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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

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ABSTRACT

In birds, optic flow is analyzed by two retinal-recipient nuclei: the nucleus of the basal optic root (nBOR) of the accessory optic system (AOS), and the pretectal nucleus, lentiformis mesencephali (LM). Previous anatomical studies have shown that both of these nuclei have descending projections to structures involved in oculomotor, head movement, and postural control. In this report, using biotinylated dextran amine (BDA) and cholera toxin subunit B (CTB) for anterograde and retrograde labelling, respectively, we investigated projections from the nBOR and LM to the dorsal thalamus. After injections of BDA into the nBOR and LM, terminals were consistently found in the nucleus dorsolateralis anterior pars lateralis and pars medialis, and the nucleus dorsalis intermedius ventralis anterior of the thalamus. Some terminals were also found in the nucleus dorsolateralis anterior, nucleus dorsomedialis anterior pars magnocellularis, nucleus dorsolateralis posterior, nucleus superficialis parvocellularis, and the ventrointermediate area. Injections of CTB into the dorsal thalamus resulted in retrogradely labelled cells in the pretectal region, including LM. Numerous cells were also seen in the nBOR pars lateralis and pars dorsalis, but fewer were seen in the nBOR proper. We suggest that the AOS is providing input to a thalamotelencephalic system that may be involved in several functions including: (1) multi-sensory analysis of self-motion, (2) perception of self-motion, (3) perception of the three-dimensional layout of the environment, (4) distinguishing object-motion from self-motion, and (5) spatial cognition. J. Comp. Neurol. 391:456–469, 1998.

Indexing terms: self-motion; optic flow; multisensory integration; basal optic root; lentiformis mesencephali; optokinetic

Because the environment consists of stationary objects and surfaces, as one moves through the environment, optic flow results across the entire retina (Gibson, 1954, 1958). The accessory optic system (AOS) and associated pretectum comprise a distinct visual system dedicated to the analysis of the optic flow (Frost et al., 1994; Grasse and Cynader, 1990; Simpson, 1984; Simpson et al., 1988). In pigeons, this system consists of two major retinal recipient nuclei (Fite et al., 1981; Gamlin and Cohen, 1988a; Karten et al., 1977; Reiner et al., 1979): the nucleus of the basal optic root (nBOR) of the AOS and the pretectal nucleus lentiformis mesencephali (LM). Electrophysiological and 2-deoxyglucose studies have shown that most nBOR and LM neurons have large receptive fields and exhibit direction selectivity in response to moving largefield visual stimuli (random dot patterns or checkerboards; Burns and Wallman, 1981; Gioanni et al., 1984; McKenna and Wallman, 1981, 1985a; Morgan and Frost, 1981; Winterson and Brauth, 1985; Wolf-Oberhollenzer and Kirschfeld, 1994; Wylie and Frost, 1990a,b, 1996).

Previous anatomical studies have shown that the nBOR and LM are the source of descending projections to structures involved in oculomotor, collimotor, and postural control. Such nuclei include the oculomotor nuclei (from nBOR: Brecha and Karten, 1979; Brecha et al., 1980; Wylie

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et al., 1997), the vestibulocerebellum (from nBOR: Brauth and Karten, 1977; Brecha et al., 1980; Wylie et al., 1997; from LM: Clarke, 1977; Gamlin and Cohen, 1988b), the accessory oculomotor and peri-rubral areas (from nBOR: Brecha et al., 1980; Wylie et al., 1997; from LM: Gamlin and Cohen, 1988b), the inferior olive (from nBOR: Brecha et al., 1980; Wylie et al., 1997; from LM: Clarke, 1977; Gamlin and Cohen, 1988b) and the pontine nuclei (from nBOR: Wylie et al., 1997; from LM: Clarke, 1977; Gamlin and Cohen, 1988b). Wylie et al. (1997) reported a projection from the nBOR to areas of the dorsal thalamus including the nucleus dorsolateralis anterior thalami (DLA), DLA pars lateralis (DLL), and DLA pars medialis (DLM). A few terminals were also seen in the DLA pars magnocellularis (DLAmc) and nucleus dorsolateralis posterior thalami (DLP). We suggested that this AOS-thalamocortical pathway might be involved in distinguishing object-motion from self-motion, and the perception of self-motion. Gamlin and Cohen (1988b) noted a projection to the DLAmc, ventral DLL and DLM from the griseum tectale (GT) which is adjacent to the LM. Wild (1989) found that DLL and, to a lesser extent DLM, received a projection from LM.

In this study, we further investigated the connections from the nBOR and the pretectum to the dorsal thalamus by injecting the anterograde tracer biotinylated dextran amine (BDA) into the nBOR and LM. This tracer has a major advantage over techniques used in previous studies in that small injections can be made with iontophoresis. Moreover, recordings were made with the injection electrode ensuring that the injection site was in an area containing cells responsive to optic flow. We confirmed our findings with injections of the retrograde tracer cholera toxin subunit B (CTB) into the dorsal thalamus.

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. Silver King Pigeons were anesthetized with a ketamine (90 mg/kg) - xylazine (15 mg/kg) mixture (i.m.), and supplemental doses were administered as necessary. The animals were placed in a stereotaxic device with pigeon ear bars and beak adapter so that the orientation of the skull conformed with the atlas of Karten and Hodos (1967).

Injections of BDA into LM and nBOR

The nBOR or LM was located based on stereotaxic coordinates in Karten and Hodos (1967). On initial penetrations, extracellular recordings were made with glass micropipettes (4-µm tip diameter) filled with 2 M NaCl. nBOR and LM neurons typically exhibit direction selectivity in response to largefield stimuli moving in the contralateral visual field. Once cells responsive to largefield motion were identified, BDA (Molecular Probes, Eugene, OR; 10% in 0.1 M phosphate-buffered saline [PBS] pH 7.4) was iontophoretically injected (+3µ amps, 1 sec ON, 1 sec OFF) for 2-5 minutes by using micropipettes with tip diameters of 8-12 µm. Recordings were first made with the injection electrode to ensure that the tip was within the nBOR or LM. Subsequent to the injection, the electrode was left undisturbed for an additional 5 minutes. After a survival time of 3-6 days, the animals were given an overdose of sodium pentobarbitol (100 mg/kg) and immediately perfused with saline (0.9%) followed by 4% paraformaldehyde in 0.1 M PB, pH 7.4. The brains were extracted, embedded in gelatin, cryoprotected in sucrose (20% in 0.1 M PB), and 40-µm-thick frozen sections were cut with a microtome. Sections were washed in PBS, incubated in 1% H_2O_2 in 25% methanol for 30 minutes, washed several times in PBS, incubated in *ExtrAvidin* peroxidase (Sigma Chemical Co., St. Louis, MO; 1:1,000) and Triton X-100 (0.4%) for 1.5 hours at room temperature, washed in PBS, then visualized with diaminobenzidine (DAB). Sections were first placed in 0.025% DAB in 0.1 M PBS for 10 minutes, then in 0.025% DAB, 0.005% H_2O_2 in 0.1 M PBS for 2-4 minutes (Veenman et al., 1992; Wild, 1993). The tissue was subsequently washed several times with PBS, then mounted onto gelatin-coated slides, dried, lightly counterstained with neutral red, and coverslipped with Permount.

