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Projections of the Nucleus of the Basal Optic Root in Pigeons (*Columba livia*) Revealed With Biotinylated Dextran Amine

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ABSTRACT

The nucleus of the basal optic root (nBOR) of the accessory optic system is known to be involved in the analysis of the visual consequences of self-motion. Previous studies have shown that the nBOR in pigeons projects bilaterally to the vestibulocerebellum, the inferior olive, the interstitial nucleus of Cajal, and the oculomotor complex and projects unilaterally to the ipsilateral pretectal nucleus lentiformis mesencephali and the contralateral nBOR. By using the anterograde tracer biotinylated dextran amine, we confirmed these projections and found (previously unreported) projections to the nucleus Darkshewitsch, the nucleus ruber, the mesencephalic reticular formation, and the area ventralis of Tsai as well as ipsilateral projections to the central gray, the pontine nuclei, the cerebellar nuclei, the vestibular nuclei, the processus cerebellovestibularis, and the dorsolateral thalamus. In addition to previous studies, which showed a projection to the dorsomedial subdivision of the contralateral oculomotor complex, we found terminal labelling in the ventral and dorsolateral subdivisions.

Individual fibers were reconstructed from serial sections, and collaterals to various nuclei were demonstrated. For example, collaterals of fibers projecting to the vestibulocerebellum terminated in the vestibular or cerebellar nuclei; collaterals of fibers to the inferior olive terminated in the pontine nuclei; many individual neurons projected to the interstitial nucleus of Cajal, the nucleus Darkshewitsch, and the central gray and also projected to the nucleus ruber and the mesencephalic reticular formation; collaterals of fibers to the contralateral nucleus of the basal optic root terminated in the mesencephalic reticular formation and/or the area ventralis of Tsai; neurons projecting to the nucleus lentiformis mesencephali also terminated in the dorsolateral thalamus. The consequences of these data for understanding the visual control of eye movements, neck movements, posture, locomotion, and visual perception are discussed. J. Comp. Neurol. 384:517–536, 1997.

Indexing terms: optokinetic; oculomotor; visual motion; visual-vestibular integration; accessory optic system

The accessory optic system (AOS) and associated pretectum comprise a distinct visual system dedicated to the analysis of the visual consequences of self-motion and the control of gaze stabilization (Simpson, 1984; Simpson et al., 1988a; Frost et al., 1994). In pigeons, this system consists of two major nuclei: the nucleus of the basal optic root (nBOR) of the AOS and the pretectal nucleus lentiformis mesencephali (LM). Lesion, neuroanatomy, and electrophysiology studies have implicated the nBOR and LM in the control of the optokinetic response (OKR) and gaze stabilization. Lesions of the nBOR and LM result in impairments of the OKR (Fite et al., 1979; Wallman et al., 1981; Gioanni et al., 1983a,b). Electrophysiology and 2-deoxyglucose studies have shown that most nBOR and LM neurons have large receptive fields and exhibit direction selectivity in response to moving, large-field visual stimuli (random-dot patterns or checkerboards; Burns and Wall-

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man, 1981; McKenna and Wallman, 1981, 1985; Morgan and Frost, 1981; Gioanni et al., 1984; Winterson and Brauth, 1985; Wylie and Frost, 1990a,b, 1996; Wolf-Oberhollenzer and Kirschfeld, 1994). Anatomy studies have shown that the nBOR and LM project to vestibular and oculomotor structures (Brauth and Karten, 1977; Clarke, 1977; Brecha and Karten, 1979; Brecha et al., 1980; Gamlin and Cohen, 1988).

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

A series of studies by Karten and colleagues (Brauth and Karten, 1977; Brecha and Karten, 1979; Brecha et al., 1980) that used tritiated amino acids for anterograde tracing and horseradish peroxidase (HRP) for retrograde tracing found that the nBOR complex projects bilaterally to the vestibulocerebellum [VbC; the uvula (folia IXc,d) and auricle], the inferior olive (IO), the interstitial nucleus of Cajal (IC); ipsilaterally to the LM and the ventral subdivision of the oculomotor complex (OMv); and contralaterally to the nBOR and the dorsolateral subdivision of the oculomotor complex (OMdl). In an attempt to determine whether individual nBOR neurons provide input into one or more of these structures, small amounts of the anterograde tracer biotinylated dextran amine (BDA) were injected iontophoretically into the nBOR. We confirmed all of the major projections described above, and we found numerous other projection sites, including other subdivisions of the oculomotor complex (OMC). In addition, we reconstructed individual axons to illustrate branching patterns to multiple nuclei. A preliminary report of the mossy fiber projection to the VbC has been published (Wylie and Linkenhoker, 1996).

