Telencephalic projections to the nucleus of the basal optic root and pretectal nucleus lentiformis mesencephali in pigeons

DOUGLAS R.W. WYLIE,[1,2] CATHERINE J. OGILVIE,[3] NATHAN A. CROWDER,[2,*]
RYAN R. BARKLEY,[1] AND IAN R. WINSHIP[1]

[1]Department of Psychology, University of Alberta, Edmonton, Alberta, Canada
[2]University Centre for Neuroscience, University of Alberta, Edmonton, Alberta, Canada
[3]Department of Psychiatry, University of Alberta, Edmonton, Alberta, Canada

Abstract

In birds, the nucleus of the basal optic root (nBOR) of the accessory optic system (AOS) and the pretectal nucleus lentiformis mesencephali (LM) are involved in the analysis of optic flow and the generation of the optokinetic response. In several species, it has been shown that the AOS and pretectum receive input from visual areas of the telencephalon. Previous studies in pigeons using anterograde tracers have shown that both nBOR and LM receive input from the visual Wulst, the putative homolog of mammalian primary visual cortex. In the present study, we used retrograde and anterograde tracing techniques to further characterize these projections in pigeons. After injections of the retrograde tracer cholera toxin subunit B (CTB) into either LM or nBOR, retrograde labeling in the telencephalon was restricted to the hyperpallium apicale (HA) of the Wulst. From the LM injections, retrograde labeling appeared as a discrete band of cells restricted to the lateral edge of HA. From the nBOR injections, the retrograde labeling was more distributed in HA, generally dorsal and dorso-medial to the LM-projecting neurons. In the anterograde experiments, biotinylated dextran amine (BDA) was injected into HA and individual axons were reconstructed to terminal fields in the LM and nBOR. Those fibers projecting to the nBOR also innervated the adjacent ventral tegmental area. However, tracing of BDA-labeled axons revealed no evidence that individual neurons project to both LM and nBOR. In summary, our results suggest that the nBOR and LM receive input from different areas of the Wulst. We discuss how these projections may transmit visual and/or somatosensory information to the nBOR and LM.

Keywords: Optokinetic, Optic flow, Accessory optic system, Pretectum, Visual Wulst

Introduction

Because the visual world consists of numerous stationary objects and surfaces, self-motion produces characteristic patterns of optic flow across the retina (Gibson, 1954). Together, nuclei in the accessory optic system (AOS) and pretectum analyze this optic flow information, and generate the optokinetic response (OKR) to facilitate retinal image stabilization (Simpson, 1984; Simpson et al., 1988a; Grasse & Cynader, 1990). This image stabilization is necessary for optimal visual acuity (Westheimer & McKee, 1975; Carpenter, 1988) and velocity discrimination (Nakayama, 1981).

The AOS and pretectum are highly conserved in vertebrates. The mammalian pretectal nucleus of the optic tract (NOT) is homologous to the nucleus lentiformis mesencephali (LM) in birds, and the avian nucleus of the basal optic root (nBOR) of the

AOS is homologous to the medial and lateral terminal nuclei (MTN, LTN) of the mammalian AOS (Simpson, 1984; McKenna & Wallman, 1985a; Fite, 1985; Weber, 1985; Simpson et al., 1988a). It has been shown in several species that AOS and pretectal neurons have large receptive fields in the contralateral visual field and exhibit direction selectivity to large-field moving visual stimuli (e.g., NOT: Collewijn, 1975a,b; Hoffmann & Schoppmann, 1975, 1981; Hoffmann et al., 1988; Hoffmann & Distler, 1989; Volchan et al., 1989; Mustari & Fuchs, 1990; Distler & Hoffmann, 1993; Ibbotson et al., 1994; Ilg & Hoffmann, 1996; LM: Katte & Hoffmann, 1980; McKenna & Wallman, 1985b; Winterson & Brauth, 1985; Fite et al., 1989; Fan et al., 1995; Wylie & Frost, 1996; Wylie & Crowder, 2000; MTN/LTN: Grasse & Cynader, 1982, 1984; Cooper & Magnin, 1986; Natal & Britto, 1987; Soodak & Simpson, 1988; nBOR: Burns & Wallman 1981; Morgan & Frost 1981; Gioanni et al., 1984; Rosenberg & Ariel, 1990; Wylie & Frost, 1990a).

The nBOR and LM receive primary input from the contralateral retina (Karten et al., 1977; Reiner et al., 1979; Fite et al., 1981; Gamlin & Cohen, 1988a), and nonretinal afferents include (1) a heavy reciprocal connection between LM and nBOR (Clarke,

1977; Brecha et al., 1980; Gamlin & Cohen, 1988*b*; Wylie et al., 1997), (2) a projection from the lateral cerebellar nucleus to both LM and nBOR (Arends & Zeigler, 1991), and (3) a telencephalic projection to both LM and nBOR. Miceli et al. (1979, 1987) and Rio et al. (1983) demonstrated this telencephalic projection in pigeons with injections of anterograde tracers into the visual Wulst, the putative homolog of mammalian primary visual cortex (e.g., Karten & Shimizu, 1989; Medina & Reiner, 2000). A telencephalic projection to the pretectum and AOS originating from several cortical visual areas, including primary visual cortex and extrastriate cortices (e.g., area MT), has been found in some mammals (e.g., cats and monkeys: Berson & Graybiel, 1980; Schoppmann, 1981; Marcotte & Updyke, 1982; Hoffmann et al., 1991; Grasse & Cynader, 1990; Ilg & Hoffmann, 1993; Mustari et al., 1994; rats: Shintani et al., 1999; guinea pigs: Lui et al., 1994; rabbits: Hollander et al., 1979) but not others (opossum: Pereira et al., 2000; hamster: Lent, 1982; tree shrew: Huerta et al., 1985).

In the present study, we investigated the projections of the telencephalon to the nBOR and LM in pigeons using the retrograde tracer cholera toxin subunit B (CTB) and the anterograde tracer biotinylated dextran amine (BDA). These experiments were performed to determine (1) if telencephalic areas other than the Wulst project to LM and nBOR; and (2) if there is a differential input from the Wulst to LM and nBOR.

Materials and methods

The methods reported herein conformed to the guidelines established by the Canadian Council on Animal Care and were approved by the Biosciences Animal Care and Policy Committee at the University of Alberta. Pigeons, obtained from a local supplier, were anesthetized with an intramuscular injection of a ketamine (65 mg/kg)/xylazine (8 mg/kg) cocktail, and were given supplemental as needed to maintain anesthesia. The animals were placed in a stereotaxic device with pigeon ear bars and beak adapter so that the orientation of the skull conformed to the atlas of Karten and Hodos (1967).

Retrograde tracer experiments

Retrograde experiments were performed on nine pigeons. CTB was injected into the nBOR and LM to examine the pattern of retrograde labeling in the telencephalon. Sufficient skull and dura were removed to expose the surface of the brain and allow access to the nBOR and/or LM with a vertical penetration. Four birds received unilateral injections in nBOR and four birds received unilateral injections in LM. One pigeon received two injections, one into nBOR in the left hemisphere and one into LM in the right hemisphere. Stereotaxic coordinates were used to approach LM and nBOR, but localization was confirmed by recording the responses of neurons to moving large-field visual stimuli and, occasionally, constructing directional tuning curves using drifting sine-wave gratings as stimuli (for details regarding visual stimuli and unit recording, see Crowder et al., 2003; Wylie & Crowder, 2000). Single-unit recordings were made with glass micropipettes (tip diameters 4–5 μm) filled with 2 M NaCl that were advanced using an hydraulic microdrive. After recording from optic flow-sensitive cells in the LM or nBOR, the recording electrode was replaced with a micropipette (tip diameter 20 μm) filled with CTB [low-salt version, Sigma, St. Louis, MO; 1% in 0.1 M phosphate-buffered saline (PBS, pH 7.4)] and the nucleus was located again by isolating cells responsive to large-field visual stimuli. When

targeting LM and nBOR, cells responsive to optic flow stimuli were found along the track at several depths so that the injection could be placed at a depth between the most dorsally and ventrally identified cells. The CTB was injected iontophoretically for 10–15 min (+4 μA, 7 s ON, 7 s OFF).

Anterograde tracer experiments

BDA was injected into the Wulst in three animals to examine the pattern of anterograde labeling in LM and nBOR. In two cases the HA was injected bilaterally and in the other case the injection was unilateral. We targeted those areas of the Wulst that contained highest density of CTB-labeled cells in our retrograde tracing experiments. Sufficient skull and dura were removed to expose the surface of the Wulst, bilaterally. A micropipette (tip diameter 20 μm) filled with BDA [Molecular Probes, Eugene, OR; MW = 10000; 10% in 0.1 M phosphate buffer (PB; pH = 7.4)] was lowered into the Wulst (depth, 0.4–1.5 mm). The BDA was injected iontophoretically for 15–30 min (+3 μA, 1 s ON, 1 s OFF).

Following the injections of BDA or CTB, the micropipette was left in place for 5 min. Once the micropipette was removed, the exposures were filled with bone wax and the wound was cleaned and sutured closed. Once the animal regained consciousness buprenorphine (2 mg/kg, i.m.) was administered as an analgesic.

