micropipettes filled with a solution containing 2 M NaCl and 100 mM CoCl₂, having 1–3 μm tip diameter and 5–15 MΩ impedance. Neuronal signals were conventionally amplified and fed into a storage oscilloscope and a computer for further data processing. A two-barreled micropipette was used to locate the ION and apply an anesthetic. The recording channel was filled with 2 M NaCl and 100 mM CoCl₂, and the other, which was connected to a pneumatic picopump (World Precision Instruments, Sarasota, FL, USA, PV800), contained 2% lidocaine hydrochloride. Guided by the stereotaxic coordinates of the ION (Karten & Hodoss, 1967), the two-barreled pipette was driven into the nucleus using a stepping motor attached to the stereotaxic apparatus. An isthmo-optic cell was identified and the location and extent of its RF were plotted with a 1-deg moving light spot (contrast = 0.98) on a screen, which was 110 deg (horizontal) × 100 deg (vertical) in size and 40 cm away from the viewing eye. The pipette was withdrawn from the brain, its tip was broken to 15–20 μm in diameter, and it was then re-inserted at the same stereotaxic coordinates in preparation for injecting lidocaine. To examine centrifugal effect of the ION on the visual responses of tectal cells, 10–15 nl of lidocaine solution was pressure injected (Fig. 1). The location and extent of each tectal cell's RF were also drawn on the screen. A computer-generated light spot (2 deg) was rear projected through a three-color projector (Electrohome ECP400) on the screen, and moved at angular velocities 10–20 deg/s randomly in eight directions (0 deg—nasal, 45 deg, 90 deg—dorsal, 135 deg, 180 deg—temporal, 225 deg, 270 deg—ventral, and 315 deg). The light spot scan path was longer than the largest extent of RF. There was a 4- to 6-s interval between consecutive stimulations to prevent fatigue. Three sweeps were usually superimposed for each direction. Com-

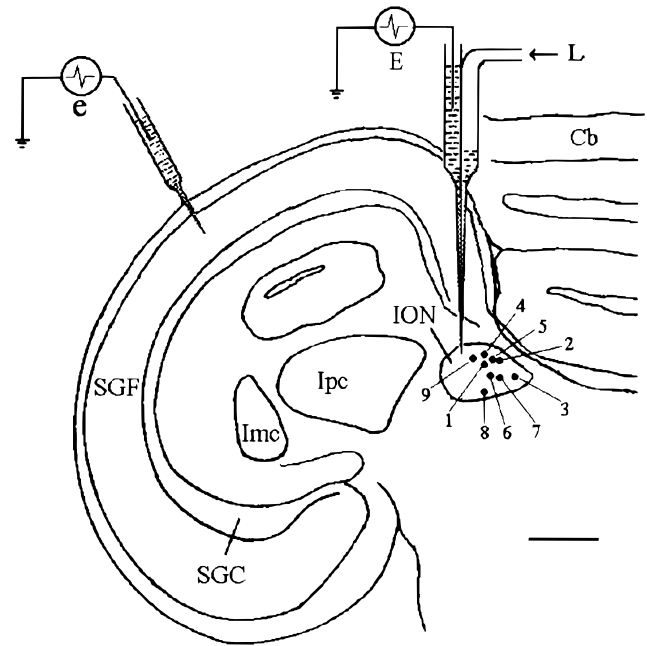


Fig. 1. Experimental arrangement and distribution of cobalt-sulfide marked lidocaine injection sites within the left isthmo-optic nucleus (ION). A two-barreled pipette was used both for recording (E) visual activity from the ION and injecting lidocaine (L) at the sites where visual activity was found. Solid spots numbered 1–9 represent locations of nine isthmo-optic cells and sites of injection in the rostrocaudal extent. Their receptive fields are shown in Fig. 3 with corresponding numbers. Second pipette (e) was used for recording tectal activity. Cb: cerebellum; Imc: nucleus isthmi pars magnocellularis; Ipc: nucleus isthmi pars parvocellularis; SGC: stratum griseum centrale; and SGF: stratum griseum et fibrosum superficiale. Scale bar = 1.0 mm.

parisons were made between response strengths of tectal cells recorded before, during, and after the injection of lidocaine into the isthmo-optic nucleus. In some experiments, physiological saline solution (0.9% NaCl) was injected into the nucleus as a control.