Injections of CTB into the dorsal thalamus

Based on the pattern of terminal labelling in the dorsal thalamus, we attempted to center the injections on the DLL/DLM by using stereotaxic coordinates in Karten and

Abbreviations

AOS	accessory optic system
AVT	area ventralis of Tsai
BDA	biotinylated dextran amine
CTB	cholera toxin subunit B
DAB	diaminobenzidine
DIVA	nucleus dorsalis intermedius ventralis anterior
DLA	nucleus dorsolateralis anterior thalami
DLAmc	nucleus dorsolateralis anterior thalami, pars magnocellularis
DLL	nucleus dorsolateralis anterior thalami, pars lateralis
DLM	nucleus dorsolateralis anterior thalami, pars medialis
DLP	nucleus dorsolateralis posterior thalami
GLv	nucleus geniculatus lateralis, pars ventralis
GT	griseum tectale
ICT	nucleus intercalatus thalami
IO	inferior olive
LM	nucleus lentiformis mesencephali
LMl	nucleus lentiformis mesencephali, pars lateralis
LMm	nucleus lentiformis mesencephali, pars medialis
LPC	nucleus laminaris precommissuralis
nBOR	nucleus of the basal optic root
nBORd	nucleus of the basal optic root, pars dorsalis
nBORl	nucleus of the basal optic root pars lateralis
nBORp	nucleus of the basal optic root, proper
nDSV	nucleus decussatio supraoptic ventralis
OPT	nucleus opticus principalis thalami
Ov	nucleus ovoidalis
PPC	nucleus principalis precommissuralis
PV	nucleus posteroventralis thalami
Rt	nucleus rotundus
SME	stria medularis
SOp	stratum opticum
SP	nucleus subpretectalis
SPC	nucleus superficialis parvocellularis
SRt	nucleus subrotundus
T	nucleus triangularis
TrO	tractus opticus
TSM	tractus septomesencephalicus
VbC	vestibulocerebellum
VIA	ventrointermediate area
VLT	nucleus ventrolateralis thalami

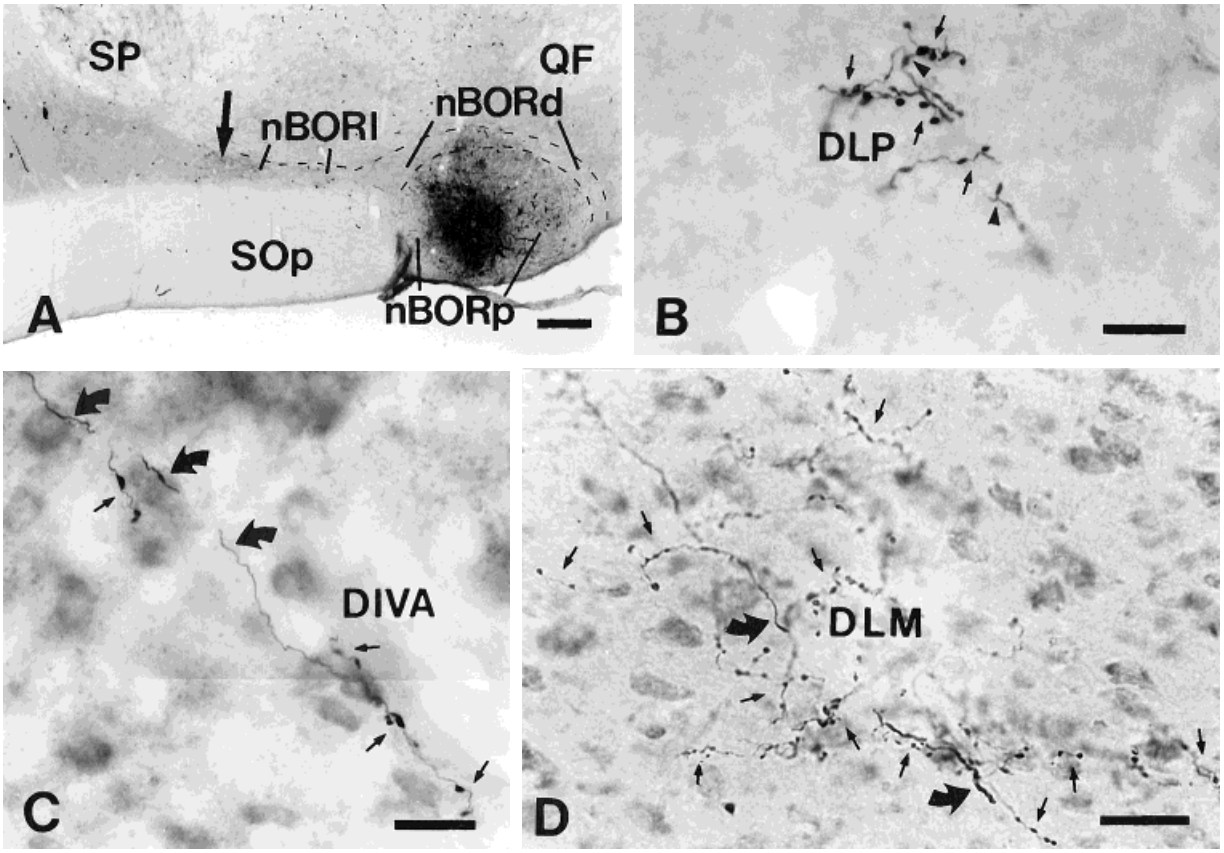

Fig. 1. **A–D:** Projections from the nucleus of the basal optic root (nBOR) to the dorsolateral thalamus. A shows the injection of biotinylated dextran amine (BDA) into the nBOR in case nBOR#4. The three divisions of the nBOR complex are indicated. Note that the injection was primarily in the nBOR proper (nBORp), but also spread slightly into the nBOR dorsalis (nBORd). The arrow indicates a bundle of fibers travelling lateral from the nBORl. These fibers give rise to terminals in the pretectum and dorsolateral thalamus. B, C and D, respectively, show terminal fields in the nucleus dorsolateralis posterior thalami (DLP; case nBOR#4), nucleus dorsalis intermedius ventralis anterior (DIVA; case nBOR#4), and nucleus dosolateralis medialis thalami (DLM; case nBOR#3). In B-D the curved arrows, small arrows and arrowheads indicate the parent fiber, sites of terminal boutons, and clear examples of axonal branching, respectively. For other abbreviations see list. For all panels, the left side is lateral. Scale bars = 200 µm in A, 25 µm in B-D.

Hodos (1967). Choleratoxin subunit B (CTB; Sigma; 1% in .05 M PBS, pH 7.4) was pressure-injected through glass micropipettes (tip diameter 16-20 µm) with a *PicoSpritzer II* (General Valve Corp., Fairfield, NJ). After a survival period of 3-6 days, the animals were perfused as described above. The brains were stored in sucrose (20% in 0.1 M PB) overnight and 40-µm-thick frozen sections were cut with a microtome. Every third section was collected. The CTB protocol we used was based on Wild (1993). The sections were washed three times (10 minutes each) with .05 M PBS, then placed in 25% methanol with 1% H_2O_2 for 30 minutes. This was followed by 30 minutes in 4% rabbit serum (Sigma; in .05 M PBS) with 0.4% Triton X-100. The sections were then incubated for 20-24 hours in goat anti-CTB (List Biological Laboratories, Campell, CA; 1:20,000 in .05 M PBS) with 0.4% Triton X-100. The tissue was then placed in biotinylated rabbit anti-goat antibody with 0.4% Triton X-100 (1:600 in .05 M PBS, pH 7.4), followed by 1.5 hours in *ExtrAvidin* with 0.4% Triton X-100. The sections were rinsed three times with .05 M PBS and then visualized with an intensified DAB procedure. After 10 minutes in 0.025% DAB with 0.002% $CoCl_2$ in 0.1 M PBS, the tissue was placed in 0.025% DAB 0.005% H_2O_2 with 0.002% $CoCL_2$ in 0.1 M PBS for up to 2 minutes. The tissue was subsequently washed several times with PBS, then mounted onto gelatin-coated slides, dried, counterstained with geimsa, and coverslipped with Permount.

Nomenclature

The pigeon nBOR resides at the base of the brain at the mesodiencepahlic border and receives direct retinal input from the displaced ganglion cells (Fite et al., 1981; Karten et al., 1977; Reiner et al., 1979). Brecha et al. (1980) divided the nBOR into three subgroups based on cell morphology and spatial location (see Fig. 1A). The nBOR proper (nBORp) comprises most of the nucleus and consists mainly of large and medium-sized round cells, and a smaller number of small spindly cells. The nBOR dorsalis (nBORd) consists of a thin layer of small spindly cells lining the caudal and dorsal margins of the BORp. The nBOR lateralis (nBORl) is a small group of cells located dorsal to the stratum opticum (SOp), lateral to the rest of the nucleus. McKenna and Wallman (1981, 1985a) have shown that the nBORl is contiguous with, and functionally similar to the LM.