Histology

After a survival time of 3–5 days postsurgery, the animals were administered an overdose of sodium pentobarbital (100 mg/kg), and perfused with 0.9% saline followed by 4% paraformaldehyde in 0.1 M phosphate buffer (PB). The brain was immediately extracted from the skull and placed in a 30% sucrose in 4% paraformaldehyde solution for 5 h, then transferred to 30% sucrose in 0.1 M PB. The brain was embedded in gelatin and placed in 30% sucrose in 0.1 M PB until the block sank. Using a microtome, frozen sections in the coronal plane (45 μm thick) were collected through the telencephalon, LM, and nBOR, and sections were processed for CTB or BDA.

Visualization of the BDA and CTB was based on the protocols outlined by Wild (1993; see also Veenman et al., 1992; Wylie et al., 1997; Lau et al., 1998). To visualize CTB, sections were initially rinsed in 0.05 M phosphate-buffered saline (PBS). They were then washed in a 25% methanol/0.9% hydrogen peroxide (H_2O_2) solution for 30 min to decrease endogenous peroxidase activity. Sections were rinsed several times in PBS then placed in 4% rabbit serum with 0.4% Triton X-100 in PBS for 30 min. Tissue was subsequently incubated for 20 h in 0.005% goat anti-CHB (List Biological Laboratories, Campbell, CA) with 0.4% Triton X-100 in PBS. Sections were then rinsed in PBS (several times) and incubated for 60 min in 0.16% biotinylated rabbit anti-goat antiserum (Vector Laboratories, Burlingame, CA) with 0.4% Triton X-100 in PBS. Tissue was rinsed several times with PBS and incubated for 90 min in 0.1% ExtrAvidin (Sigma, St. Louis, MO) with 0.4% Triton X-100 in PBS. Subsequent to a few washes with PBS, the tissue was incubated for 12 min in filtered 0.025% diaminobenzidine (DAB) and 0.006% cobalt chloride in PBS. 0.005% hydrogen peroxide was added to the DAB solution and the sections were reacted for up to 6 min. The sections were then rinsed several times with PBS and then mounted onto aluminum gelatin-coated slides, lightly counterstained with Neutral Red, and coverslipped with Permount. To visualize BDA, the sections were

first rinsed and treated with methanol/H_2O_2 as described above. After several rinses with PBS, sections were incubated in ExtrAvidin, reacted with DAB as described above, mounted onto slides, counterstained, and coverslipped as described above. The tissue was examined using light microscopy and drawings were made with the aid of a drawing tube.

Nomenclature

We relied on the new avian nomenclature established by Reiner et al. (2004). With this nomenclature the Wulst is divided into the hyperpallium apicale (HA; formerly known as the hyperstriatum accessorium), the interstitial nucleus of HA (IHA; formerly known as the nucleus intercalates hyperstriatum accessorium), the hyperpallium intercalatum (HI; formerly known as the hyperstriatum intercalates superior), and the hyperpallium densocellulare (HD; formerly known as the hyperstriatum dorsale). The region medial to the nBOR is the ventral tegmental area (VTA; formerly known

as the area ventralis of Tsai). For the pretectum, we relied on Gamlin and Cohen (1988*a*,*b*) who divided the LM into medial and lateral subdivision (LMm, LMl).

Results

Retrograde tracer experiments

Retrograde experiments were performed on nine pigeons. Four animals received unilateral injections into nBOR (cases #nBOR1–4), four received unilateral injections into LM (cases #cLM1–4), and one received two injections, one into nBOR in the left hemisphere and one into LM in the right hemisphere (case #cLMBOR). The locations of nBOR and LM were confirmed by recording single-unit activity to large-field moving stimuli with the injection electrode. Fig. 1 shows the unit activity and directional tuning curve of a single unit at the location of an LM injection. Typical of most
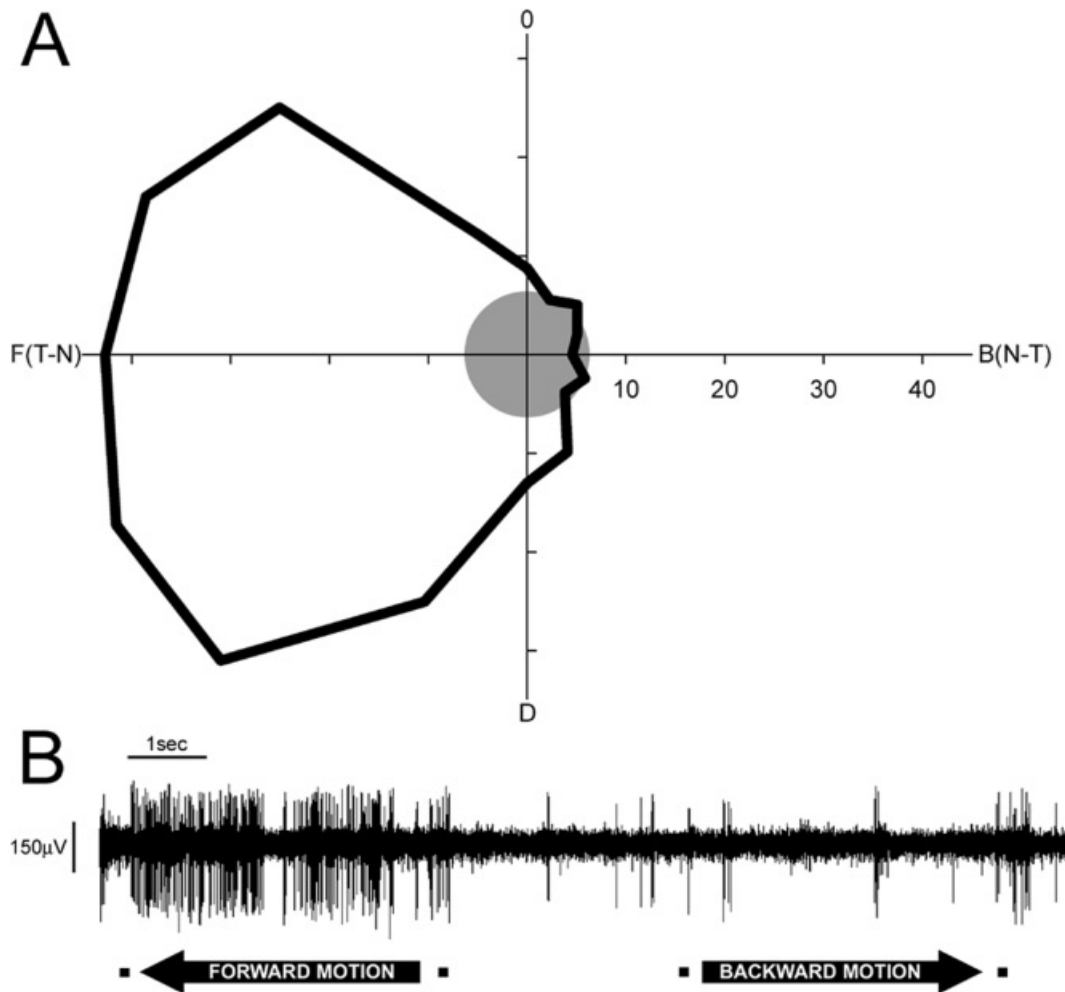

Fig. 1. Directional tuning of a unit in the nucleus lentiformis mesencephali (LM). A: A polar plot of the responses of a LM unit to large-field sine-wave gratings drifting in various directions in the contralateral visual field. Firing rate (spikes/s) is plotted as a function of the direction of motion in polar coordinates. The grey circle represents the cell's spontaneous firing rate. B: The raw trace of the same unit showing the modulation during a single sweep consisting of 4 s of temporal-to-nasal (T–N, i.e. forward) motion followed by 3 s of no motion, followed by 4 s of nasal-to-temporal (N–T, i.e. backward) motion. The small squares indicate the commencement and cessation of the motion epochs. Note the clear preference of this unit for forward motion. See text for additional details regarding recording and stimulus presentation. U, D, B, and F represent upward, downward, backward, and forward motion, respectively.

LM neurons (e.g., Winterson & Brauth, 1985), the unit preferred forward (temporal-to-nasal) motion.

From all injections, retrogradely labeled cell bodies were noted in the ipsilateral Wulst. The labeled cells were confined to HA of the Wulst, but no labeling was found in other areas of the telencephalon. No retrograde labeling was found in the contralateral telencephalon. Fig. 2 shows photomicrographs of injection sites in the LM and nBOR, and retrogradely labeled cells in HA. Within HA, there was a clear difference with respect to the pattern of labeling resulting from injections into the nBOR and LM.