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 (Palmetto Pigeon Plant, Sumter, SC) were anesthetized with a ketamine (90 mg/kg)-xylazine (15 mg/kg) mixture (i.m.), and supplemental doses were administered

Abbreviations

AOS	accessory optic system
AVT	area ventralis of Tsai
BCP	brachium conjuctivum cerebropedale
CbL	lateral cerebellar nucleus
CbM	medial cerebellar nucleus
CtG	central gray
CTz	corpus trapezoidium
D	nucleus Darkshewitsch
dl	dorsal lamella of inferior olive
DLA	anterior dorsolateral thalamus
DLAmc	anterior dorsolateral thalamus, magnocellular division
DLL	anterior dorsolateral thalamus, lateral subdivision
DLM	anterior dorsolateral thalamus, medial subdivision
DLP	anterior dorsolateral thalamus, posterior subdivision
DVN	descending vestibular nucleus
EW	Edinger-Westphal nucleus
FR	mesencephalic reticular formation
FRL	lateral mesencephalic reticular formation
FRM	medial mesencephalic reticular formation
gl	granule layer of cerebellar cortex
GLv	ventral lateral geniculate nucleus
IC	interstitial nucleus of Cajal
ICo	nucleus intercollicularis
IO	inferior olive
IPS	nucleus interstitiopretectosubpretectalis
IXa,b	folium IXa,b of the cerebellum
IXc,d	folium IXc,d of the (vestibulo)cerebellum
LM	nucleus lentiformis mesencephali
LMl	nucleus lentiformis mesencephali, pars lateralis
LMm	nucleus lentiformis mesencephali, pars medialis
LP	lateral pontine nucleus
LPC	nucleus laminaris precommisuralis
LTN	lateral terminal nucleus
mc	medial column of inferior olive
MF	mossy fiber
ml	molecular layer of cerebellar cortex
MLF	medial longitudinal fasciculus
MLv	lateral mesencephalic nucleus, pars ventralis
MP	medial pontine nucleus
MTN	medial terminal nucleus
MVN	medial vestibular nucleus
MVNmc	medial vestibular nucleus, magnocellular division
MVNpc	medial vestibular nucleus, parvocellular division
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
OKR	optokinetic response
OMC	oculomotor complex
OMdl/dl	oculomotor nucleus, dorsolateral subdivision
OMdm/dm	oculomotor nucleus, dorsomedial subdivision
OMv	oculomotor nucleus, ventral subdivision
OPT	nucleus opticus principalis thalami
OV	nucleus ovoidalis
pc	posterior commissure
PCV/pcv	processus cerebellovestibularis
Pl	Purkinje layer of cerebellar cortex
PPC	nucleus principalis precommisuralis
PST	tractus pretectosubpretectalis
PT	nucleus pretectalis
PTM	nucleus pretectalis medialis
PV	nucleus periventricularis
R	nucleus raphes
RPO	nucleus reticularis pontis oralis
Rt	nucleus rotundus
Ru	nucleus ruber (red nucleus)
SCE	stratum cellulare externum
SCI	stratum cellulare internum
SOp	stratum opticum
SP	nucleus subpretectalis
SRt	nucleus subrotundus
SVN	superior vestibular nucleus
T	nucleus triangularis
Ta	tangential (vestibular) nucleus
TrO	tractus opticus
TVM	tractus vestibulomesencephalicus
VbC	vestibulocerebellum
vl	ventral lamella of inferior olive
VTRZ	ventral tegmental relay zone
wm/cwm	cerebellar white matter