To mark the lidocaine-injection positions in the ION, and occasionally the recording sites in tectum, cobalt ions were iontophoretically ejected from the pipette tips with rectangular current pulses of 5–10 μA in intensity and 0.1–0.5 s in duration for 10–15 min (Wang et al., 1981). The brain was removed from the skull and immersed for 35–40 min in a 10% ammonium sulfide solution to form a black precipitate (CoS). The brain block was then fixed for 24 h in 4% paraformaldehyde, and immersed in 30% sucrose solution overnight. Frozen sections were cut at 100-μm thickness, and counterstained with cresyl violet. Sections were dehydrated and covered for microscope observation.

Results

In preliminary experiments, the location of the isthmo-optic nucleus in pigeons was determined both by its stereotaxic coordinates, and by visual responses characterized by sensitivity to target motion, often with minimum responses to posterior movement. Seven marked sites were all localized within the nucleus, indicating reliability of locating the ION.

Thirty-three visual cells were sampled from the optic tectum in 13 pigeons. Their recording depth ranged from 100 μm to

1000 μm , corrected for electrode angle, equivalent to the stratum griseum et fibrosum superficiale (SGFS), or tectal layers IIa-j (Cowan et al., 1961). The cobalt-sulfide marked sites of two of these cells were in layers IIg-h. The size of receptive fields of these tectal cells ranged from 7 deg to 23 deg ($13 \text{ deg} \pm 4 \text{ deg}$, mean \pm s.d.), whereas that of the ION cells' RFs had a mean diameter of $14 \text{ deg} \pm 4 \text{ deg}$, ranging from 10 deg to 23 deg. The RFs were larger than those measured by Holden and Powell (1972, 3 deg–10 deg), but similar to those by Miles (1972a, 5 deg–20 deg). The measured size probably depends on the size, contrast, and motion of the stimuli used for plotting RFs, as well as on ambient illumination and the sample of cells. The receptive fields of 31 tectal cells either overlapped with, or were close to, those of the isthmo-optic cell at the site where lidocaine was ejected. By "close to" we mean that the shortest distance between the neighboring boundary lines of two RFs was within several degrees of visual angle. The paired *t*-test was made on each cell of the 31 cells using spike numbers of three trials, and it showed that the decrease in spike number following lidocaine application was highly significant for 27 of the 31 cells ($P < 0.01$). The firing rate of these cells was steady and changed by an average of $17 \pm 6\%$ from trial to trial in control experiments. Visual responses of these cells were reduced by 59% (maximum of 96%, minimum of 43%) 0.5–4 min (average 1.9 min) after injection of lidocaine into the ION. This suppression usually recovered to 87% of pre-drug controls in 8–17 min (average 12.3 min) after stopping lidocaine injection into the ION (Fig. 2). Generally speaking, directional selectivity was not significantly changed by lidocaine. Four others did not show a significant change in their visual responsiveness to isthmo-optic lidocaine application (paired *t*-test, $P > 0.01$). It was probably due to their labile firing, which changed by an average of $34 \pm 2\%$ from control to control trial. The receptive fields of the remaining two cells were outside those of the isthmo-optic cells, separated by 26 deg and 37 deg, respectively, and their visual responses were not significantly changed (paired *t*-test, $P > 0.05$) after lidocaine application. These two cells were steadily discharging with a fluctuation of $18 \pm 5\%$ during three pre-drug trials. It appeared that the effect of lidocaine ejected into the ION on visual responses of tectal cells was not related to recording depths. Therefore, the spatial relationship between receptive fields of the tectal cells examined and those of the isthmo-optic cells whose sites were chemically blocked by lidocaine was an essential factor, in determining whether tectal activity was affected by isthmo-optic blockage (Fig. 3). Nine injection sites were marked, and all were localized within the nucleus (Fig. 1). The receptive fields of the isthmo-optic cells corresponding to these sites were distributed in the inferior visual field, more (56%) in the anterior-inferior field, which corresponded to the posterior superior retina.