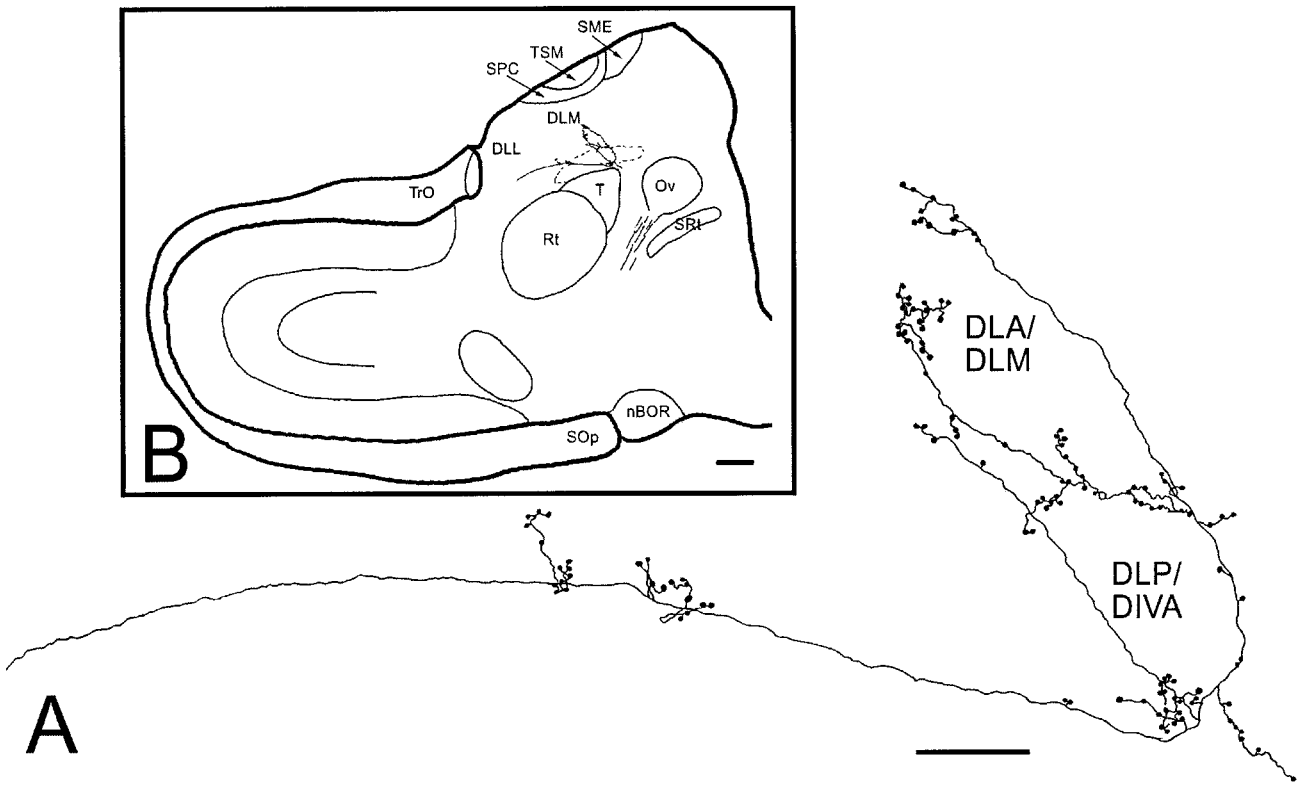

Fig. 2. Terminal field of a fiber projecting from the nucleus of the basal optic root (nBOR) to the dorsal thalamus. **A** shows the arborizing terminal field with varicosities as reconstructed from serial sections and projected onto the coronal plane. The terminals were found in the caudolateral margin of the nucleus dorsalis intermedius ventralis anterior (DIVA) and the adjacent rostral aspect of the nucleus dorsolateralis posterior thalami (DLP), as well as the caudal aspect of the nucleus dorsolateralis medialis thalami (DLM) and the nucleus dorsolateral anterior thalami (DLA). In **B**, the fiber is superimposed upon the coronal section that was midway between the rostral and caudal extents of the terminal field. The dashed line in B outlines the boundaries of the DIVA. For other abbreviations see list. Scale bars = 100 µm in A, 400 µm in B.

In pigeons, the pretectum consists of numerous nuclei, the borders of which are difficult to define (see Fig. 3A). We have adopted the description by Gamlin and Cohen (1988a). In their description, the LM consists of two subnuclei, the LM pars lateralis (LMl) and the LM pars medialis (LMm). Medial to the LMm is a strip of small cells, the nucleus laminaris precommissuralis (LPC), which appears contiguous with the internal lamina of the nucleus geniculatus lateralis, pars ventralis (GLv). Medial to the LPC is the nucleus principalis precommissuralis (PPC) which resides lateral to the nucleus rotundus (Rt). Ventrally, the LMm, LMl, and LPC course ventral to the nucleus subpretectalis (SP) and posterior to the GLv. The LMm and LMl, although virtually indistinguishable at this point, continue medially as a strip of cells which becomes the nBORl. It is believed that the most cells sensitive to optic flow in the pretectum reside within the LMl (Winterson and Brauth, 1985; Wylie and Frost, 1996), but some have been recorded in the LMm (Winterson and Brauth, 1985).

For the subdivisons of the dorsal thalamus, we relied on Karten and Hodos (1967). We also included the nucleus dorsalis intermedius ventralis anterior (DIVA) described by Wild (1987a), which resides dorsal to the nucleus triangularis (T) and the medial portions of the rostral half of Rt. Just ventral to DIVA and medial to T is the ventrointermediate area (VIA) described by Medina et al. (1997). In our previous report of projections to the dorsal thalamus from nBOR (Wylie et al., 1997), we had not differentiated DIVA and VIA. Some of the terminals we previously ascribed to DLM, DLL, and DLA may actually have resided within DIVA or VIA.

RESULTS

nBOR injections

BDA was injected into the nBOR in 4 pigeons, 3 of which have been described in a previous report (Wylie et al., 1997). However, given that we previously used the atlas of Karten and Hodos (1967) to delineate the subnuclei, we have reexamined the terminal labelling in the dorsal thalamus and included DIVA (Wild et al., 1987a) and VIA (Medina et al., 1997). We were confident that the injection did not extend beyond the nBOR complex in any of the cases. In all cases, a fiber bundle consisting of 15-30 axons travelled laterally from the nBOR providing a massive input to the LMl (Wylie et al., 1997; see Fig. 1A). Terminals from this fiber bundle were also found in the nBORl, LMm, LPC, PPC, GLv, GT, and the tectum (Wylie et al., 1997). Some of these fibers, about a half dozen in each case, continued dorsally and entered the dorsal thalamus.

In case nBOR#1, the injection was centered in the ventral portion of nBORp. In the dorsal thalamus terminal labelling was prevalent in the ventral and lateral areas of

the DLL. Some fibers travelled more medially and terminal labelling was found in the DIVA and rostral DLP. A few terminals were found in ventral DLM and VIA, and a single terminal field was found in the DLAmc.

In case nBOR#2, the injection was centered in dorsal margin of the nBORp and included the overlying nBORd. Terminals were abundant in the DLL and slightly fewer were found in the DIVA. In the DLM some terminals were observed, and we noted a few terminals in the DLP and nucleus superficialis parvocellularis (SPC).

In case nBOR#3, the injection was just medial to the center of the nBORp. Terminals were prevalent in the DLL, and some were found in the DLM.

In case nBOR#4, the injection was located just lateral to the center of the nBORp, although there was some spread into the nBORd (see Fig. 1A). Terminal labelling in the dorsal thalamus was abundant in the DLL, particularly ventrally, and numerous terminal fields were found in the DIVA. Some terminal fields were also found in the DLP, particularly rostrally, and a few terminal fields were also found in the DLM, DLA, and VIA. A single terminal field was found in each of the SPC and DLAmc. Figure 2A shows the terminal arborizations of a fiber from case nBOR#4 that was reconstructed from serial sections. As illustrated, the fiber is projected onto the coronal plane. In fact the terminal field extended about 400 µm rostrocaudally. In Figure 2B, to clearly show the position of this terminal field within the dorsal thalamus, the fiber has been superimposed upon the coronal section that was at the midpoint of the rostrocaudal extent of the terminal field. The broken line in Figure 2B denotes the boundary of the DIVA. Terminals from this fiber were found in the caudolateral margin of the DIVA and the adjacent DLP, and in the caudal aspects of the DLM and the adjacent DLA.