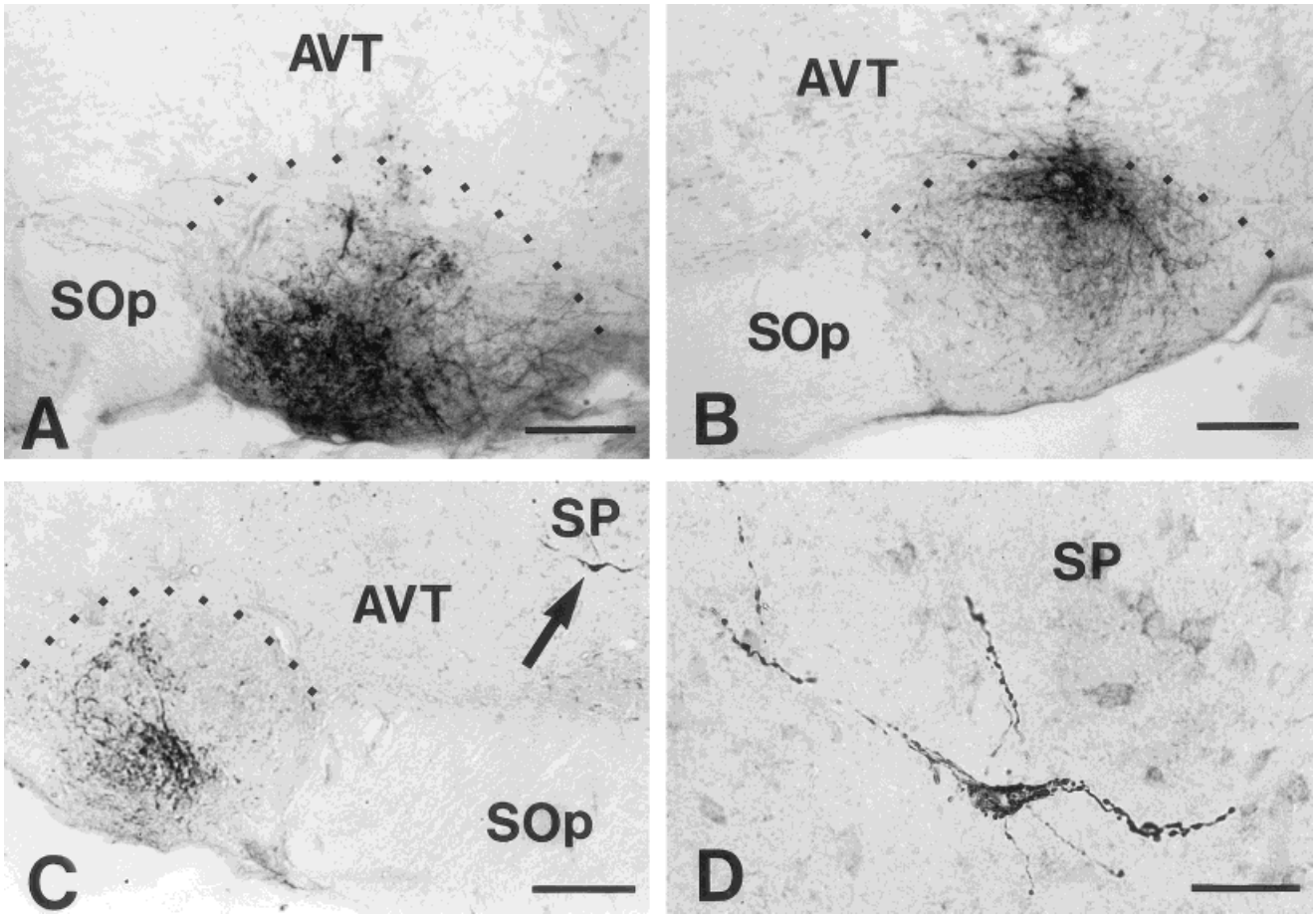


Fig. 1. Injections of biotinylated dextran amine (BDA) into the pigeon nucleus of the basal optic root (nBOR). **A–C:** Injection sites of cases 1–3, respectively. The dotted lines indicate the approximate border of the nBOR proper (nBORp). The stratum opticum (SOp) lies lateral to the nBOR. **D:** A terminal field surrounding a cell in the nucleus subpretectalis (SP) from case 3, as indicated by the arrow in C. AVT, area ventralis of Tsai. Scale bars = 250 μm in A–C, 50 μm in D.

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). The location of the nBOR was 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 neurons typically exhibit direction selectivity in response to large-field stimuli moving in the contralateral visual field. Once nBOR was localized, BDA (Molecular Probes, Eugene OR; MW 10,000, 10% in 0.1 M phosphate-buffered saline; PBS) was injected iontophoretically (+3 μamps, 1 second on, 1 second off) for 2–5 minutes by using micropipettes with tip diameters of 8–12 μm. First, recordings were made with the injection electrode to ensure that the tip was within the nBOR. Subsequent to the injection, the electrode was left undisturbed for an additional 5 minutes. After a survival time of 4–6 days, the animals were given an overdose of sodium pentobarbital (100 mg/kg) and were immediately perfused with saline (0.9%) followed by 4% paraformaldehyde in 0.1 M PB. The brains were extracted, embedded in gelatin, and cryoprotected in sucrose (30% in 0.1 M PB). Coronal sections (50 μm thick) were cut with a microtome. Sections were washed in PBS, incubated in ExtrAvidin peroxidase (1:1,000; Sigma, St. Louis, MO) and Triton X-100 (0.3%) for 1.5 hours at room temperature, washed again in PBS, and then visualized with diaminobenzidine (DAB). Sections were first placed in 0.025% DAB in 0.1 M PBS for 10 minutes and then placed 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 mounted onto gelatin-coated slides, dried, lightly counterstained with neutral red, and coverslipped with Permount. The slides were viewed by using light microscopy, and, in some cases, individual axons were reconstructed from serial sections with the aid of a drawing tube.

RESULTS

The nBOR was injected in three pigeons (see Fig. 1). In case 1, the injection was confined to the ventral half of the nBORp (diameter ~ 500 μm). In case 2, the injection was in the dorsal portion of the nBORp and the overlying nBORd (diameter ~ 300 μm). In case 3, the injection was contained within the nBORp and was located slightly medial to the center (diameter ~ 400 μm). Terminal labelling was clear and abundant, but retrogradely la-