As a control, we examined the action of physiological saline solution injected into the ION on visual responses of three tectal cells in two pigeons, whose receptive fields overlapped with those of the isthmo-optic cells. The total number of visual spikes before and during saline application was not significantly changed ($P > 0.05$), indicating that hydraulic pressure or saline itself had no effect at all on tectal firings. In three additional pigeons, possible effects of lidocaine diffusion on tectal activity were examined on three cells by ejecting 2–3 times the normal volume of lidocaine into a region dorsal to the ION. Changes of visual responsiveness in these tectal cells averaged 13%, statistically showing the absence of lidocaine diffusion effects (paired *t*-test on each cell, $P > 0.05$). In fact, the injection sites were usually 5–7 mm away from the recording sites, and this distance is too long for such a small

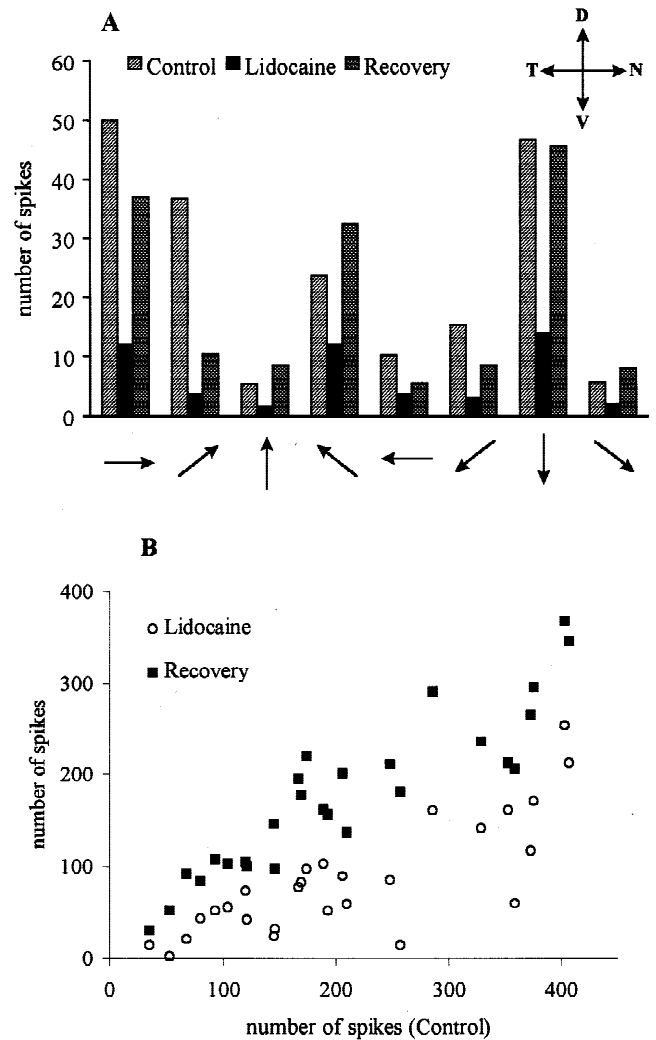


Fig. 2. Effects of lidocaine injected into ION on visual responses of a tectal cell to a 2-deg light spot moving through its RF in randomly ordered eight directions (arrows) (A). Note that visual responses were significantly reduced by lidocaine and then recovered in every direction. Each bar gives the activity evoked by three sweeps of the stimulus. N, D, T, and V represent nasal, dorsal, temporal, and ventral, respectively. Visual responses were significantly reduced by lidocaine (circles), and recovered (squares) after stopping lidocaine application (B). The abscissa represents the average of the total number of spikes calculated in all eight directions for three sweeps, and the ordinate represents the average number of spikes recorded during and after lidocaine application.

volume of lidocaine to diffuse to the tectal cells (Wang et al., 1995). Also, the above-mentioned topography of lidocaine effects with respect to spatial relationship between RFs of the isthmo-optic and tectal cells implied that lidocaine diffusion was unlikely to play a role in depressing tectal activity.

Discussion

By showing that lidocaine injected into the isthmo-optic nucleus significantly depressed visual activity in the optic tectum, the present study clearly indicates that the avian centrifugal pathway exerts powerful control over visual responses of tectal cells. In fact, lidocaine is a local anesthetic, which operates as a sodium-ion channel