In summary, injections of BDA in the nBOR resulted in terminal labelling in the dorsal thalamus. Most of these fibers terminated in the DLL, but many were also seen in the DIVA and DLM. The terminals in the DIVA were generally in the lateral half. Still fewer terminals were observed in the DLP, DLA, VIA, SPC and DLAmc. Figure 1B-D shows representative cases of these BDA labelled terminals.

LM injections

BDA was injected into the pretectal area in 4 cases. In all cases the injection was centered on the LMl. We expected this, as most cells sensitive to optic flow were believed to reside in the LMl (Winterson and Brauth, 1985; Wylie and Frost, 1996). Typically, many retrogradely labelled cells and labelled fibers were seen throughout the dorsoventral extent of the LMl in each case. We inferred spread to other pretectal areas based on the appearance of fiber bundles traversing the dorsoventral extent of the LMm, LPC, PPC, or GT (see Fig. 3A). The presence of many terminals in the pontine nuclei indicated the injection spread to the LPC (Gamlin and Cohen, 1988b). Likewise, heavy terminal labelling in the nucleus intercalatus thalami (ICT), nucleus posteroventralis thalami (PV), nucleus ventrolateralis thalami (VLT), and nucleus decussatio supraoptic ventralis (nDSV) suggested that the injection spread into the adjacent GT (Gamlin and Cohen, 1988b).

In case LM#1, the injection was found in the rostral extreme of ventral LMl, just posterior to GLv, and may have spread into the adjacent LMm, but did not involve LPC, PPC, or GT. In the dorsal thalamus, terminal labelling was abundant in DLL, and one terminal field was found in DLAmc. At caudal levels the terminals were restricted to ventral DLL, but more rostrally labelling was found throughout DLL.

In case LM#2 the injection site was again centered in the ventral LMl, but was not located as far rostral as case LM#1. This was the largest of the injection sites and it appeared that the tracer leaked up the pipette shaft into the overlying LMm and LPC, and perhaps the PPC. A moderate amount of labelling in the VLT, ICT, nDSV, and PV suggested that the injection site may also have encroached upon the GT, and heavy labelling in the pontine nuclei confirmed that the LPC was injected. In the dorsal thalamus, terminal labelling was abundant in the DLL as in case LM#1, particularly ventrally, and there was substantial labelling in the DLM, DIVA, and DLA. Caudally, there were a few terminals observed within the SPC and rostral DLP.

In case LM#3 the injection was located in the extreme dorsal LMl, which appears as a wedge between the isthmo-optic tract and the tractus opticus (TrO). The injection infringed upon the LMm (see Fig. 3A). This injection resulted in the fewest terminal fields in the dorsal thalamus from about a half dozen fibers. Terminal labelling was found in the DLL, DIVA, DLA, and SPC. A few terminal fields were also observed in the DLM.

In case LM#4, the injection was located in dorsal LMl and may have encroached slightly upon the LMm and certainly involved the PPC (see Fig. 4A). Many fibers coursed dorsoventrally in the PPC but not through the LPC. Terminals were virtually absent from the pontine nuclei. It did not appear that the injection spread into the GT, but there were numerous fibers and terminals in the VLT, ICT, and PV. The nDSV was heavily labelled. Thus, it is difficult not to conclude that the GT received a substantial part of the injection. This injection resulted in the greatest amount of terminal labelling in the dorsal thalamus, arising from between two and three dozen fibers. Terminal labelling was abundant in the DLAmc and some were found in the nucleus lateralis anterior thalami. However, it appeared that these terminal fields arose from fibers terminating in the ventral thalamus. Terminal fields were abundant in the DLL, particularly ventrally, and many were observed in the DIVA and VIA. Some terminal fields were also found in the DLM (mostly ventral) and SPC; few were found in the DLA, and a single fiber terminated in the DLP. Figure 4 shows a series of coronal sections illustrating the extent of the injection site and the terminal labelling in the dorsal thalamus from case LM#4.

To summarize, after injections of BDA centered on the LMl, terminal labelling in the dorsal thalamus was most abundant in the DLL (particularly ventrally). Many terminal fields were also seen in the DIVA and DLM, and some were found in the DLA, SPC, DLP, DLAmc, and VIA. Figure 3B-D shows representative cases of these BDA-labelled terminals. As with the injections in the nBOR, the terminals in the DIVA were only found in the lateral regions, and relatively fewer terminals were seen in the DIVA from the LM injections. Clearly, injections that extended into the GT resulted in a greater amount of labelling in the dorsal thalamus.

Dorsal thalamus injections

CTB was injected into the dorsal thalamus of 4 animals. Examples of retrogradely labelled cells in the nBOR and

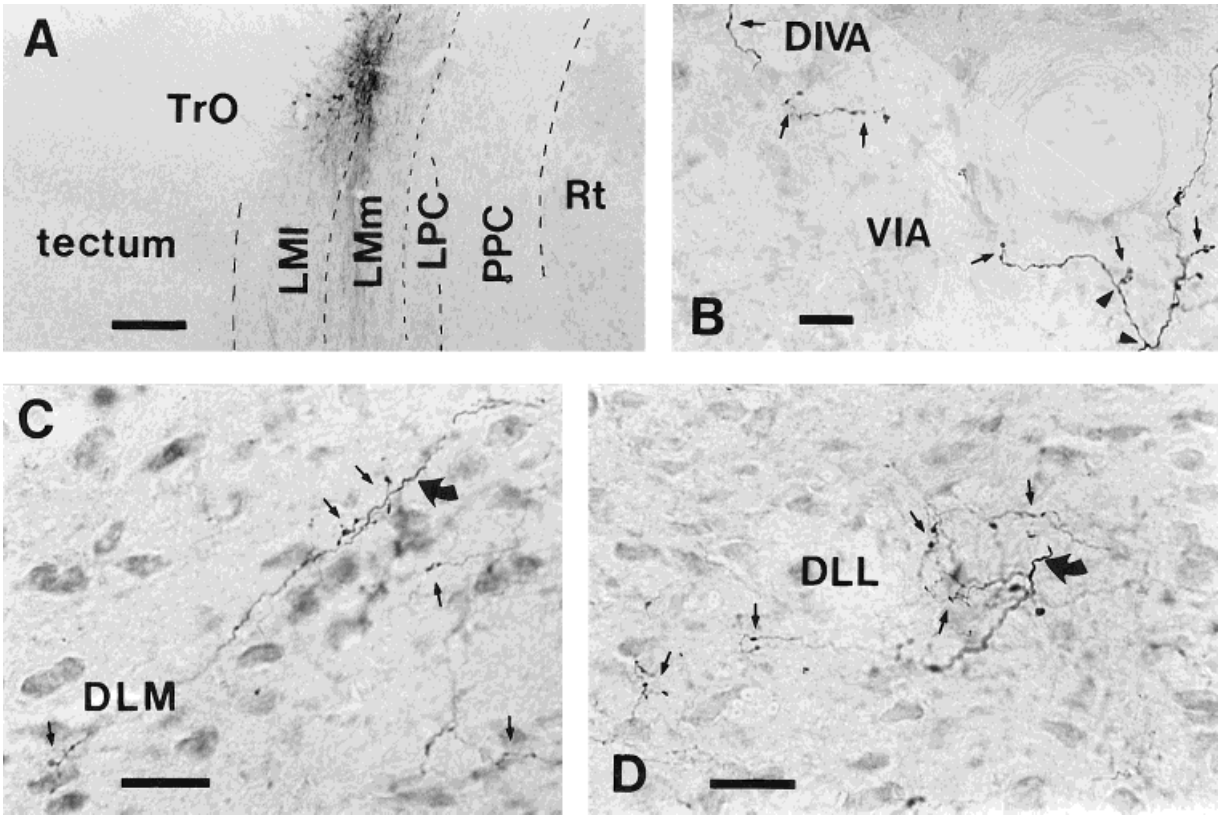

Fig. 3. **A–D:** Projections from the nucleus lentiformis mesencephali (LM) to the dorsolateral thalamus. A shows the injection of biotinylated dextran amine (BDA) into the LM in case LM#3. The four divisions of the pretectum are indicated (dashed lines). Note that the injection was centered in the dorsal extreme of the LM lateralis (LMl), but the presence of a dorsoventral strip of fibers traversing the LM medialis (LMm) suggests spread of the injection to the LMm. B, C and D, respectively, show terminal fields in the nucleus dorsalis intermedius ventralis anterior (DIVA; case LM#4), nucleus dosolateralis medialis thalami (DLM; case LM#2) and the ventral portion of the nucleus dorsolateralis anterior thalami pars lateralis (DLL; case LM#4). In B-D the curved arrows, small arrows, and arrowheads indicate the parent fiber, sites of terminal boutons, and clear examples of axonal branching, respectively. For all panels, the left side is lateral. For other abbreviations see list. Scale bars = 200 μm in A, 25 μm in B-D.