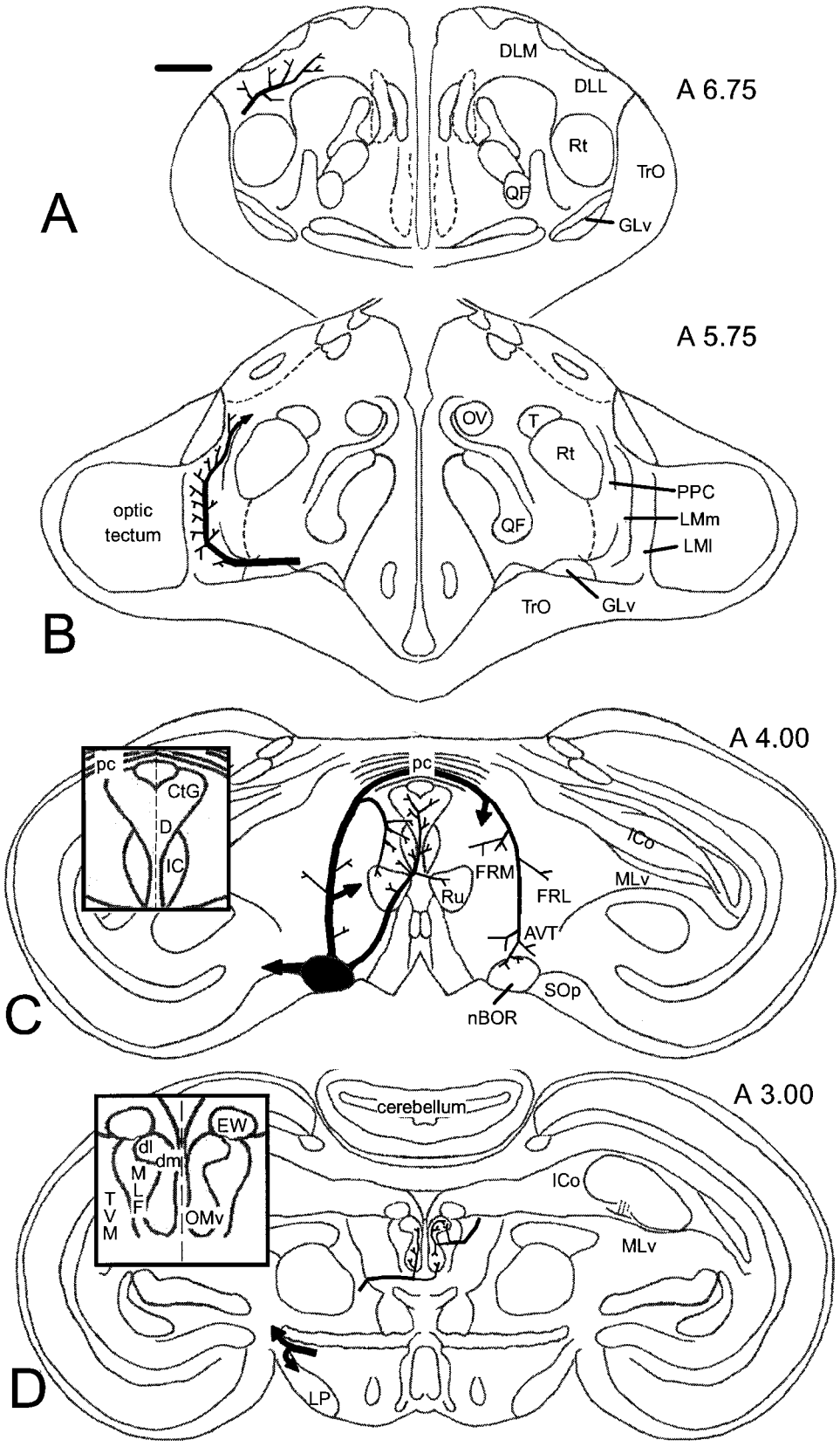


Fig. 2. **A–G:** Projections of the pigeon nBOR shown in a series of schematic sections (from rostral to caudal) of the axon pathways to the terminal areas. Arrows indicate the direction of the fibers continuing in subsequent sections. The approximate location of each section relative to interaural zero (0.00, E) is indicated by the numerals to the right in A–G (A = anterior; P = posterior). The **insets** in C, D, and G magnify the accessory oculomotor area, the oculomotor complex (OMC), and the inferior olive, respectively. The dashed lines in the insets for B and C indicate the midline. Cross-hatched areas represent cranial nerves. Drawings adapted from Karten and Hodos (1967). See text for details. For other abbreviations, see list.