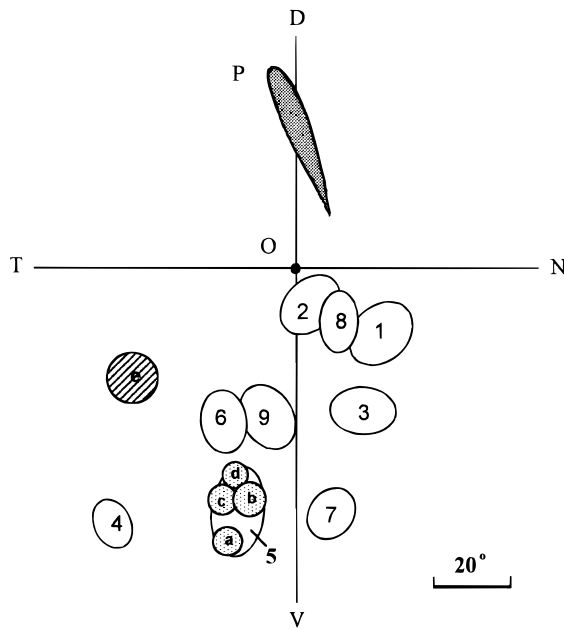


Fig. 3. Locations and extents of receptive fields of nine isthmo-optic cells (1–9; open ovals) where lidocaine was injected. Case 5 is an example in which the RFs of tectal cells a–d (stippled) overlapped with the RF of ION cell 5, whereas that of tectal cell e (hatched) was outside the RF of ION cell 5. The visual responses decreased for cells a–d, but not for cell e following lidocaine injection into the site where ION cell 5 was localized. Locations of these ION cells are marked in Fig. 1 with corresponding numbers. Pecten (P) in the lower retina was plotted with an ophthalmoscope in the upper visual field on the screen. N, D, T, and V represent nasal, dorsal, temporal, and ventral, respectively. O: optic axis. Scale bar = 20 deg.

blocker. Lidocaine blockage is not due to hydraulic pressure of injections in the ION, as shown in control experiments in which saline injection had no effect on tectal firings. It is most unlikely that lidocaine action on tectal cells is mediated by drug diffusion from its injection sites to cells recorded in tectum, because there exists a retinotopic relationship between the receptive fields of the isthmo-optic cells where lidocaine is injected and those of the tectal cells responding to chemical blockage. This is reminiscent of the previous finding that lidocaine injected into the nucleus isthmi pars magnocellularis (Imc) in pigeons significantly (75%) decreases visual responses of the tectal cells whose RFs are located within RFs of the isthmic cells where lidocaine is injected (Wang et al., 1995). It appears that there exist at least two positive feedback actions on visual cells of the tectum, one being exerted *via* the direct tectum-Imc-tectum pathway and the other *via* the indirect tectum-ION-retina-tectum route. It is interesting to note that axonal projection from the ION directly to tectum is present in the chick embryo but absent in the hatched chick. Moreover, some of the embryonic isthmo-tectal fibers are collaterals of axons normally projecting to the retina (Wizenmann & Thanos, 1990). The present results are in accordance with the findings by Pearlman and Hughes (1976) that cooling the ION results in depression of visual activity of retinal ganglion cells, but not with Miles (1972c). It seems likely that the probe the latter author used for cold blocking the isthmo-optic tract was too thick (1.7 mm × 0.8 mm). Cooling may have failed if the static pressure exerted on tract by the probe may have already depressed transmission to the retina. Our results are also indirectly supported by the fact that activation of the centrifu-

gal system enhances visual responses of retinal ganglion cells (Galifret et al., 1971; Miles, 1972b; Uchiyama & Barlow, 1994).

Immunocytochemical studies have shown that centrifugal fibers to the avian retina contain nitric oxide (Morgan et al., 1994), but not GABA (Miceli et al., 1995), and that their recipient cells are immunostained for aspartate and glutamate, two excitatory amino acids as neurotransmitters (Uchiyama et al., 1995). These findings are supported by intracellular recordings showing that excitatory postsynaptic potentials (EPSPs) are evoked in the turtle ganglion cells and amacrine cells by activation of centrifugal fibers, suggesting that the centrifugal pathway exerts significant influence on the retinal output (Marchiafava, 1976). These may explain the present results and the suppression of visual activity of ganglion cells by cooling the ION (Pearlman & Hughes, 1976), as well as the enhanced responsiveness of ganglion cells by activation of the centrifugal system (Galifret et al., 1971; Miles, 1972b; Uchiyama & Barlow, 1994). These observations could be also explained by the suggestion that centrifugal fibers activate the association amacrine cells which make inhibitory contacts with ordinary amacrine cells that in turn exert inhibitory action on retinal ganglion cells (Uchiyama, 1989). This proposed model of centrifugal modulation of retinal ganglion cells in birds is in accordance with neuroanatomical findings (Ramon y Cajal, 1889; Uchiyama & Ito, 1993). These two types of connections are similarly proposed in the circuit model for visual attention switching by Clarke et al. (1996).