LM injections

The right side of Fig. 3 shows camera lucida drawings of coronal sections through the Wulst, indicating the location of the
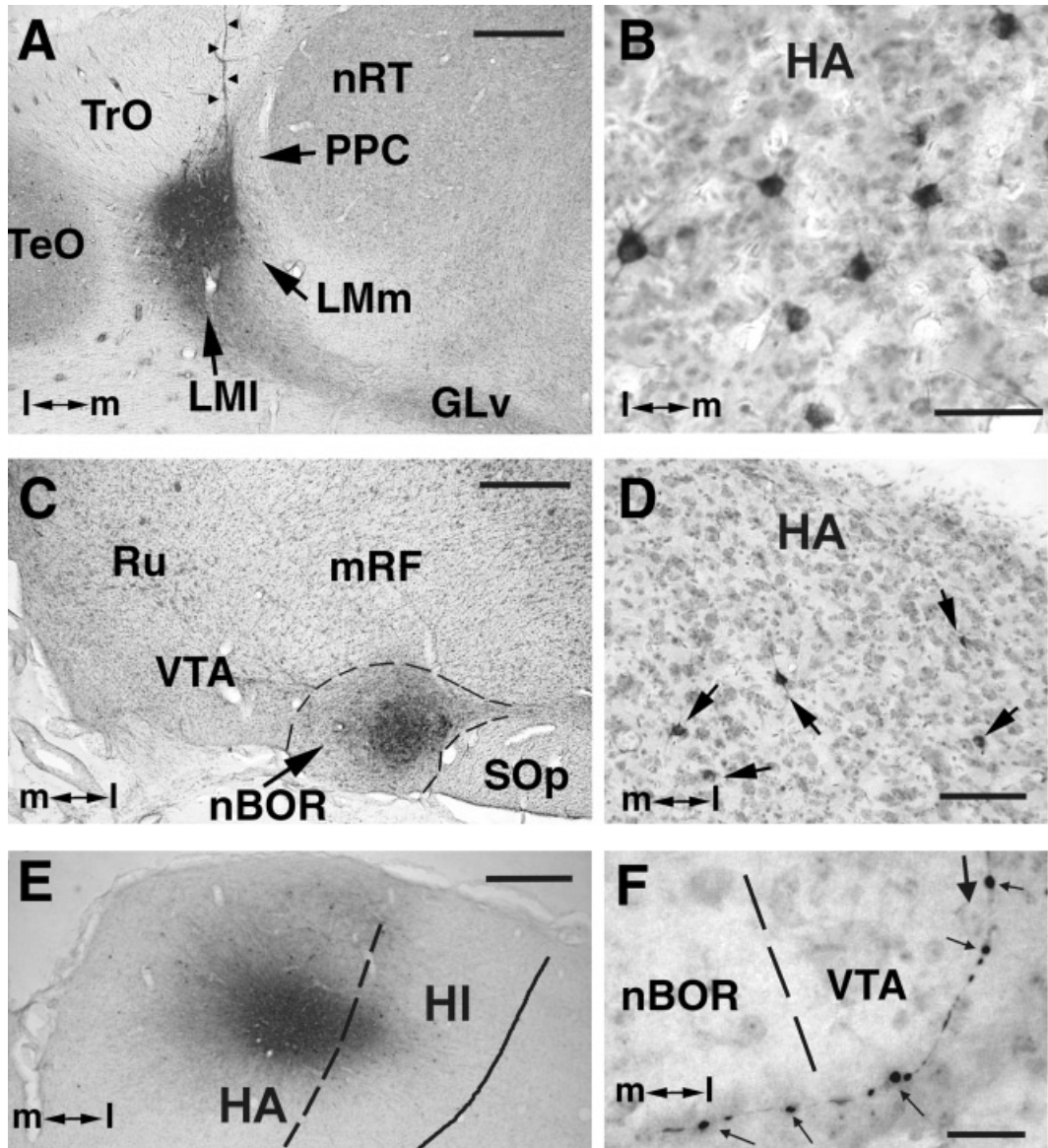

Fig. 2. Photomicrographs of retrograde and anterograde labeling. A: The CTB injection site in the nucleus lentiformis mesencephali (LM) from case #cLMBOR. The injection occupied both the medial and lateral subnuclei of LM (LMm, LMl). The small arrowheads highlight the electrode track through the tractus opticus (TrO). B: A cluster of cells in the hyperstriatum apicale (HA) retrogradely labeled from an injection of CTB in LM (case #cLMBOR). C: The CTB injection site in the nucleus of the basal optic root (nBOR) from case #nBOR2. The injection was confined to the lateral half of nBOR. D: Cells in HA retrogradely labeled from an injection of CTB in nBOR (case #nBOR1). Note the edge of the brain in the upper right of this photo, to illustrate that these cells were found superficially. E: The injection site of biotinylated dextran amine (BDA) in the HA from case #antwu3. The broken and solid lines respectively represent the approximate borders between HA and the hyperpallium intercalatum (HI), and HI and the hyperpallium densocellulare. F: Terminal labeling at the border of the nucleus of the basal optic root (nBOR) and the ventral tegmental area (VTA) from an injection of BDA in HA (from case #antwu4). The small arrows indicate variscosities, and the large arrow indicates the direction of the fiber from the injection site. Scale bars: A, C, E = 500 μm; B = 50 μm; D = 100 μm; F = 25 μm. l = lateral, m = medial. GLv, nucleus geniculatus lateralis, pars ventralis; mRF, mesencephalic reticular formation; nRT, nucleus rotundus; PPC, nucleus principalis precommisuralis; Ru, nucleus ruber; SOp; statum opticum; and TeO, optic tectum.
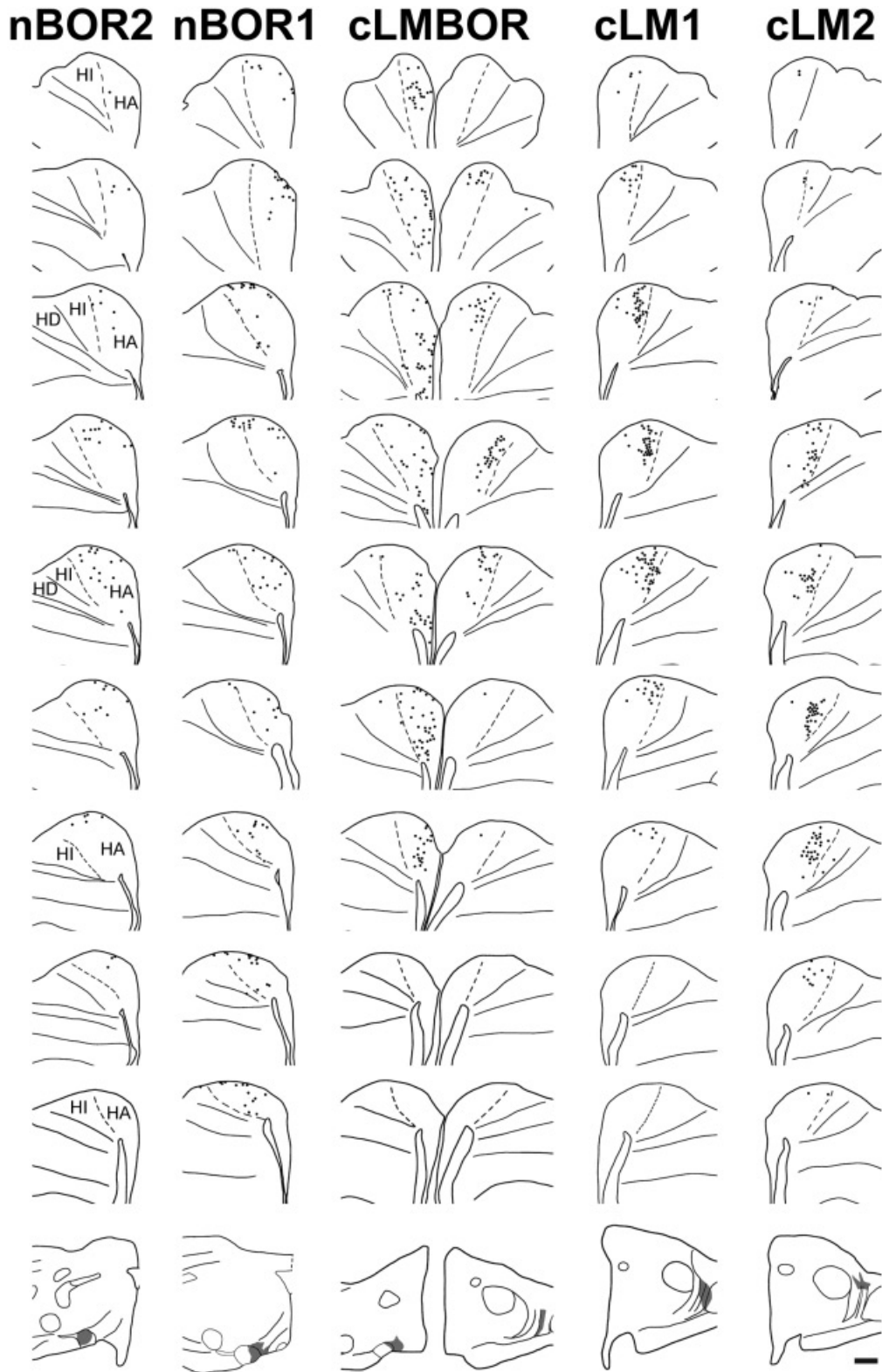
nBOR2 nBOR1 cLMBOR cLM1 cLM2

Fig. 3. Pattern of retrograde labeling in the visual Wulst (hyperpallium apicale, HA) from injections of the retrograde tracer in the nucleus lentiformis mesencephali (LM) and the nucleus of the basal optic root (nBOR). Coronal sections, rostral (top) to caudal and approximately 265 μm apart, through the Wulst are shown from five cases. The injection sites are shown in the bottom row. In cases #nBOR1 and #nBOR2, the injections of cholera toxin subunit B (CTB) were in the nBOR. In cases #cLM1 and #cLM2, the injections were in the pretectal nucleus lentiformis mesencephali (LM). In case #cLMBOR, CTB was injected in the left nBOR and the right LM. For aesthetic purposes the nBOR injections are shown as if on the left side of the brain, and the LM injections are shown as if on the right side of the brain. Each dot represents the location of a retrogradely labeled cell in HA. For identification of structures in the drawings of the injection sites, see Figs. 2A and 2C. See text for details. Scale bar = 1 mm.