pretectal area are shown in Figure 5. In case CTB#1, the injection was large, and centered in the rostral dorsal thalamus just ventral to the tractus septomesencephalicus (TSM) and appeared to involve the rostral portion of the DLM, the medial portion of the DLL, the DIVA, and the SPC (see Fig. 6A). Consistent with an injection including these areas, anterograde CTB-labelled terminals were abundant in the wulst (Bagnoli and Burkhalter, 1983; Karten et al., 1973; Wild, 1987a) and area parahippocampalis (Casini et al., 1986). There were also terminals in the medial parts of lobus paraolfactorius and the neostriatum internum, suggesting that the injection also involved more medial regions of the dorsal thalamus (Wild, 1987b). Numerous retrogradely labelled cells were seen in the lateral cerebellar nucleus and ventrolateral superior vestibular nucleus indicating involvement of the rostral DLP (Arends and Zeigler, 1991; Wild, 1988). As shown by drawings of coronal sections in Figure 6, numerous retrogradely labelled cells were found in the nBOR complex and the pretectal region. The nBORp contained few retrogradely labelled cells, but was surrounded by abundant labelling in the nBORd (Figs. 5D,6D,E). The area dorsal to the nBORd was also labelled. We have previously (Wylie et al., 1997) considered the areas adjacent to the nBORd as a lateral extension of the area ventralis of Tsai (AVT; see Discussion). The labelling did continue more medially, and cells in the AVT adjacent to the third cranial nerve were labelled. The nBORl was also heavily labelled (Figs. 5E,6C-E), and the labelling continued rostrally and laterally, just posterior to the GLv. Where the nBORl meets the ventral portion of the LM, the labelling all but stopped. Only a few cells in the ventral LMl were labelled and fewer were seen in the ventral LMm. Just lateral to the ventral LMl, numerous cells were labelled in the GT (Figs. 5B, 6C,D). The labelling in the GT appeared as a strip of cells oriented parallel to the adjacent (rostral) LM. There were numerous cells labelled in the LMl along the border of the GT (Figs. 5A, 6B). In the dorsal pretectal area, cells were found scattered in the LMl, LPC and PPC, but were virtually absent from the LMm (Figs. 5C, 6B). More rostrally, the labelling continued in the PPC, and cells in the stratum internum of the GLv were labelled.

The injection site of CTB#2 was located more caudally, in the DLP, but rostrally included the DLM. Consistent with this, anterograde labelling in the telencephalon was most prevalent in the neocortex, the paleostriatum augmentatum, and the hyperstriatum ventrale (Karten et al., 1977; Wild, 1987b). Also consistent with this injection, was the presence of heavy retrograde labelling in the lateral cerebellar nucleus, the lateral superior vestibular nucleus,

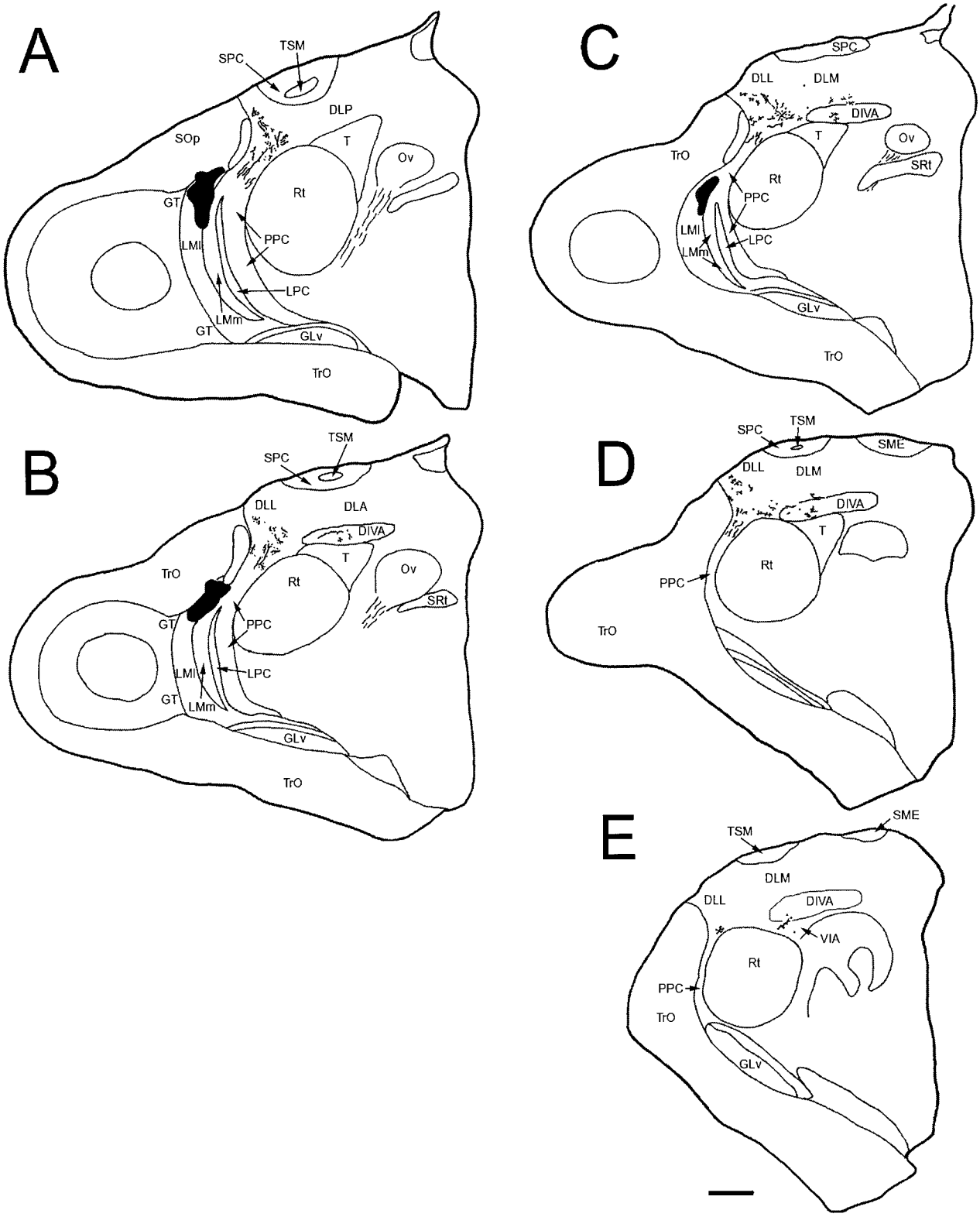

Fig. 4. **A-E:** Anterograde labelling in the dorsal thalamus after injections of biotinylated dextran amine in the pretectal nucleus lentiformis mesencephali (LM). Five coronal sections through the dorsal thalamus from case LM#4 are shown in a caudal (A) to rostral (E) sequence. Fine lines and dots represent labelled fibers and terminal boutons, respectively. The injection site, indicated by the solid black area in A-C, was centered in the dorsal margin of LMl. Terminal labelling was abundant in the ventral and lateral margins the of nucleus dorsolateralis anterior thalami pars lateralis (DLL; A-E) and some was also seen in the lateral aspect of the nucleus dorsalis intermedius ventralis anterior (DIVA; B-E), nucleus dosolateralis medialis thalami (DLM; C-D) and the ventrointermediate area (VIA; E). In other sections from this case, a few terminals were also seen in the nucleus superficialis parvocellularis (SPC), nucleus dorsolateralis anterior thalami (DLA), and the nucleus dorsolateralis posterior thalami (DLP). For other abbreviations see list. Scale bar = 600 µm.