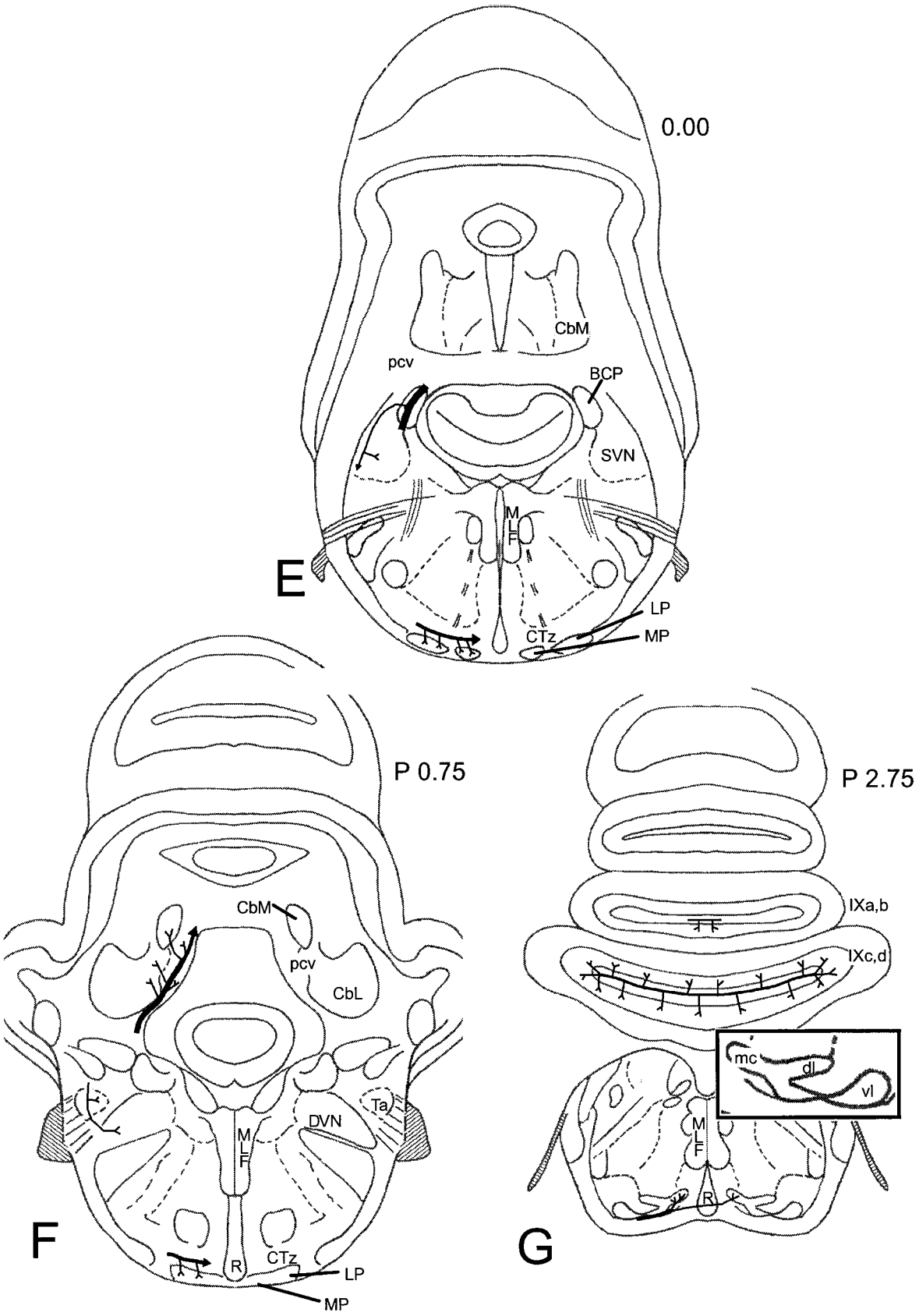


Figure 2 (Continued.)

belled cell bodies were rarely seen. (In total, only four retrogradely labelled cell bodies were noted.)

Figure 2 shows a schematic illustration of the axon pathways to the terminal areas discussed below. Axons that travelled dorsally and medially from the nBOR innervated the ipsilateral mesencephalic reticular formation (FR; Fig. 2C), the OMC (bilateral; Fig. 2D), and the accessory oculomotor nuclei and perirubral areas (bilateral; Fig. 2C). Some of these axons crossed the midline via the posterior commissure (pc) and terminated in the contralateral OMC (Fig. 2D), contralateral nBOR, FR, and area ventralis of Tsai (AVT; Fig. 2C). Numerous axons left laterally from the nBOR, coursed rostrally, and terminated heavily in the pretectum and the anterior dorsolateral thalamus (Fig. 2A,B). Other axons exited the nBOR laterally and coursed caudally to terminate in the pontine nuclei and IO (Fig. 2E–G), whereas others innervated the cerebellar and vestibular nuclei and the cerebellar cortex of the VbC (Fig. 2F,G). Table 1 summarizes the location of terminal fields found in each of the three cases.

Projections to the cerebellum, cerebellar nuclei, and vestibular nuclei

In all cases, labelled axons travelled laterally and joined the ipsilateral brachium conjuctivum cerebropedale (BCP) and ascended into the VbC to terminate as mossy fiber (MF) rosettes in the granule layer throughout the mediolateral extent of folium IXc,d (Fig. 3A). To a lesser extent, rosettes were found in folium IXa,b, (particularly in the ventral lamella), and a few were also found in folium VIII. Fewer still were found in the contralateral anterior vermis (folia I, II, and III; see Table 1).

In case 1, two MFs branched at the rostral end of the vestibular complex, dorsal to the superior vestibular nucleus (SVN), and collaterals descended and terminated in the SVN. One of these fibers continued caudally and terminated in the tangential nucleus (Ta) and the descending vestibular nucleus (DVN). The parent MFs continued into the cerebellum and branched in the cerebellar nuclei. Terminals were observed in the medial cerebellar nucleus (CbM), the lateral cerebellar nucleus (CbL), and the processus cerebellovestibularis (PCV; Fig 3B,C; see also Wylie and Linkenhoker, 1996). Most of these terminals were seen in a relatively circumscribed area just lateral to the fourth ventricle, as indicated in Figure 3B. This area includes the ventral margin of the CbM, the dorsomedial margin of CbL, and the adjacent PCV.