retrogradely labeled cells from the LM injections. Drawings of the injection sites are also shown (bottom). This figure shows drawings from two unilateral cases (cases #cLM1 and #cLM2) and the one bilateral case (case #cLMBOR). All of the LM injections were confined to the medial and lateral subnuclei (Gamlin & Cohen, 1988*a,b*) with little encroachment laterally on adjacent structures. As can be seen in Fig. 3, for case #cLM1 there was a little spread of the injection laterally into the tectal grey. This was also the situation for case #cLM3 (not shown). For cases #cLM2 (Fig. 3) and #cLM4 (not shown), there was a little spread medially into the nucleus laminaris precommisuralis (LPC). The amount and pattern of retrograde labeling in HA was similar after all five LM injections. A rather discrete cluster of cells was seen forming an elongated strip in the lateral HA extending dorso-ventrally along the entire lateral border with HI. IHA is a thin strip of granule cells that resides between HA and HI, but was very difficult to see in neutral red-stained sections. The retrogradely labeled cells that we observed were round or ovoid multipolar cells, and measured on average $16.3 \pm 2.4 \times 10.9 \pm 2.8$ μm (mean $\pm$ S.E.M.; $n = 30$). This indicates that the cells were not in the IHA, where the cells typically measure <10 μm in diameter (Karten et al., 1973).

nBOR injections

The left side of Fig. 3 shows camera lucida drawings of coronal sections through the Wulst, indicating the location of the retrogradely labeled cells from the nBOR injections. The injections sites are also shown at the bottom. In addition to the bilateral case (case #cLMBOR), drawings from two of the four unilateral cases are shown (cases #nBOR2 and #nBOR1). The retrogradely labeled cells from the nBOR injections were ovoid, and measured $15.9 \pm 1.8 \times 11.7 \pm 2.1$ μm (mean $\pm$ S.E.M.). These were not significantly different from those HA cells labeled from the LM injections. Compared to that from the LM injections, the retrograde labeled cells were more dispersed, and generally found dorsal and medial to those labeled from the LM injections. Unlike that from the LM injections, there was also more variability with respect to the distribution of cells labeled from the nBOR injections. Moreover, there was more variability with respect to the injections themselves and more spread outside the target nucleus. In case #nBOR2 (Fig. 3), the injection was confined to the nBOR, and the labeled cells were found superficially in HA, dorsal and medial to those labeled from the LM injections. With case #nBOR1 (Fig. 3), the injections spread medially into the rostrolateral part of VTA. More retrograde labeling was seen in HA compared to case #nBOR2 but the distribution was similar. With case #cLMBOR (Fig. 3), the injection was heavier in the VTA than in the nBOR itself. Much more retrograde labeling was seen in HA compared to cases #nBOR1 and #nBOR2. This labeling extended into the rostral and ventormedial regions of HA. In case #nBOR3 (not shown) the injection was confined to nBOR with minimal spread into the VTA, and in case #nBOR4 (not shown) the injection was quite small and confined to the medial half of nBOR. From these cases, the pattern of retrograde labeling in HA was similar to that seen with cases #nBOR1 and #nBOR2, but fewer cells were observed.

Anterograde tracer experiments

Anterograde experiments were performed on three animals. In two cases the HA was injected bilaterally (cases #antwu4, #antwu5), and in the other case the injection was unilateral (case #antwu3). The injection was aimed at the location where the most abundant

retrograde labeling was observed from the CTB experiments. Using the atlas of Karten and Hodos (1967), we targeted the coordinates A-P = 12.2–12.5 mm, L-M =1.5–1.8 mm, and a depth of 0.5–1.5 mm. This corresponds to the 3rd to 5th sectioned from the top in Fig. 3. The injection sites were all similar in size and location and one of these is shown in Fig. 2E. These injections appear to be smaller than those of Miceli et al. (1979, 1987) and Rio et al. (1983).

From all five injections, varicosities, indicative of terminal labeling, were found in and around LM. The labeling was seen throughout the LMl and LMm, but was slightly heavier in the rostral half. In case #antwu5, where the injections were slightly rostral to the intended target, the labeling in LM was sparse compared to the other cases. Terminal labeling was seen in and around nBOR from two of the injections (cases #antwu3 and #antwu4-left). More labeling was found medial to nBOR, in the rostral VTA, rather than nBOR itself (see Fig. 4B). A photomicrograph of terminal labeling at the border of VTA and nBOR is shown in Fig. 2F. In both cases where there was labeling in nBOR/VTA, the terminal labeling was heavier in LM, but clearly the major efferent target in the diencephalon was the ventral leaflet of the lateral geniculate nucleus (GLv). Terminal labeling was very heavy in the GLv in all cases, particularly in the rostral half.

The course of the fibers from HA to the diencephalon was as described previously by Miclei et al. (1979, 1987). Fibers descended in the tractus septopallio-mesencepahlicus (TSM) to reach the dorsal margin of the rostral diencephalon. From this point there were two major courses. Most fibers took a dorsal root (TSMd) and travelled medially and coursed caudally. Fewer fibers took a ventral root (TSMv) and travelled caudally through the ventrolateral thalamus (VLT). From both the TSMd and TSMv terminal labeling was seen in LM and GLv. The TSMd fibers travelled medial to nucleus rotundas (nRt) and many coursed ventrally and numerous terminals were seen in the rostral half of GLv. Other TSMd fibers coursed more caudally through the dorsal thalamus to enter the LM at its dorso-rostral extreme. These fibers continued to course ventrally and caudally and terminal labeling was seen in LMm and LMl, and some was seen in the adjacent LPC. Few fibers continued caudally into the ventral aspect of LM, which resides lateral to the caudal part of GLv. In each case only one or two TSMd fibers continued caudally and coursed laterally though the caudal GLv. The lateral subnucleus of nBOR (nBORl), which is regarded as an extension of LM (McKenna & Wallman, 1985*b*), is found just caudal and medial to the caudal GLv. From the few TSMd fibers that did reach the caudal GLv, terminals were not seen in the nBORl, and they did not continue caudo-laterally to reach the main parts of nBOR, the dorsal and proper subnuclei (nBORd, nBORp; Brecha et al., 1980).

The TSMv fibers coursed ventrally, through, or more commonly lateral to, the lateral anterior nucleus. They continued ventrally and caudally into through the VLT and the intercalated nucleus of the thalamus (ICT). Most fibers then coursed medially to enter and terminate within the LM and GLv. A few fibers, numbering about ten in case #antwu4-left and two in case #antwu3, travelled more laterally through the ventral thalamus and gave rise to terminals in the vicinity of nBOR. These fibers appeared to course caudally and ventrally in the tractus quintofrontalis or the ansa lenticularis and at the dorso-medial border of nBOR. At this point the fibers terminated medial to nBOR, in what is best described as the ventro-rostro-lateral region of VTA, and some fibers then coursed laterally to terminate in nBOR. In case #antwu4-left, the terminals that were clearly within the boundaies of nBOR
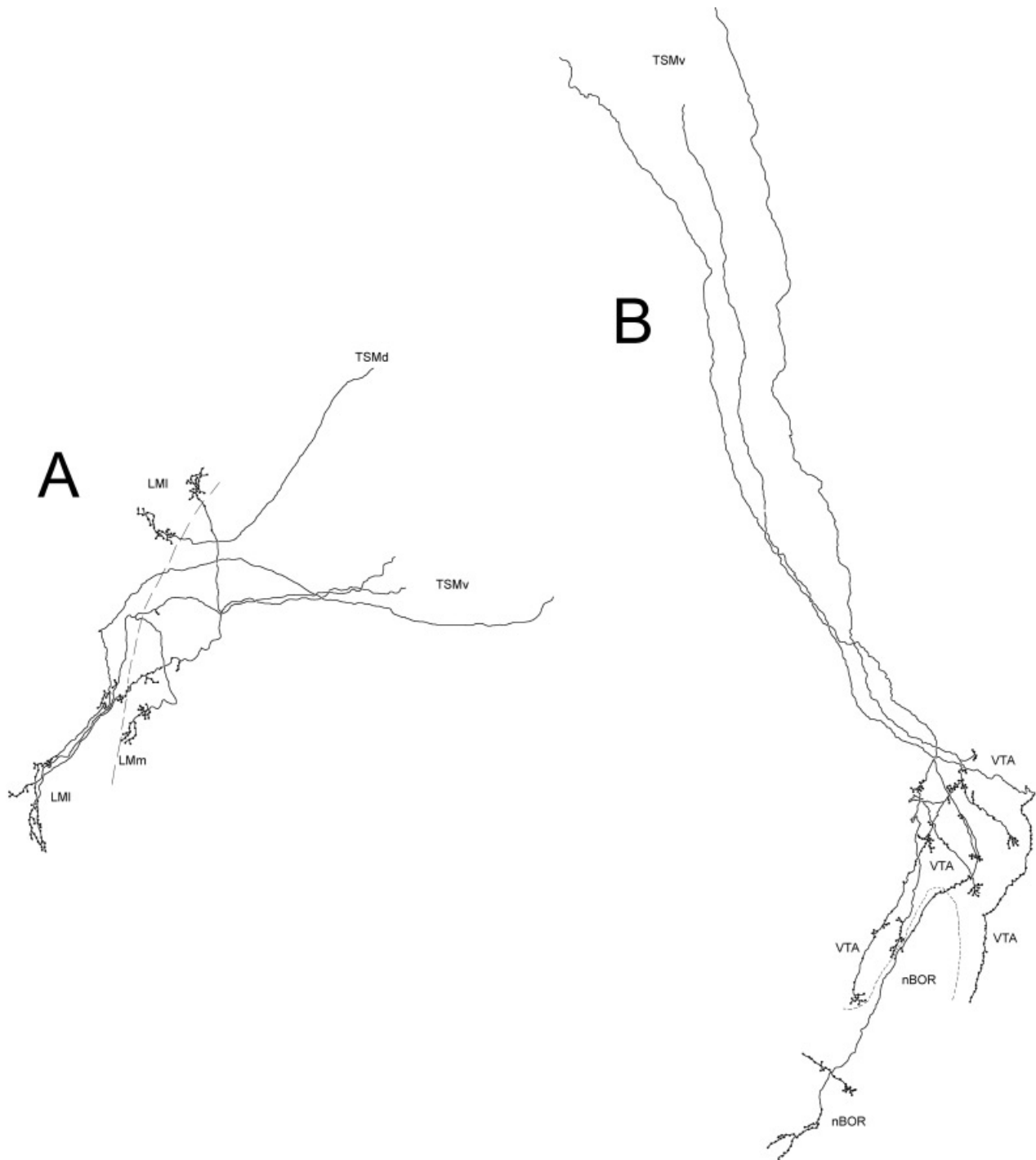
Fig. 4. Projections of the hyperpallium apicale (HA) on the medial and lateral subnuclei of lentiformis mesencephali (LM), the nucleus of the basal optic root (nBOR), and the ventral tegmental area (VTA). A traverse view of seven axons reconstructed from case #antwu4-left are shown. The size of the terminal varicosities has been exaggerated. A shows four axons that terminated in LM, whereas B shows three axons that terminated in VTA. One of these three fibers also terminated in the nBOR. See text for details. TSM(d,v); tractus septomesencephalicus (dorsal root, ventral root).