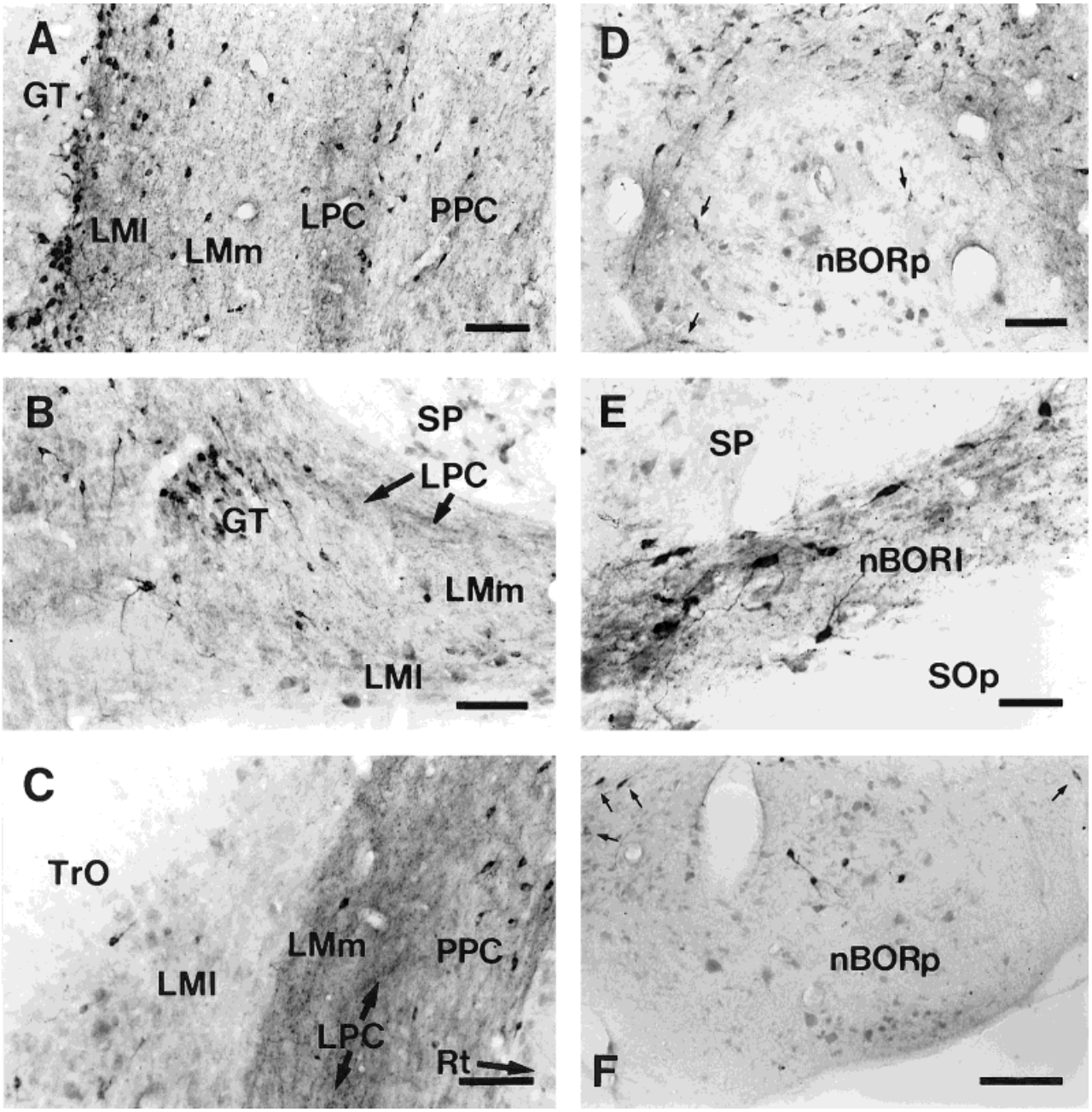

Fig. 5. Retrogradely labelled neurons in the nucleus of the basal optic root (nBOR; **D-F**) and pretectum (**A-C**) after injections of cholera toxin subunit B (CTB) into the dorsolateral thalamus. A shows retrogradely labelled cells in the pretectum from case CTB#1. Note the abundance of labelled cells on the border of the nucleus lentiformis mesencephali pars lateralis (LMl) and the griseum tectale (GT). Note also several labelled cells in the nucleus principalis precommissuralis (PPC) and fewer labelled cells in the nucleus laminaris precommissuralis (LPC) and nucleus lentiformis mesencephali pars medialis (LMm). B shows labelling in the area just ventral to the nucleus subpretectalis (SP). Note the presence of some labelled cells in the LMl and LMm, but clearly more labelling was present in the GT. C shows labelled cells in the dorsal aspects of the pretectum. Some labelled cells were found in the LMl and LPC, but more were present in the PPC and few were found in the LMm. D shows labelled cells in the nucleus of the basal optic root (nBOR). Although, as indicated by the small arrows, a few cells were observed in the nBOR proper (nBORp), many more cells were seen in the nBOR dorsalis (nBORd). E shows several retrogradely labelled cells in the nBOR lateralis (nBORl). F shows four labelled cells in the nBORp and a few labelled cells in the nBORd indicated by the small arrows. For all panels, the left side is lateral. For other abbreviations see list. Scale bars = 100 μm in A-D,F, 50 μm in E.

and throughout the tectum (Arends and Zeigler, 1991; Gamlin and Cohen, 1986; Wild, 1988). In the pretectal region and nBOR, the pattern of labelling resembled that of case CTB#1. There were several cells labelled in the nBORp (Fig. 5F), but clearly the labelling was heavier in the nBORd and nBORl. A few cells in the ventral LMl and LMm were labelled, but throughout the rest of the LM, labelling was absent from the LMm, except for a few cells