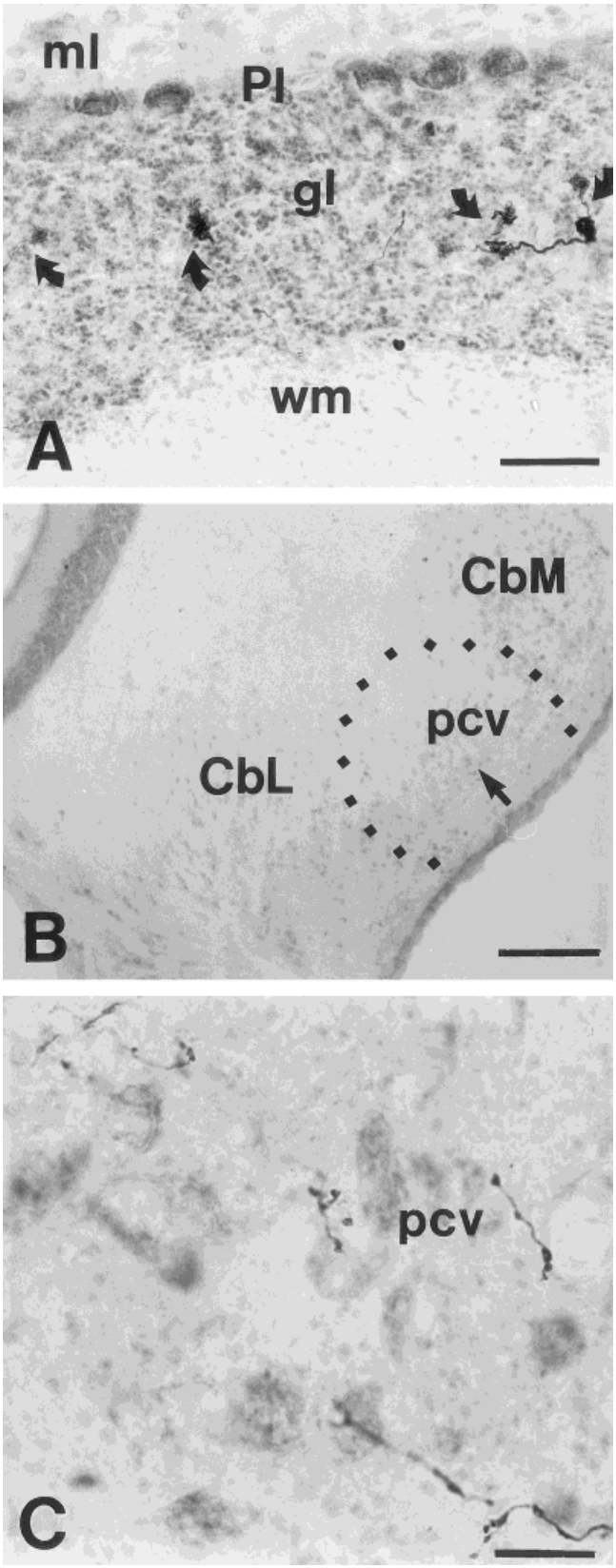
Figure 4 shows a reconstruction of one of the MFs from case 2 that gave off collaterals in the cerebellar nuclei. This MF initially split into two branches dorsal to the SVN and then ascended into the cerebellum. Both branches gave off collaterals to the circumscribed area (ventral CbM/dorsomedial CbL) described above. One of these collaterals travelled quite laterally, and terminals were seen in the cerebellar white matter (cwm) lateral to the CbL. In case 3, one MF gave off a small terminal field in the processus cerebellovestibularis (PCV) immediately dorsal to the SVN, and several MFs branched and terminated in the area of the ventral CbM/dorsomedial CbL and the adjacent PCV. In none of the cases were terminals found in the infracerebellar nucleus described by Arends and Zeigler (1991a,b).

Terminal fields were also seen in the vestibular nuclei in case 1 from a fiber that did not ascend into the cerebellum.

TABLE 1. Summary of the Projection Sites of All Biotinylated Dextran Amine Injections[1]

Site	Case 1	Case 2	Case 3
Cerebellar cortex			
folium IXc,d	**i, c**	**i, c**	**i, c**
folium IXa,b	**i, c**	**i, c**	**i, c**
Other	Folia VIII, I, II, III (c)	Folium I	Lateral unfoliated cortex (i, c)
Cerebellar nuclei			
CbM	**i**	**i**	**i**
CbL	**i**	**i**	—
PCV	**i**	**i**	**i**
Vestibular nuclei			
DVN	i	—	—
MVNmc	c	—	—
MVNpc	c	i	—
SVN	i, c	—	—
Ta	i	—	—
Lateral vestibular nucleus	—	—	—
Dorsolateral nucleus	—	—	—
Inferior olive	—	**i,** c	—
Pontine nuclei			
Medial	**i**	**i,** c	**i**
Lateral	—	**i**	**i**
Adjacent CTZ	—	i, c	i
Oculomotor complex			
OMdl	**c**	—	**i, c**
OMdm	**c**	**—**	**c**
OMv	**c**	**i, c**	**c**
MLF	—	i	i, c
Edinger-Westphal	—	—	—
Trochlear nucleus	—	—	—
Abducens nucleus	—	—	—
Accessory oculomotor and perirubral areas			
CtG	**i**	**i**	**i, c**
D	**i, c**	**i, c**	**i, c**
IC	**i, c**	**i, c**	**i, c**
Rn	**i, c**	**i, c**	**i**
SCE	—	i	i, c
SCI	—	i	i, c
Contralateral nBORd	+	−	+
Mesencephalic reticular formation			
Medial (FRM)	**i, c**	**i, c**	**i, c**
Lateral (FRL)	**i, c**	**i**	**i, c**
AVT	—	i	i, c
Pretectum			
LMl	**i**	**i,** c	**i**
LMm	**i**	**i**	**i**
nBORl	**i**	**i**	**i,** c
LPC	i	i	i
PPC	i	i	i
IPS	i	i	i
PT	—	—	i
SP	—	i	i
ICo	i	i	—
MLv	i	—	—
PtM	i	—	—
PV	i	—	—
PT	—	i	—
PST	—	i, c	—
Tectum	i	—	i
Tectal gray	i	—	i
SOP	—	i	i
TrO	—	—	i
Thalamus			
DLA	**i**	**i**	**i**
DLM	**i**	**i**	**i**
DLL	**i**	**i**	**i**
DLAmc	i	i	i
DLP	—	i	—
GLv	i	i	i
T	i	i	—
Rt	i	i	—
Miscellaneous			
TTD	i		
Nucleus solitarius	i		
External cuneate	i		
TVM	i		
Medial lemniscus			i

[1]Summary of the projection sites of all biotinylated dextran amine (BDA) injections into the nucleus of the basal optic root (nBOR). Labelling in the structure ipsilateral (i) or contralateral (c) to the injection site is indicated for each case. — Indicates no labelling, and structures indicated in boldface are considered among the more significant projections. For abbreviations, see list.