were located in ventrolateral nBORp and appeared to originate from one fiber (see Fig. 4). In case #antwu3, one of the fibers coursed medially to terminate in VTA, whereas the other turned laterally and terminated in nBORl, just medial to the caudal GLv.

In Fig. 4, we show the course of seven fibers from case #antwu4-left, reconstructed from serial sections with the aid of the drawing tube. Fig. 4A shows four fibers that terminated in LM, and Fig. 4B shows three others that terminated in nBOR and/or VTA. The purpose of the recontructions was to determine if individual fibers project to both LM and nBOR. One of the fibers to the LM originated in the TSMd, but the other six fibers traveled in the TSMv. They were reconstructed from the terminals back to the

dorsal areas of the ventral thalamus, at which point there were too many fibers to reliably continue tracing. We saw no evidence of individual fibers giving off collaterals to both LM and nBOR/VTA.

Discussion

Numerous studies have examined the afferent and efferent projections of the avian visual Wulst (Karten et al., 1973; Miceli et al., 1979, 1987, 1990; Wilson, 1980; Nixdorf & Bischof, 1982; Bagnoli & Burkhalter, 1983; Reiner & Karten, 1983; Rio et al., 1983; Miceli & Reperant, 1983; Bagnoli et al., 1990; Casini et al., 1992; Shimizu et al., 1995; Veenman et al., 1995; Alpar & Tombol, 1998; Kroner & Güntürkün, 1999; Deng & Rogers, 2000). In the present study, we injected CTB into the nBOR and LM and examined retrogradely labeled neurons in the telencephalon. We found that labeling was restricted to HA in the visual Wulst. From the LM, labeling was confined to a relatively discrete area, along the lateral border of HA. In contrast, from nBOR, the labeling was more distributed, but most was found superficially in HA. The nBOR-projecting HA cells could be described as complimentary to the LM-projecting HA cells: the former are generally found dorsal and medial to the latter. Our anterograde studies also emphasized a separation of the nBOR- and LM-projecting cells: there was no evidence of axons collateralizing to both the LM and nBOR.

Using anterograde techniques, Miceli and colleagues (Miceli et al., 1979, 1987; Rio et al., 1983) described the projections of the Wulst upon LM and nBOR. Our results are consistent with these previous studies with perhaps one small difference. The projection to the nBOR that we observed is closer to that described by Miceli et al. (1979). They note that fibers travel medially through VLT and aggregate dorsomedial to nBOR, but the termination of these fibers was not determined. We found that these fibers terminated in this region, in the VTA, and some travelled laterally and terminated in nBOR. Subsequent reports by Rio et al. (1983) and Miceli et al. (1987) described fibers from the Wulst reaching the nBOR laterally, by traversing the pretectum and caudal GLv. We observed a few fibers travelling medially through the caudal GLv but the terminals in the nBOR were not observed. Thus, it is possible that there are two routes to the nBOR from the Wulst: a pathway through the VLT which congregates dorsomedial to nBOR and a second pathway traversing the GLv and pretectum that enters the lateral nBOR. The former pathway was observed in the present study and described by Miceli et al. (1979). The latter pathway described by Rio et al. (1983) and Miceli et al. (1987) was not observed in the present study. The injections in the present study were purposefully smaller than those of Rio et al. (1983) and Miceli et al. (1987) because we were interested in reconstructing individual fibers. With the small injections, it is possible that we simply missed this second pathway to the nBOR.

The input from the Wulst to the nBOR and VTA

We wish to emphasize that the input from the Wulst to the ventral mesencephalon is to both the nBOR and the adjacent VTA. Indeed most of the injections in nBOR also involved the VTA, and there was more retrograde labeling in the HA in these cases. Moreover, the anterograde injections showed that fibers originating in HA projected to both nBOR and VTA. This is not necessarily a concern given that this area of VTA is functionally similar to nBOR, insofar as there are cells in the VTA that are sensitive to optic flow. In fact, the VTA cells seem to have more complex properties than those cells in the nBOR itself. The VTA cells respond to particular patterns of optic flow that result from either self-translation or self-rotation (Wylie & Frost, 1990*b*, 1999), and project to the optic flow-sensitive areas of the inferior olive (Wylie, 2001). A similar situation exists in mammals. The homologue of the nBOR is the medial terminal nucleus (MTN). Cells in the ventral tegmentum just outside the MTN project to the inferior olive (Maekawa & Takeda, 1979; Giolli et al., 1984, 1985) and respond best to complex patterns of optic flow (Simpson et al., 1988*b*). This area has been dubbed the visual tegmental relay zone (VTRZ), and we have previously noted that the VTRZ is functionally similar to the avian VTA (Wylie, 2001).

There is one potential caveat regarding the interpretations of the CTB injections into nBOR. Wild and Williams (2000) investigated the projections of the rostral Wulst, which is generally somatosensory and motor in nature (e.g., Wild, 1987; Medina & Reiner, 2000). Wild and Williams (2000) identified an avian pyramidal tract originating in the rostral HA and projecting to various regions in the mesencephalon and diencephalon. Some of these fibers passed just dorsal and dorso-medial to the nBOR and the adjacent VTA. Because CTB can be taken up by fibers of passage (Chen & Aston-Jones, 1995), it is possible that some of the retrogradely labeled cells from the nBOR injections were due to uptake by pyramidal fibers originating in the rostral HA. However, injections of retrograde tracers into the target sites of the pyramidal tract labeled cells primarily in the ventral aspect of the rostral HA. The only cases in which we observed labeling in this region from an nBOR injection was case #cLMBOR (see Fig. 3). There was clearly labeling in the ventral aspect of rostral Wulst that was not seen in the other cases. Thus, we are confident that this potential caveat was only an issue for this one case.

Comparison to mammals

In mammals, a telencepahlic projection to the AOS and/or pretectum has been shown in several species including cats, primates, rats, guinea pigs, and rabbits (Hollander et al., 1979; Berson & Graybiel, 1980; Schoppmann, 1981; Marcotte & Updyke, 1982; Hoffmann et al., 1991; Ilg & Hoffmann, 1993; Mustari et al., 1994; Lui et al., 1994; Shintani et al., 1999). These projections originate in various visual regions including primary visual cortex, but the bulk of the input arises from extrastriate areas that are involved in complex motion analysis: the suprasylvian areas in cats (Marcotte & Updyke, 1982) and middle temporal (MT) and middle superior temporal (MST) areas in primates (Hoffmann et al., 1991; Ilg & Hoffmann, 1993). It is somewhat surprising then that in the present study the input to the LM and nBOR from the telencephalon was restricted to the Wulst, which is regarded as the equivalent to primary visual cortex (e.g., Karten & Shimizu, 1989; Medina & Reiner, 2000). The putative avian equivalent of MT/MST is the caudal region of the entopallium (Nguyen et al., 2004; see also Karten & Shimizu, 1989; Shimizu & Karten 1991, 1993; Butler & Hodos, 1996; Shimizu & Bowers, 1999), which was not retrogradely labeled from injections into LM and nBOR.

Function of the Wulst to LM/nBOR projection

It is known that the Wulst provides a direct excitatory connection to about one-third of the neurons in both LM (Crowder et al., 2004) and nBOR (Nogueira & Britto, 1991) but the function of these projections is unknown. Britto and colleagues (Britto et al., 1990; Hamassaki et al., 1988) suggested that the Wulst contributes to the directional tuning of nBOR neurons. They noted that the

distribution of the direction preferences of neurons was different for animals with lesions to the Wulst compared to normal animals. A recent study by Crowder et al. (2004) definitively showed that this is not the function of the Wulst-LM projections. They recorded the activity of individual LM neurons before and after the Wulst was inactivated with lidocaine. Neither the directional tuning nor the spatio-temporal tuning of the LM neurons was affected in this manipulation. What then could be the function of this projection?