The fact that the ION in ground-feeding birds is much more developed than that in birds of prey (Cowan & Clarke, 1976; Wolf-Oberhollenzer, 1987; Weidner et al., 1987; Feyerabend et al., 1994) may give some cues to reveal its functional significance. This centrifugal system is postulated to act as a “searchlight” in ground-feeding birds, highlighting or alerting them to threatening stimuli in their upper visual field (Uchiyama, 1989; Holden, 1990). In fact, this system has a heterotopic organization, i.e. ION receives its major input from the dorsal retina *via* tectum and projects primarily to the ventral retina (Holden, 1990; Woodson et al., 1995; Clarke et al., 1996). The interconnection between the two parts of the retina might be mediated by intrinsic interneurons (Woodson et al., 1991), or by the propriorectal neurons which project long axons from the ventral retina to the dorsal retina and make contacts with ordinary amacrine cells there. These amacrine cells could inhibit ganglion cells throughout the dorsal retina involved in ground feeding. Therefore, local enhancement of the ventral retina and long-range inhibition in the dorsal retina would result in visual attention switching (Clarke et al., 1996). Our findings lend considerable support to the notion that the ventral retina is somehow connected to the dorsal retina.

Acknowledgments

This work was supported by the National Natural Science Foundation of China and the Chinese Academy of Sciences.

References

- CLARKE, P.G.H., GYGER, M. & CATSICAS, S. (1996). A centrifugally controlled circuit in the avian retina and its possible role in visual attention switching. *Visual Neuroscience* **13**, 1043–1048.
- COWAN, W.M. (1970). Centrifugal fibers to the avian retina. *British Medicine Bulletin* **26**, 112–118.
- COWAN, W.M., ADAMSON, L. & POWELL, T.P.S. (1961). An experimental study of the avian visual system. *Journal of Anatomy* **95**, 545–563.
- COWAN, W.M. & CLARKE, P.G.H. (1976). The development of the isthmo-optic nucleus. *Brain, Behavior, and Evolution* **13**, 345–375.