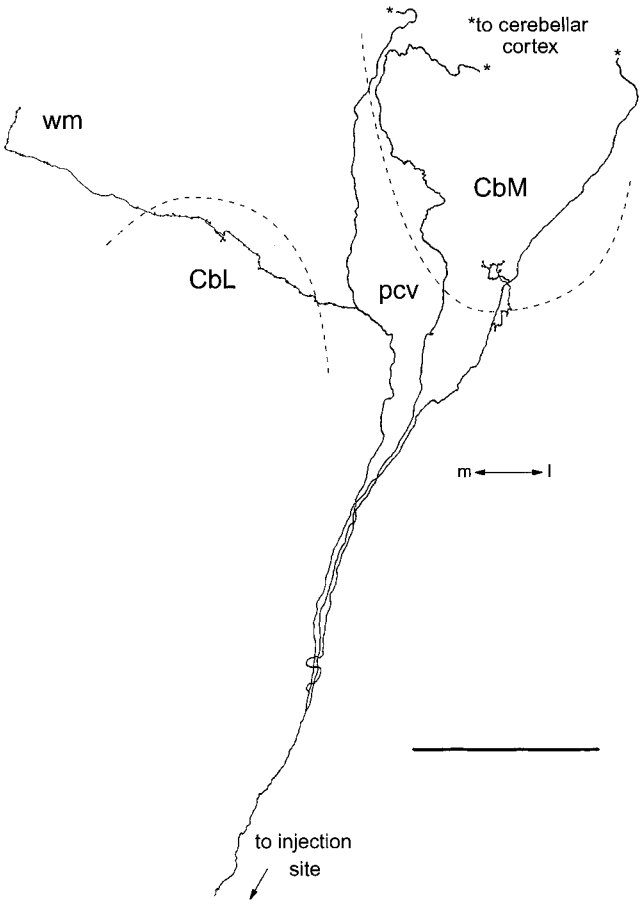


Fig. 4. MF collaterals to the cerebellar nuclei. A single MF, which was reconstructed from serial sections, is shown (case 2). The MF split into three branches just before it ascended into the cerebellum and eventually terminated as MF rosettes (asterisks). Two of the branches also gave off collaterals to the cerebellar nuclei and the adjacent pcv. In and in subsequent figures of serial reconstructions, dashed lines are used to approximate the boundaries of the target nuclei. m, medial; l, lateral. Scale bar = 500 μm.

This fiber crossed the midline at the nucleus decussationis brachiorum conjuctivorum, coursed ventrally, and branched at the nucleus centralis superior. One branch crossed back to the ipsilateral side, coursed laterally through the nucleus reticularis pontis oralis (RPO), ascended, and terminated in the tractus vestibulomesencephalicus (TVM). The other branch coursed dorsally through the RPO on the border of nucleus linearis caudalis, then turned laterally, and travelled caudally to the contralateral vestibular nuclei. Termi-

Fig. 3. **A–C:** Mossy fibers (MFs) from the nBOR to the cerebellar cortex. In A, the curved arrows indicate MF rosettes in the granule layer of the dorsal lamella of folium IXc,d (case 1). C shows terminals from MF collaterals in the processus cerebellovestibularis (pcv) between the lateral cerebellar nucleus (CbL) and the medial cerebellar nucleus (CbM; case 1). The location of these terminals is indicated by the arrow in B. The dotted line in B encompasses an area that includes the parts of pcv, CbM, and CbL where most of the collaterals from the MFs terminated in cases 1 and 2. For other abbreviations, see list. Scale bars = 50 μm in A, 200 μm in B, 25 μm in C.