One possibility is related to the visual properties of the Wulst. Unfortunately very little is known about the neurophysiology of Wulst neurons. HA neurons in pigeons have small receptive fields that respond to motion and orientation of small stimuli (Miceli et al., 1979). Early lesion studies failed to find a function for the Wulst in various visual tasks (e.g., Hodos et al., 1984; Watanabe, 1992; Hodos, 1993). However, Hahmann and Güntürkün (1993) showed the Wulst is important for acuity in the lateral but not the frontal visual field (see also Remy & Güntürkün, 1991). A recent study by Budzynski and Bingman (2004) showed that pigeons with Wulst lesions were impaired at pattern discrimination for far-field (i.e. more distant) stimuli. In light of these two studies, it is possible that the projection to the LM and nBOR is to adjust the gain of a subset of optic flow-sensitive neurons when the animal is attending to small object-like stimuli in the lateral field. Alternatively, perhaps the role of this projection is to modify the optokinetic responses in the LM and nBOR such that a far depth plane is preferentially stabilized.

Another possibility is that the projection of the Wulst to the nBOR and LM is multimodal in nature (Crowder et al., 2004). Generally, the caudal Wulst is visual in function, whereas the rostral tip is somatosensory and motor (Wild, 1987, 1997; Funke, 1989; Medina & Reiner, 2000). However, Deng and Wang (1992, 1993) demonstrated that there is significant overlap between areas of the Wulst that process visual and somatosensory information, and some neurons responded to both visual and somatosensory stimuli (also see Medina & Reiner, 2000). Based on the location of the retrogradely labeled neurons from LM and nBOR injections shown in Fig. 3, it appears that the LM- and nBOR-projecting HA neurons overlap with those areas of the Wulst where somatosensory responses are evoked (Wild, 1987; Deng & Wang, 1992, 1993). As self-motion would undoubtedly induce concurrent optic flow and somatosensory stimuli, for example, air passing through the pigeon's feathers, it is possible that the Wulst is providing visual-somatosensory information during self-motion.

Finally, there is a region in the ventromedial Wulst, the posterior Whs (Shimizu & Karten, 1990), that receives input from nonsensory thalamic nuclei, including the nucleus dorsomedialis anterior and the nucleus dorsolateralis pars medialis. Because these thalamic nuclei receive input from the medial forebrain bundle, Karten et al. (1973) have compared the Whs to limbic cortex in mammals (see also Berk & Hawkin, 1985). If the LM- and nBOR-projecting neurons reside in Whs, it is possible that this projection is involved in a general arousal of the optokinetic response. We would argue that most of the neurons retrogradely labeled from injections into LM and nBOR are not within the Whs. The Whs is posterior, ventral, and medial to most of theses neurons (Shimizu & Karten, 1990).

Acknowledgments

References

ALPAR, A. & TOMBOL, T. (1998). Telencephalic connections of the visual system of the chicken: Tracing the interrelation of the efferents of the visual Wulst and the hyperstriatum ventrale. *Annals of Anatomy* **180**, 529–536.

ARENDS, J.J.A. & ZEIGLER, H.P. (1991). Organization of the cerebellum in the pigeon (*Columba livia*): II. Projections of the cerebellar nuclei. *Journal of Comparative Neurology* **306**, 245–272.

BAGNOLI, P. & BURKHALTER, A. (1983). Organization of the afferent projections to the Wulst in the pigeon. *Journal of Comparative Neurology* **214**, 103–113.

BAGNOLI, P., FONTANESI, G., CASINI, G. & PORCIATTI, V. (1990). Binocularity in the little owl, Athene noctua. I. Anatomical investigation of the thalamo-Wulst pathway. *Brain, Behavior and Evolution* **35**, 31–39.

BERK, M.L. & HAWKIN, R.F. (1985). Ascending projections of the mammillary region in the pigeon: Emphasis on telencephalic projections. *Journal of Comparative Neurology* **239**, 330–340.

BERSON, D.M. & GRAYBIEL, A.M. (1980). Some cortical and subcortical fiber projections to the accessory optic nuclei in the cat. *Neuroscience* **5**, 2203–2217.

BRECHA, N., KARTEN, H.J. & HUNT, S.P. (1980). Projections of the nucleus of basal optic root in the pigeon: An autoradiographic and horseradish peroxidase study. *Journal of Comparative Neurology* **189**, 615–670.

BRITTO, L.R., GASPAROTTO, O.C. & HAMASSAKI, D.E. (1990). Visual telencephalon modulates directional selectivity of accessory optic neurons in pigeons. *Visual Neuroscience* **4**, 3–10.

BUDZYNSKI, C.A. & BINGMAN, V.P. (2004). Participation of the thalamofugal pathway in a coarse pattern discrimination task in an open arena. *Behavioral Brain Research* **153**, 543–556.

BURNS, S. & WALLMAN, J. (1981). Relation of single unit properties to the oculomotor function of the nucleus of the basal optic root (AOS) in chickens. *Experimental Brain Research* **42**, 171–180.

BUTLER, A.B. & HODOS, W. (1996). *Comparative Vertebrate Neuroanatomy: Evolution and Adaptation*. New York: Wiley-Liss.

CARPENTER, R.H.S. (1988). *Movements of the Eye* (2nd edition). London: Pion.

CASINI, G., PORCIATTI, V., FONTANESI, G. & BAGNOLI, P. (1992). Wulst efferents in the little owl Athene noctua: An investigation of projections to the optic tectum. *Brain, Behavior and Evolution* **39**, 101–115.

CHEN, S. & ASTON-JONES, G. (1995). Evidence that cholera toxin B subunit (CTb) can be avidly taken up and transported by fibers of passage. *Brain Research* **674**, 107–111.

CLARKE, P.G.H. (1977). Some visual and other connections to the cerebellum of the pigeon. *Journal of Comparative Neurology* **174**, 535–552.

COLLEWIJN, H. (1975a). Direction-selective units in the rabbit's nucleus of the optic tract. *Brain Research* **100**, 489–508.

COLLEWIJN, H. (1975b). Oculomotor areas in the rabbit's midbrain and pretectum. *Journal of Neurobiology* **6**, 3–22.

COOPER, H.M. & MAGNIN, M. (1986). A common mammalian plan of accessory optic system organization revealed in all primates. *Nature* **324**, 457–459.

CROWDER, N.A., DAWSON, M.R.W. & WYLIE, D.R.W. (2003). Temporal frequency and velocity-like tuning in the pigeon accessory optic system. *Journal of Neurophysiology* **90**, 1829–1841.

CROWDER, N.A., DICKSON, C.T. & WYLIE, D.R.W. (2004). Telencephalic input to the pretectum of pigeons: An electrophysiological and pharmacological inactivation study. *Journal of Neurophysiology* **191**, 274–285.

DENG, C. & ROGERS, L.J. (2000). Organization of intratelencephalic projections to the visual Wulst of the chick. *Brain Research* **856**, 152–162.

DENG, C. & WANG, B. (1992). Overlap of somatic and visual response areas in the Wulst of pigeon. *Brain Research* **582**, 320–322.

DENG, C. & WANG, B. (1993). Convergence of somatic and visual afferent impulses in the Wulst of pigeon. *Experimental Brain Research* **96**, 287–290.

DISTLER, C. & HOFFMANN, K.P. (1993). Visual receptive field properties in kitten pretectal nucleus of the optic tract and dorsal terminal nucleus of the accessory optic tract. *Journal of Neurophysiology* **70**, 814–827.

FAN, T.X., WEBER, A.E., PICKARD, G.E., FABER, K.M. & ARIEL, M. (1995).

Visual responses and connectivity in the turtle pretectum. *Journal of Neurophysiology* **73**, 2507–2521.

FITE, K.V. (1985). Pretectal and accessory-optic visual nuclei of fish, amphibia and reptiles: Themes and variations. *Brain, Behavior and Evolution* **26**, 71–90.

FITE, K.V., BRECHA, N., KARTEN, H.J. & HUNT, S.P. (1981). Displaced ganglion cells and the accessory optic system of pigeon. *Journal of Comparative Neurology* **195**, 279–288.

FITE, K.V., KWEI-LEVY, C. & BENGSTON, L. (1989). Neurophysiological investigation of the pretectal nucleus lentiformis mesencephali in *Rana pipiens. Brain, Behavior and Evolution* **34**, 164–170.

FUNKE, K. (1989). Somatosensory areas in the telencephalon of the pigeon. I. Response characteristics. *Experimental Brain Research* **76**, 603–619.

GAMLIN, P.D.R. & COHEN, D.H. (1988*a*). Retinal projections to the pretectum in the pigeon (*Columba livia*). *Journal of Comparative Neurology* **269**, 1–17.

GAMLIN, P.D.R. & COHEN, D.H. (1988*b*). Projections of the retinorecipient pretectal nuclei in the pigeon (*Columba livia*). *Journal of Comparative Neurology* **269**, 18–46.

GIBSON, J.J. (1954). The visual perception of object motion and subjective movement. *Psychological Review* **61**, 304–314.

GIOANNI, H., REY, J., VILLALOBOS, J. & DALBERA, A. (1984). Single unit activity in the nucleus of the basal optic root (nBOR) during optokinetic, vestibular and visuo-vestibular stimulations in the alert pigeon (Columba livia). *Experimental Brain Research* **57**, 49–60.

GIOLLI, R.A., BLANKS, R.H. & TORIGOE, Y. (1984). Pretectal and brain stem projections of the medial terminal nucleus of the accessory optic system of the rabbit and rat as studied by anterograde and retrograde neuronal tracing methods. *Journal of Comparative Neurology* **227**, 228–251.