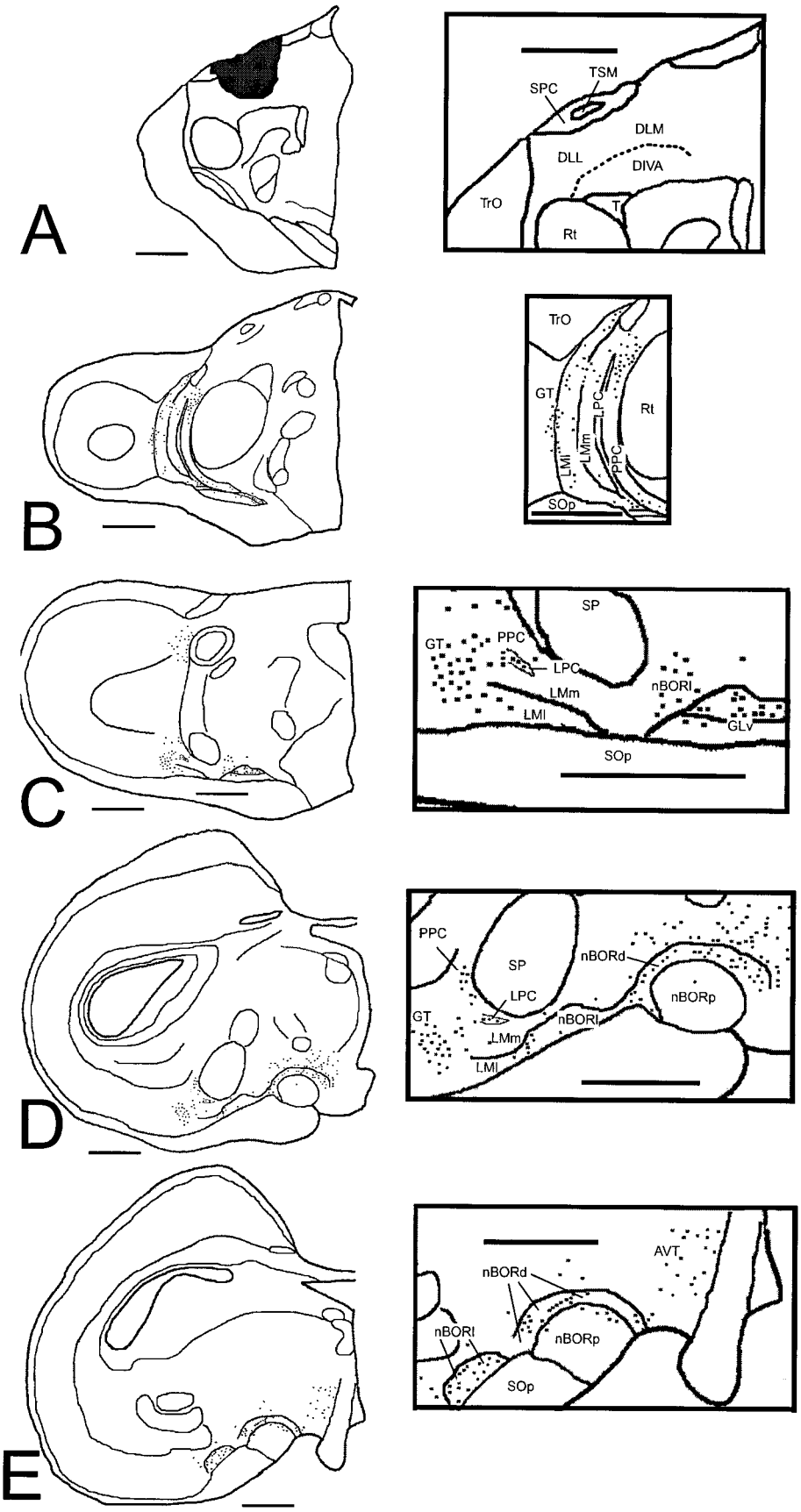

Fig. 6. Retrogradely labelled cells in the pretectal area and nucleus of the basal optic root (nBOR) after injections of cholera toxin subunit B (CTB) into the dorsal thalamus. **A** shows the injection site (blackened area) and **B-E** show the location of labelled cells in the nucleus lentiformis mesencephali pars lateralis and pars medialis (LMl, LMm), nucleus laminaris precommissuralis (LPC), nucleus principalis precommissuralis (PPC), griseum tectale (GT), the nucleus geniculatus lateralis pars ventralis (GLv), the area ventralis of Tsai (AVT) and the three subdivisions of the nBOR, pars lateralis (nBORl), pars dorsalis (nBORd) and proper (nBORp). Retrogradely labelled cells found in other areas were not included in these drawings. The **insets** on the right highlight areas of interest. These data are from case CTB#1. See text for details. For other abbreviations see list. Scale bars = 1 mm.

dorsally. Cells were scattered throughout the LMl and LPC, but clearly there were more cells in the PPC.

In case CTB#3, the injection site was small and centered in the dorsal margin of the Rt, but there was evidence of some spread into the overlying ventral DLL. One retrogradely labelled cell was found in the nBORp but more than a dozen were found in the nBORl and several were found laterally in the nBORd. The ventral margin of the LM contained few retrogradely labelled cells, but dorsally several cells were found in the LMl and a few were seen in the LMm. Retrogradely labelled cells were more abundant in the LPC, PPC and GT than in the LM.

In case CTB#4, the injection was very small and centered on the TSM but spread into the adjacent SPC and perhaps the extreme dorsal portion of the DLL. Very little retrograde labelling was seen, but one cell was seen in the nBORl, 8 cells were found in the nBORd and a few were seen in the adjacent AVT. In the pretectum, more cells were seen dorsally than ventrally. Five cells were found in the LMl, 4 were seen in the LMm, but several were noted in the LPC, PPC and GT.

DISCUSSION

In this report we have shown that the LM and nBOR, two retinal recipient areas specialized for the analysis of optic flow, project to the anterior dorsolateral thalamus in pigeons.

Projection from the nBOR to the dorsal thalamus

Injections of BDA into the nBOR resulted in abundant anterograde terminal labelling in the DLL and DIVA, and to a lesser extent in the DLM. Some terminals were also found in the DLP, DLA, DLAmc, VIA, and SPC. Retrograde experiments with CTB revealed that the projection from the nBOR was largely from the nBORd and nBORl. We have previously described the projection from nBOR to the dorsal thalamus (Wylie et al., 1997), but in this report we have clarified that the projection is from the nBORd and nBORl, and our reanalysis of the material indicates that the projection is largely to the DLL and DIVA, and somewhat to the DLM. Previously, using the atlas of Karten and Hodos (1967), we reported that the projection was to the DLL, DLA, and DLM. Most of the terminals we had ascribed to the DLA and DLM were found ventrally, in the DIVA described by Wild (1987a).

Previously it has been argued that cells in the nBORp and nBORd have different response properties. Whereas cells in the nBORp have large monocular receptive fields responsive to largefield motion (Wylie and Frost, 1990a), cells in the nBORd and the adjacent area, (which Wylie et al., 1997 have included as part of the AVT), have binocular receptive fields and respond best to particular patterns of optic flow resulting from either self-translation or self-rotation (Wylie and Frost, 1990b). The nBORd is known to project to the medial column of the inferior olive (IO; Brecha et al., 1980; Wylie et al., 1997) which in turn projects to the vestibulocerebellum (VbC; Arends and Voogd, 1989). Neurons in the VbC have binocular receptive fields and respond best to particular patterns of optic flow resulting from self-translation and self-rotation (Wylie and Frost, 1991, 1993; Wylie et al., 1993). Thus, it is likely that the same highly processed information specifying self-rotation and self-translation that reaches the olivocerebellar system from the nBORd also reaches the dorsal thalamus. However, further experiments will have to be performed to determine if individual cells within the nBORd project to either the IO or the dorsal thalamus, or both structures.

Projection from the LM to the dorsal thalamus

Most cells in the LM have monocular receptive fields (Winterson and Brauth, 1985; Wylie and Frost, 1996), but we have recorded from binocular cells in the LMl that, like neurons in the nBORd, respond to particular patterns of optic flow (unpublished observations). In fact, one such cell was recorded at the injection site of case LM#1.

Injections of BDA into the LM resulted in abundant anterograde labelling in the DLL, and to a lesser extent in the DLM and DIVA. Some terminals were also found in the DLAmc, DLP, SPC, and VIA. Retrograde experiments showed that the projection from the LM was greater from the LMl than from the LMm. Moreover, clearly the GT and PPC provided a greater input to the dorsal thalamus than did the adjacent LM. Gamlin and Cohen (1988b) investigated the projections of the pretectal area using horseradish peroxidase (HRP) and did find terminal labelling in the dorsal thalamus; however, they concluded that it was from the GT. Wild (1989) studied the projection of the pretectum to the dorsal thalamus in pigeons and concluded that the projection was largely to the DLL but also to the DLAmc and DLM, but not to the DIVA. Our results are in agreement with those of Wild (1989) in that we found that the LM projected largely to the DLL. However, in some cases we did find projections, albeit weaker, to other areas in the dorsal thalamus, including the DIVA. It is noteworthy that we found the projection to the DIVA to be restricted to its lateral margin overlying T and the medial half of Rt. The illustrations in Wild (1989) show some terminal labelling in this area. Thus, the apparent differences in the two studies might be due to the difficulties in localizing the boundaries of DIVA in Nissl-stained sections. Wild (1989) also used a different nomenclature for the pretectum than we did in the present study. What Gamlin and Cohen (1988b) include as part of the GT, Wild (1989) includes as part of the LM (LM parvocellularis; compare Fig. 2 of Wild, 1989 to Fig. 6 of the present study).

Comparison with mammals

We are not aware of any studies that show projections from the AOS to the dorsal thalamus in mammals, but there is an extensive literature demonstrating a pretectal projection from the nucleus of the optic tract (NOT) to the dorsal lateral geniculate nucleus (LGNd; Berman, 1977; Graybiel and Berson, 1980; Harting et al., 1986; Holstege and Collewijn, 1982; Kubota et al., 1987, 1988; Mackay-Sim et al., 1983; van der Want et al., 1992). Based on functional and anatomical grounds, the NOT is homologous to the avian LM (Hoffmann and Schoppmann, 1981; McKenna and Wallman, 1985a,b; Winterson and Brauth, 1985). The LGNd is homologous to the retinorecipient nuclei in the thalamus providing input to telencephalon, namely the DLL and DLAmc (Karten et al., 1973; Karten and Shimizu, 1989). Thus, the NOT-LGNd and LM-DLL projections are equivalent, suggesting that it may have evolved in a common ancestral reptile. There is currently a debate as to whether the NOT neurons projecting to LGNd are gamma aminobutyric acid (GABA)ergic (Cucchiaro et al., 1991; Nabors and Mize, 1991). It would be interesting

to see if the LM and nBOR neurons projecting to the dorsal thalamus are GABAergic. Britto et al. (1989) have shown that GABAergic neurons represent a small population of nBOR neurons.