- FEYERABEND, B., MALZ, C.R. & MEYER, D.L. (1994). Birds that feed-on-the-wing have few isthmo-optic neurons. *Neuroscience Letters* **182**, 66–68.
- FRITZSCH, B., CRAPON DE CAPRONA, M.D. & CLARKE, P.G. (1990). Development of two morphological types of retinopetal fibers in chick embryos, as shown by the diffusion along axons of a carbocyanine dye in the fixed retina. *Journal of Comparative Neurology* **300**, 405–421.
- GALIFRET, Y., CONDÉ-COURTINE, F., REPÉRANT, J. & SERVIÈRE, J. (1971). Centrifugal control in the visual system of the pigeon. *Vision Research (Suppl.)* **3**, 185–200.
- HAHMANN, U. & GÜNTÜRKÜN, O. (1992). Visual discrimination deficits after lesions of the centrifugal visual system in pigeons (*Columba livia*). *Visual Neuroscience* **9**, 225–233.
- HAYES, B.P. & WEBSTER, K.E. (1981). Neurons situated outside the isthmo-optic nucleus and projecting to the eye in adult birds. *Neuroscience Letters* **26**, 107–112.
- HOLDEN, A.L. & POWELL, T.P.S. (1972). The functional organization of the isthmo-optic nucleus in the pigeon. *Journal of Physiology* **223**, 419–447.
- HOLDEN, A.L. (1990). Centrifugal pathway to the retina: Which way does the “search light” point? *Visual Neuroscience* **4**, 493–495.
- KARTEN, H.J. & HODOS, W. (1967). *A Stereotaxic Atlas of the Brain of the Pigeon (Columba livia)*. Baltimore, Maryland: The Johns Hopkins Press.
- KNIPLING, R.R. (1978). No deficit in near-field visual acuity of pigeons after transection of the isthmo-optic tract. *Brain Research* **22**, 813–816.
- MALZ, C.R. & MEYER, D.L. (1994). Interspecific variation of isthmo-optic projections in poikilothermic vertebrates. *Brain Research* **661**, 259–264.
- MARCHIAFAVA, P.L. (1976). Centrifugal actions on amacrine and ganglion cells in the retina of the turtle. *Journal of Physiology* **255**, 137–155.
- MATURANA, H.R. & FRENK, S. (1965). Synaptic connections of the centrifugal fibers in the pigeon retina. *Science* **150**, 359–362.
- MICELI, D., REPÉRANT, J., RIO, J.-P. & MEDINA, M. (1995). GABA immunoreactivity in the nucleus isthmo-opticus of the centrifugal visual system in the pigeon: A light and electron microscopic study. *Visual Neuroscience* **12**, 425–441.
- MILES, F.A. (1972a). Centrifugal control of the avian retina. II. Receptive field properties of cells in the isthmo-optic nucleus. *Brain Research* **48**, 93–113.
- MILES, F.A. (1972b). Centrifugal control of the avian retina. III. Effects of electrical stimulation of the isthmo-optic tract on the receptive field properties of retinal ganglion cells. *Brain Research* **48**, 115–129.
- MILES, F.A. (1972c). Centrifugal control of the avian retina. IV. Effects of reversible cold block of the isthmo-optic tract on the receptive field properties of cells in the retina and isthmo-optic nucleus. *Brain Research* **48**, 131–145.
- MORGAN, I.G., MIETHKE, P. & LI, Z.K. (1994). Is nitric oxide a transmitter of the centrifugal projection to the avian retina? *Neuroscience Letters* **168**, 5–7.
- NICKLA, D.L., GOTTLIEB, M.D., MARIN, G., ROJAS, X., BRITTO, L.R.G. & WALLMAN, J. (1994). The retinal targets of centrifugal neurons and the retinal neurons projecting to the accessory optic system. *Visual Neuroscience* **11**, 401–409.
- PEARLMAN, A.L. & HUGHES, C.P. (1976). Functional role of efferents to the avian retina. II. Effects of reversible cooling of the isthmo-optic nucleus. *Journal of Comparative Neurology* **166**, 123–132.
- RAMON Y CAJAL, S. (1889). *The Structure of the Retina* (translated by THORPE, S.A. & GLICKSTEIN, M.). Springfield: Charles C. Thomas Publisher, 1972.
- SHORTESS, G.K. & KLOSE, E.F. (1977). Effects of lesions involving efferent fibers to the retina in pigeon (*Columba livia*). *Physiology and Behavior* **18**, 409–414.
- UCHIYAMA, H. (1989). Centrifugal pathways to the retina: Influence of the optic tectum. *Visual Neuroscience* **3**, 183–206.
- UCHIYAMA, H. & BARLOW, R.B. (1994). Centrifugal inputs enhance responses of retinal ganglion cells in the Japanese quail without changing their spatial coding properties. *Vision Research* **34**, 2189–2194.
- UCHIYAMA, H. & ITO, H. (1993). Target cells for the isthmo-optic fibers in the retina of the Japanese quail. *Neuroscience Letters* **154**, 35–38.
- UCHIYAMA, H., ITO, H. & TAUCHI, M. (1995). Retinal neurons specific for centrifugal modulation of vision. *Neuroreport* **6**, 889–892.
- WANG, S.R., YAN, K. & WANG, Y.T. (1981). Visual field topography and binocular responses in the frog's nucleus isthmi. *Scientia Sinica* **9**, 1292–1301.
- WANG, S.R., WANG, Y.C. & FROST, B.J. (1995). Magnocellular and parvocellular divisions of pigeon nucleus isthmi differentially modulate visual responses in the tectum. *Experimental Brain Research* **104**, 376–384.
- WEIDNER, C., REPÉRANT, J., DESROCHES, A.M., MICELI, D. & VESSELKIN, N.P. (1987). Nuclear origin of the centrifugal visual pathway in birds of prey. *Brain Research* **436**, 153–160.
- WIZENMANN, A. & THANOS, S. (1990). The developing chick isthmo-optic nucleus forms a transient efferent projection to the optic tectum. *Neuroscience Letters* **113**, 241–246.
- WOLF-OBERHOLLENZER, F. (1987). A study of the centrifugal projections to the pigeon retina using two fluorescent markers. *Neuroscience Letters* **73**, 16–20.
- WOODSON, W., REINER, A., ANDERSON, K. & KARTEN, H.J. (1991). Distribution, laminar location, and morphology of tectal cells projecting to the isthmo-optic nucleus and the nucleus isthmi, pars parvocellularis in the pigeon (*Columba livia*) and chick (*Gallus domesticus*): A retrograde labeling study. *Journal of Comparative Neurology* **305**, 470–488.
- WOODSON, W., SHIMIZU, T., WILD, J.M., SCHIMKE, J., COX, K. & KARTEN, H.J. (1995). Centrifugal projections upon the retina: An anterograde tracing study in the pigeon (*Columba livia*). *Journal of Comparative Neurology* **362**, 489–509.