GIOLLI, R.A., BLANKS, R.H.I., TORIGOE, Y. & WILLIAMS, D.D. (1985). Projections of the medial terminal nucleus, ventral tegmental nuclei and substantia nigra of rabbit and rat as studied by retrograde axonal transport of horseradish peroxidase. *Journal of Comparative Neurology* **232**, 99–116.

GRASSE, K.L. & CYNADER, M.S. (1982). Electrophysiology of medial terminal nucleus of accessory optic system in the cat. *Journal of Neurophysiology* **48**, 490–504.

GRASSE, K.L. & CYNADER, M.S. (1984). Electrophysiology of lateral and dorsal terminal nuclei of the cat accessory optic system. *Journal of Neurophysiology* **51**, 276–293.

GRASSE, K.L. & CYNADER, M.S. (1990). The accessory optic system in frontal-eyed animals. In *Vision and Visual Dysfunction, Vol. IV, The Neuronal Basis of Visual Function*, ed. Leventhal, A., pp. 111–139. New York: MacMillan.

HAHMANN, U. & GUNTURKUN, O. (1993). The visual acuity for the lateral visual field of the pigeon (Columba livia). *Vision Research* **33**, 1659–1664.

HAMASSAKI, D.E., GASPAROTTO, O.C., NOGUEIRA, M.I. & BRITTO, L.R.G. (1988). Telencephalic and pretectal modulation of the directional selectivity of accessory optic neurons in the pigeon. *Brazilian Journal of Medical and Biological Research* **21**, 649–652.

HODOS, W. (1993). The visual capabilities of birds. In *Vision, Brain, and Behavior in Birds*, ed. ZEIGLER, H.P. & BISCHOF, H.J., pp. 36–76. Cambridge, Massachusetts: The MIT Press.

HODOS, W., MACKO, K.A. & BESSETTE, B.B. (1984). Near-field acuity changes after visual system lesions in pigeons. II. Telencephalon. *Behavioral Brain Research* **13**, 15–30.

HOFFMANN, K.P. & DISTLER, C. (1989). Quantitative analysis of visual receptive fields of neurons in nucleus of the optic tract and dorsal terminal nucleus of the accessory optic tract in macaque monkey. *Journal of Neurophysiology* **62**, 416–428.

HOFFMANN, K.P., DISTLER, C. & ERICKSON, R.G. (1991). Functional projections from striate cortex and superior temporal sulcus to the nucleus of the optic tract (NOT) and dorsal terminal nucleus of the accessory optic tract (DTN) of macaque monkeys. *Journal of Comparative Neurology* **313**, 707–724.

HOFFMANN, K.P., DISTLER, C., ERICKSON, R.G. & MADER, W. (1988). Physiological and anatomical identification of the nucleus of the optic tract and dorsal terminal nucleus of the accessory optic tract in monkeys. *Experimental Brain Research* **69**, 635–644.

HOFFMANN, K.P. & SCHOPPMANN, A. (1975). Retinal input to direction selective cells in the nucleus tractus opticus of the cat. *Brain Research* **99**, 359–366.

HOFFMANN, K.P. & SCHOPPMANN, A. (1981). A quantitative analysis of the direction-specific response of neurons in the cat's nucleus of the optic tract. *Experimental Brain Research* **42**, 146–157.

HOLLANDER, H., TIETZE, J. & DISTEL, H. (1979). An autoradiographic study of the subcortical projections of the rabbit striate cortex in the adult and during postnatal development. *Journal of Comparative Neurology* **184**, 783–794.

HUERTA, M.F., WEBER, J.T., ROTHSTEIN, L.R. & HARTING, J.K. (1985). Subcortical connections of area 17 in the tree shrew: An autoradiographic analysis. *Brain Research* **340**, 163–170.

IBBOTSON, M.R., MARK, R.F. & MADDESS, T.L. (1994). Spatiotemporal response properties of direction-selective neurons in the nucleus of the optic tract and the dorsal terminal nucleus of the wallaby, Macropus eugenii. *Journal of Neurophysiology* **72**, 2927–2943.

ILG, U.J. & HOFFMANN, K.-P. (1993). Functional grouping of the cortico-pretectal projection. *Journal of Neurophysiology* **70**, 867–869.

ILG, U.J. & HOFFMANN, K.-P. (1996). Responses of neurons of the nucleus of the optic tract and the dorsal terminal nucleus of the accessory optic tract in the awake monkey. *European Journal of Neuroscience* **8**, 92–105.

KARTEN, H.J., FITE, K.V. & BRECHA, N. (1977). Specific projection of displaced retinal ganglion cells upon the accessory optic system in the pigeon (Columba livia). *Proceedings of the National Academy of Sciences of the U.S.A.* **74**, 1752–1756.

KARTEN, H.J. & HODOS, W. (1967). *A Stereotaxic Atlas of the Brain of the Pigeon* (*Columba livia*). Baltimore, Maryland: Johns Hopkins Press.

KARTEN, H.J., HODOS, W., NAUTA, W.J. & REVZIN, A.M. (1973). Neural connections of the "visual Wulst" of the avian telencephalon. Experimental studies in the pigeon (*Columba livia*) and owl (*Speotyto cunicularia*). *Journal of Comparative Neurology* **150**, 253–278.

KARTEN, H.J. & SHIMIZU, T. (1989). The origins of neocortex: Connections and lamination as distinct events in evolution. *Journal of Cognitive Neuroscience* **1**, 290–301.

KATTE, O. & HOFFMANN, K.-P. (1980). Direction specific neurons in the pretectum of the frog (Rana esculenta). *Journal of Comparative Physiology* **140**, 53–57.

KRONER, S. & GUNTURKUN, O. (1999). Afferent and efferent connections of the caudolateral neostriatum in the pigeon (*Columba livia*): A retro- and anterograde pathway tracing study. *Journal of Comparative Neurology* **407**, 228–260.

LAU, K.L., GLOVER, R.G., LINKENHOKER, B. & WYLIE, D.R.W. (1998). Topographical organization of inferior olive cells projecting to translation and rotation zones in the vestibulocerebellum of pigeons. *Neuroscience* **85**, 605–614.

LENT, R. (1982). The organization of subcortical projections of the hamster's visual cortex. *Journal of Comparative Neurology* **206**, 227–242.

LUI, F., GIOLLI, R.A., BLANKS, R.H.I. & TOM, E.M. (1994). Pattern of striate cortical projections to the pretectal complex in the guinea pig. *Journal of Comparative Neurology* **344**, 598–609.

MAEKAWA, K. & TAKEDA, T. (1979). Origin of descending afferents to the rostral part of the dorsal cap of the inferior olive which transfers contralateral optic activities to the flocculus. A horseradish peroxidase study. *Brain Research* **172**, 393–405.

MARCOTTE, R.R. & UPDYKE, B.V. (1982). Cortical visual areas of the cat project differentially onto the nuclei of the accessory optic system. *Brain Research* **242**, 205–217.

MCKENNA, O. & WALLMAN, J. (1985*a*). Accessory optic system and pretectum of birds: Comparisons with those of other vertebrates. *Brain, Behavior and Evolution* **26**, 91–116.

MCKENNA, O.C. & WALLMAN, J. (1985*b*). Functional postnatal changes in avian brain regions responsive to retinal slip: A 2-deoxy-D-glucose study. *Journal of Neuroscience* **5**, 330–342.

MEDINA, L. & REINER, A. (2000). Do birds possess homologues of mammalian primary visual, somatosensory and motor cortices? *Trends in Neuroscience* **23**, 1–12.

MICELI, D., GIOANNI, H., REPERANT. J. & PEYRICHOUX, J. (1979). The avian visual Wulst: I. An anatomical study of afferent and efferent pathways. II. An electrophysiological study of the functional properties of single neurons. In *Neural Mechanisms of Behavior of the Pigeon*, ed. GRANDA, A.M. & MAXWELL, J.H., pp. 223–254. New York: Plenum Press.

MICELI, D., MARCHAND, L., REPERANT, J. & RIO, J.P. (1990). Projections of the dorsolateral anterior complex and adjacent thalamic nuclei upon the visual Wulst in the pigeon. *Brain Research* **518**, 317–323.

MICELI, D. & REPERANT, J. (1983). Hyperstriatal-tectal projections in the pigeon (Columba livia) as demonstrated by the retrograde double-label fluorescence technique. *Brain Research* **276**, 147–153.

MICELI, D., REPERANT, J., VILLALOBOS, J. & DIONNE, L. (1987). Extra-telencephalic projections of the avian visual Wulst. A quantitative autoradiographic study in the pigeon Columbia livia. *Journal fur Hirnforschung* **28**, 45–57.

MORGAN, B. & FROST, B.J. (1981). Visual response properties of neurons in the nucleus of the basal optic root of pigeons. *Experimental Brain Research* **42**, 184–188.

MUSTARI, M.J. & FUCHS, A.F. (1990). Discharge patterns of neurons in the pretectal nucleus of the optic tract (NOT) in the behaving primate. *Journal of Neurophysiology* **64**, 77–90.

MUSTARI, M.J., FUCHS, A.F., KANEKO, C.R. & ROBINSON, F.R. (1994). Anatomical connections of the primate pretectal nucleus of the optic tract. *Journal of Comparative Neurology* **349**, 111–128.

NAKAYAMA, K. (1981). Differential motion hyperacuity under conditions of common image motion. *Vision Research* **21**, 1475–1482.