Function of the AOS-dorsal thalamic projection

There is an extensive literature on the anatomy of the AOS and associated pretectum in numerous species (McKenna and Wallman, 1985b). Most studies of the AOS have considered its role with regard to optokinetic nystagmus and generation of compensatory eye movements (Simpson, 1984; Simpson et al., 1988). As such, investigation has focused on those subsystems concerned with oculomotor control, namely the olivocerebellar pathway, the vestibular nuclei, and to a lesser extent, the pontine nuclei (see Simpson, 1984; Simpson et al., 1988; Waespe and Henn, 1987). Wylie et al. (1997) suggested that the AOS should be considered in its broader sense: a system dedicated to the analysis of the visual consequences of self-motion (Frost et al., 1990, 1994; Grasse and Cynader, 1990; Simpson et al., 1988). Gibson (1954, 1958) emphasized that there is an abundance of information available in the optic flowfield as one moves through the environment. This information can be used to control posture, influence the mechanisms responsible for locomotion through the environment, and contribute to the perception of the three-dimensional layout of the environment, one's orientation relative to the environment, and the perception of self-motion (see also Nakayama, 1985). Below we address the findings of the present study with respect to various potential functions of a system responsible for the analysis of optic flow.

Multimodal analysis of self-motion. Self-motion is obviously a multimodal event. As one moves, proprioceptive feedback arises from: (1) the vestibular system due to stimulation of the otolith organs and semicircular canals; (2) the somatosensory system due to the limbs contacting the ground or, in the pigeon's case, the wind stimulating the feathers during flight; (3) muscle senses due to feedback from the limbs responsible for locomotion; and (4) the visual system due to the induced motion of the entire visual world. As such, it would not be surprising to find neural systems responsive to optic flow as well as other sensory stimuli. Brainstem neurons responsive to both optic flow and vestibular stimulation are abundant, although they are usually described in the context of oculomotor control rather than self-motion per se (for review see Waespe and Henn, 1987). Recently, in monkeys, neurons in the medial superior temporal area of the cerebral cortex have been shown to respond to both vestibular stimulation and optic flow (e.g., Duffy, 1996; Graf et al., 1996).

We believe that the projection described in the present study might, in part, represent an integration of optic flow analysis with the somatosensory, muscle proprioceptive, and vestibular systems. The somatosensory system in pigeons is represented by two telencephalic areas that receive input from the dorsal thalamus: the anterior hyperstriatum and the medial neostriatum (Delius and Bennetto, 1972). The anterior hyperstriatum receives most of its thalamic input from the DIVA (Wild, 1987a), and the medial neostriatum receives a heavy input from the caudal DLP (Wild, 1987a). The caudal DLP is known to receive input from the spinal cord and dorsal column nuclei (Arends et al., 1984; Wild, 1987a). The SPC has also been implicated in the processing of somatosensory and spinal information (Bagnoli and Burkhalter, 1983; Delius and Bennetto, 1972; Karten and Revzin, 1966). In the present study, while we found a few projections from the nBOR and LM to the caudal DLP and SPC, we found a significant projection to the DIVA. This may permit the integration of somatosensory and optic flow information. Recently, Medina et al. (1997) have also concluded that the DIVA and VIA might be involved in self-motion based on the fact that they are connected with somatomotor areas of the telencephalon, and the cerebellum. Medina et al. (1997) suggested that the DIVA is comparable to the caudal ventroposterolateral nucleus in mammals, and VIA is comparable to the motor area of the ventral tier.

The rostral DLP could also be a site of the integration of optic flow and vestibular information. Wild (1988) has shown that the rostral DLP and, to a lesser extent, the caudal aspect of the DIVA, receive projections from the vestibular nuclei.

Perception of self-motion. When observers are presented with optic flow stimulation encompassing large parts of the visual field, they experience "vection" or "illusory self-motion." The observer perceives that the objects moving in the visual display are stationary, and that he/she is moving through the environment (e.g., Anderson, 1986). The thalamocortical system receiving optic flow information from the LM and nBOR might be involved in the perception of self-motion. It is noteworthy that the perception of vection is enhanced by concurrent stimulation of the somatosensory and/or vestibular systems (Wong and Frost, 1981).

Perception of the three-dimensional layout of the environment. In addition to providing proprioceptive information related to self-motion, Gibson (1958) also emphasized that the optic flowfield affords the observer with a rich source of exteroceptive information related to the three-dimensional layout of the environment, particularly during self-translation. During translation, objects nearer the observer move "faster" in the flowfield than do more distant objects. This relative motion (or "velocity edges," Nakayama, 1985) is a powerful cue in assigning the relative depth of various objects and surfaces, and contributes to our phenomenal percept of a three-dimensional world. We propose that the connection from the AOS and the pretectum to the DLL might be involved in this function.

The DLL is part of the nucleus opticus principalis thalami (OPT) described by Karten et al. (1973). The DLL is a retinal recipient area that projects bilaterally to the visual wulst of the telencephalon (Bagnoli and Burkhalter, 1983; Hunt and Webster, 1972; Karten et al., 1973; Miceli et al., 1979a; Meier et al., 1974). This pathway is thought to be equivalent to the geniculostriate system in mammals (Karten and Shimizu, 1989). Physiological experiments have revealed that the DLL and the visual areas of the wulst have small receptive fields and respond best small moving or stationary stimuli (Britto et al., 1975; Denton, 1981; Miceli et al., 1979b; Revzin, 1969; Wilson, 1980). As such, the thalamofugal system is performing a "local" analysis of the optic array, of small stationary and moving stimuli. Perhaps those neurons in the DLL receiving input from the AOS and pretectum are analyzing local motion in the context of an optic flowfield and using this information to construct a three-dimensional world.

Distinguishing object-motion from self-motion. Neurons in the DLL receiving input from the AOS and pretectum might also be involved in distinguishing object from self-motion (see Frost, 1982, 1985; Frost et al., 1990, 1994). A moving edge could be due to movement of an object in the environment, self-translation of the observer, or a combination of object and self-motion. The AOS and pretectum might simply be conveying information to local movement detectors in the DLL that self-motion is occurring. Such an analysis may also take place in the DLP which has been shown to receive input from the tectum (Gamlin and Cohen, 1986). Tectal cells are involved in the analysis of small moving stimuli (Frost, 1982, 1985; Frost et al., 1990, 1994).

Spatial cognition. Most animals have a sophisticated ability to remember the relative locations of various objects and to use this information to appropriately navigate. If obvious landmarks are not present, the observer must rely on "path integration" to construct a cognitive map of the environment (e.g., McNaughton et al., 1995). In many species, including birds, the hippocampus has been implicated in spatial cognition (mammals, e.g., O'Keefe and Speakman, 1987; Olton and Papas, 1979; birds, Bingman and Mench, 1990; Bingman et al., 1988a,b, 1990; Krebs et al., 1989; Sherry and Vaccarino, 1989).

Path integration simply involves the addition of vectors as an animal moves about the environment. The resultant vector at any point in time would specify the direction and distance from a starting point. To compute this, the animal must rely on information about its own self-motion. Self-motion has been shown to be important for spatial memory (Foster et al., 1989) and McNaughton et al. (1995) have proposed a model for path integration that relies on self-motion information provided by the vestibular system, noting that a thalamic structure providing input to the hippocampus in rats does receive vestibular information. However, optic flow might be a better indicator of self-motion as it occurs in situations, such as constant velocity, when the vestibular system is not necessarily active.

In birds, the parahippocampus receives thalamic input from the SPC and DLM. In the present study, we found that the nBOR and LM projected to the DLM and weakly to the SPC. We propose that these connections implicate that optic flow information is used for spatial cognition.

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