NATAL, C.L. & BRITTO, L.R.G. (1987). The pretectal nucleus of the optic tract modulates the direction selectivity of the accessory optic neurons in rats. *Brain Research* **419**, 320–323.

NGUYEN, A.P., SPETCH, M.L., CROWDER, N.C., WINSHIP, I.R., HURD, P.L. & WYLIE, D.R.W. (2004). A dissociation of motion and spatial-pattern vision in the avian telencephalon: Implications for the evolution of "visual streams". *Journal of Neuroscience* **24**, 4962–4970.

NIXDORF, B.E. & BISCHOF, H.J. (1982). Afferent connections of the ecto-striatum and visual Wulst in the zebra finch (Taeniopygia guttata castanotis Gould)—an HRP study. *Brain Research* **248**, 9–17.

NOGUEIRA, M.I. & BRITTO, L.R.G. (1991). Extraretinal modulation of accessory optic units in the pigeon. *Brazilian Journal for Medical and Biological Research* **24**, 623–631.

PEREIRA, A., VOLCHAN, E., VARGAS, C.D., PENETRA, L. & ROCHA-MIRANDA, C.E. (2000). Cortical and subcortical influences on the nucleus of the optic tract of the opossum. *Neuroscience* **95**, 953–963.

REINER, A., BRECHA, N. & KARTEN, H.J. (1979). A specific projection of retinal displaced ganglion cells to the nucleus of the basal optic root in the chicken. *Neuroscience* **4**, 1679–1688.

REINER, A. & KARTEN, H.J. (1983). The laminar source of efferent projections from the avian Wulst. *Brain Research* **275**, 349–354.

REINER, A., PERKEL, D.J., BRUCE, L.L., BUTLER, A.B., CSILLAG, A., KUENZEL, W., MEDINA, L., PAXINOS, G., SHIMIZU, T., STRIEDTER, G., WILD, M., BALL, GF., DURAND, S., GUTURKUN, O., LEE, D.W., MELLO, C.V., POWERS, A., WHITE, S.A., HOUGH, G., KUBIKOVA, L., SMULDERS, T.V., WADA, K., DUGAS-FORD, J., HUSBAND, S., YAMA-MOTO, K., YU, J., SIANG, C. & JARVIS, E.D. (2004). Avian Brain Nomenclature Forum. Revised nomenclature for avian telencephalon and some related brainstem nuclei. *Journal of Comparative Neurology* **473**, 377–414.

REMY, M. & GÜNTÜRKÜN, O. (1991). Retinal afferents to the tectum opticum and the nucleus opticus principalis thalami in the pigeon. *Journal of Comparative Neurology* **305**, 57–70.

RIO, J.P., VILLALOBOS, J., MICELI, D. & REPERANT, J. (1983). Efferent projections of the visual Wulst upon the nucleus of the basal optic root in the pigeon. *Brain Research* **271**, 145–151.

ROSENBERG, A.F. & ARIEL, M. (1990). Visual-response properties of neurons in turtle basal optic nucleus in vitro. *Journal of Neurophysiology* **63**, 1033–1045.

SCHOPPMANN, A. (1981). Projections from areas 17 and 18 of the visual cortex to the nucleus of the optic tract. *Brain Research* **223**, 1–17.

SHIMIZU, T. & BOWERS, A.N. (1999). Visual circuits of the avian telen-cephalon: evolutionary implications. *Behavioral Brain Reseach* **98**, 183–191.

SHIMIZU, T., COX, K. & KARTEN, H.J. (1995). Intratelencephalic projec-tions of the visual Wulst in pigeons (Columba livia). *Journal of Comparative Neurology* **359**, 551–572.

SHIMIZU, T. & KARTEN, H.J. (1990). Immunohistochemical analysis of the visual Wulst of the pigeon *(Columba livia). Journal of Comparative Neurology* **300**, 346–369.

SHIMIZU, T. & KARTEN, H.J. (1991). Central visual pathways in retiles and birds: Evolution of the visual system. In *Vision and Visual Dysfunction, Vol. 2*., ed. GREGORY, R. & CRONLY-DILLON, J.R., pp. 421–441. London, UK: Macmillan.

SHIMIZU, T. & KARTEN, H.J. (1993). The avian visual system and the evolution of the neocortex. In *Vision, Brain, and Behavior in Birds*, ed. ZEIGLER, H.P. & BISCHOF, H.J., pp.103–114. Cambridge, Massachu-setts: MIT.

SHINTANI, T., HOSHINO, K., MEGURO, R., KAIYA, T. & NORITA, M. (1999). A light and electron microscopic analysis of the convergent retinal and visual cortical projections to the nucleus of the optic tract (NOT) in the pigmented rat. *Neurobiology* **7**, 445–460.

SIMPSON, J.I. (1984). The accessory optic system. *Annual Review of Neuroscience* **7**, 13–41.

SIMPSON, J.I., GIOLLI, R.A. & BLANKS, R.H.I. (1988*a*). The pretectal nuclear complex and the accessory optic system. In *Neuroanatomy of the Oculomotor System*, ed. Buttner-Ennerver, J.A., pp. 335–364. Am-sterdam: Elsevier.

SIMPSON, J.I., LEONARD, C.S. & SOODAK, R.E. (1988*b*). The accessory optic system of rabbit. II. Spatial organization of direction selectivity. *Journal of Neurophysiology* **60**, 2055–2072.

SOODAK, R.E. & SIMPSON, J.I. (1988). The accessory optic system of rabbit. I. Basic visual response properties. *Journal of Neurophysiology* **60**, 2037–2054.

VEENMAN, C.L., REINER, A. & HONIG, M.G. (1992). Biotinylated dextran amine as an anterograde tracer for single- and double-labeling studies. *Journal of Neuroscience Methods* **41**, 239–254.

VEENMAN, C.L., WILD, J.M. & REINER, A. (1995). Organization of the avian "corticostriatal" projection system: A retrograde and anterograde pathway tracing study in pigeons. *Journal of Comparative Neurology* **354**, 87–126.

VOLCHAN, E., ROCHA-MIRANDA, C.E., PICANCO-DINIZ, C.W., ZINSMEIS-SER, B., BERNARDES, R.F. & FRANCA, J.G. (1989). Visual response properties of pretectal units in the nucleus of the optic tract of the opossum. *Experimental Brain Research* **78**, 380–386.

WATANABE, S. (1992). Effect of lesions in the ectostriatum and Wulst on species and individual discrimination in pigeons. *Behavioral Brain Research* **49**, 197–203.

WEBER, J.T. (1985). Pretectal complex and accessory optic system of primates. *Brain, Behavior and Evolution* **26**, 117–140.

WEBER, J.T. & HARTING, J.K. (1980). The efferent projections of the pretectal complex: An autoradiographic and horseradish peroxidase analysis. *Brain Research* **194**, 1–28.

WESTHEIMER, G. & McKEE, S.P. (1975). Visual acuity in the presence of retinal-image motion. *Journal of the Optical Society of America* **65**, 847–850.

WILD, J.M. (1987). The avian somatosensory system: Connections of regions of body representation in the forebrain of the pigeon. *Brain Research* **412**, 205–223.

WILD, J.M. (1993). Descending projections of the songbird nucleus robus-tus archistrialis. *Journal of Comparative Neurology* **338**, 225–241.

WILD, J.M. (1997). The avian somatosensory system: The pathway from wing to Wulst in a passerine (Chloris chloris). *Brain Research* **759**, 122–134.

WILD, J.M. & WILLIAMS, M.N. (2000). Rostral Wulst in passerine birds. I. Origin, course, and terminations of an avian pyramidal tract. *Journal of Comparative Neurology* **416**, 429–450.

WILSON, P. (1980). The organization of the visual hyperstriatum in the domestic chick. II. Receptive field properties of single units. *Brain Research* **188**, 333–345.

WINTERSON, B.J. & BRAUTH, S.E. (1985). Direction-selective single units in the nucleus lentiformis mesencephali of the pigeon (Columba livia). *Experimental Brain Research* **60**, 215–226.

WYLIE, D.R.W. (2001). Projections from the nucleus of the basal optic root and nucleus lentiformis mesencephali to the inferior olive in pigeons (Columba livia). *Journal of Comparative Neurology* **429**, 502–513.

WYLIE, D.R.W. & CROWDER, N.A. (2000). Spatiotemporal properties of fast and slow neurons in the pretectal nucleus lentiformis mesencephali in pigeons. *Journal of Neurophysiology* **84**, 2529–2540.

WYLIE, D.R. & FROST, B.J. (1990*a*). Visual response properties of neurons in the nucleus of the basal optic root of the pigeon: A quantitative analysis. *Experimental Brain Research* **82**, 327–336.

WYLIE, D.R. & FROST, B.J. (1990*b*). Binocular neurons in the nucleus of the basal optic root (nBOR) of the pigeon are selective for either translational or rotational visual flow. *Visual Neuroscience* **5**, 489–495.

WYLIE, D.R.W. & FROST, B.J. (1996). The pigeon optokinetic system: Visual input in extraocular muscle coordinates. *Visual Neuroscience* **13**, 945–953.

WYLIE, D.R.W. & FROST, B.J. (1999). Responses of neurons in the nucleus of the basal optic root to translational and rotational flowfields. *Journal of Neurophysiology* **81**, 267–276.

WYLIE, D.R., LINKENHOKER, B. & LAU, K.L. (1997). Projections of the nucleus of the basal optic root in pigeons (*Columba livia*) revealed with biotinylated dextran amine. *Journal of Comparative Neurology* **384**, 517–536.