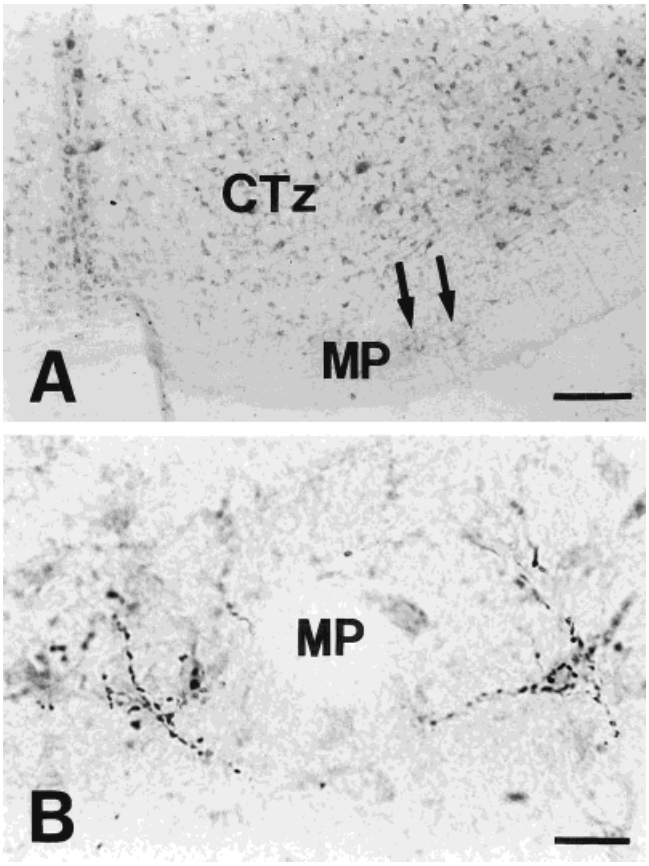


Fig. 5. Terminal labelling in the pontine nuclei. The two arrows in **A** indicate the location of the terminal fields shown in **B** in the medial pontine nucleus (MP; case 3). CTz, corpus trapezoidium. Scale bars = 250 μm in A, 25 μm in B.

nals were observed in the medial vestibular nucleus (MVN) and the SVN.

Projections to the inferior olivary complex and pontine nuclei

In all cases, terminal labelling was found in the ipsilateral pontine nuclei (see Fig. 5). Most of these terminals were found in the caudal half, and more were found in the medial pontine (MP) than in the lateral pontine (LP). A few terminals were also seen in the corpus trapezoidium (CTz) adjacent to the MP and the LP. In case 2, a few terminals were detected in the contralateral MP and adjacent CTz from a single fiber.

In case 3, one of the fibers that terminated in the MP continued caudally and ended as a small terminal field in the medial lemniscus, just ventral to the IO. Terminal labelling within the borders of the IO was observed only in case 2 (see Fig. 6). Four axons travelled with several others to the pontine nuclei but continued caudally. At the level of the IO, these four axons coursed dorsally, branched, and terminated heavily in the ipsilateral IO. Numerous terminal fields were seen in the medial column (mc), particularly in the dorsal portion, and in the medial aspects of the dorsal lamella (dl). Only one small branch was observed to terminate in the ventral lamella (vl), and it was located to the medial area. Of those terminals not in the mc, few were found lateral to nerve XII. Figure 6 shows the four axons reconstructed from serial sections. Note that terminals from a single fiber were found in both the ipsilateral and the contralateral mc. This fiber also gave off a collateral to the LP.

Projections to the FR

In all cases, fibers travelled dorsally from the nBOR through the AVT and the ipsilateral FR. Numerous terminals were found in the ipsilateral medial and lateral FR (FRM and FRL, respectively) and the AVT. In some cases, these terminal fields came from collaterals of fibers that terminated in the ipsilateral IC, the central gray (CtG), the nucleus Darkshewitsch (D), and the nucleus ruber (Ru; see below). Other fibers travelled dorsally from the nBOR and crossed the midline via the pc. It is possible that some of these fibers gave off collaterals to the ipsilateral FRL, FRM, and AVT, although it has not been confirmed. After crossing the midline, these fibers terminated in the contralateral OMC or the nBOR (see below; Figs. 9, 10), and numerous terminal fields were also observed in the contralateral FRL, FRM, and AVT. It was evident that the fibers to the contralateral nBOR gave off collaterals to the FRL, FRM, and/or AVT en route (see below; Figs. 11, 12). It was not determined whether such collaterals arose from fibers to the OMC.

Projections to the OMC

In all cases, terminal fields were observed in the OMC (see Fig. 7). In case 1, terminal labelling was found in all three subdivisions of the contralateral OMC. The terminals arose from fibers that crossed the midline via the pc. Figure 8A shows a fiber from case 1 that was reconstructed from serial sections. The fiber crossed the midline in the pc, descended, and coursed laterally through the medial longitudinal fasciculus (MLF) to the OMC. Figure 8B shows that the fiber terminated heavily in the dorsomedial subdivision (OMdm) and in the caudal portions of the OMdl. One branchlet continued rostrally and ended as a small terminal field in the rostral margin of the dorsal OMv.

In case 2, terminal labelling was seen bilaterally in the OMv, but more was seen on the ipsilateral side. On the contralateral side, the terminals were confined to the lateral margin of the caudal half of the OMv and arose from fibers that crossed the midline ventral to the OMC or, in a few instances, via the pc. On the ipsilateral side, the fibers coursed laterally, and terminals were found throughout the rostrocaudal extent of the lateral margin and the rostral half of the medial margin of the ipsilateral OMv. Figure 8C shows a fiber from case 2 that was reconstructed from serial sections. Note that this fiber projected to both the ipsilateral (dorsomedial) and the contralateral (ventrolateral) OMv.

In case 3, the contralateral OMC was heavily labelled, but only one faintly labelled fiber was seen to terminate in the OMdl on the ipsilateral side. On the contralateral side, fibers that crossed in the pc terminated throughout the rostrocaudal extent of the OMdm and OMdl, with the heaviest labelling on the border of the OMdl/dm. In the contralateral OMv, the lateral margin was labelled in the rostral half. At caudal levels, terminals were located ventrally in both the lateral and the medial aspects of the OMv.

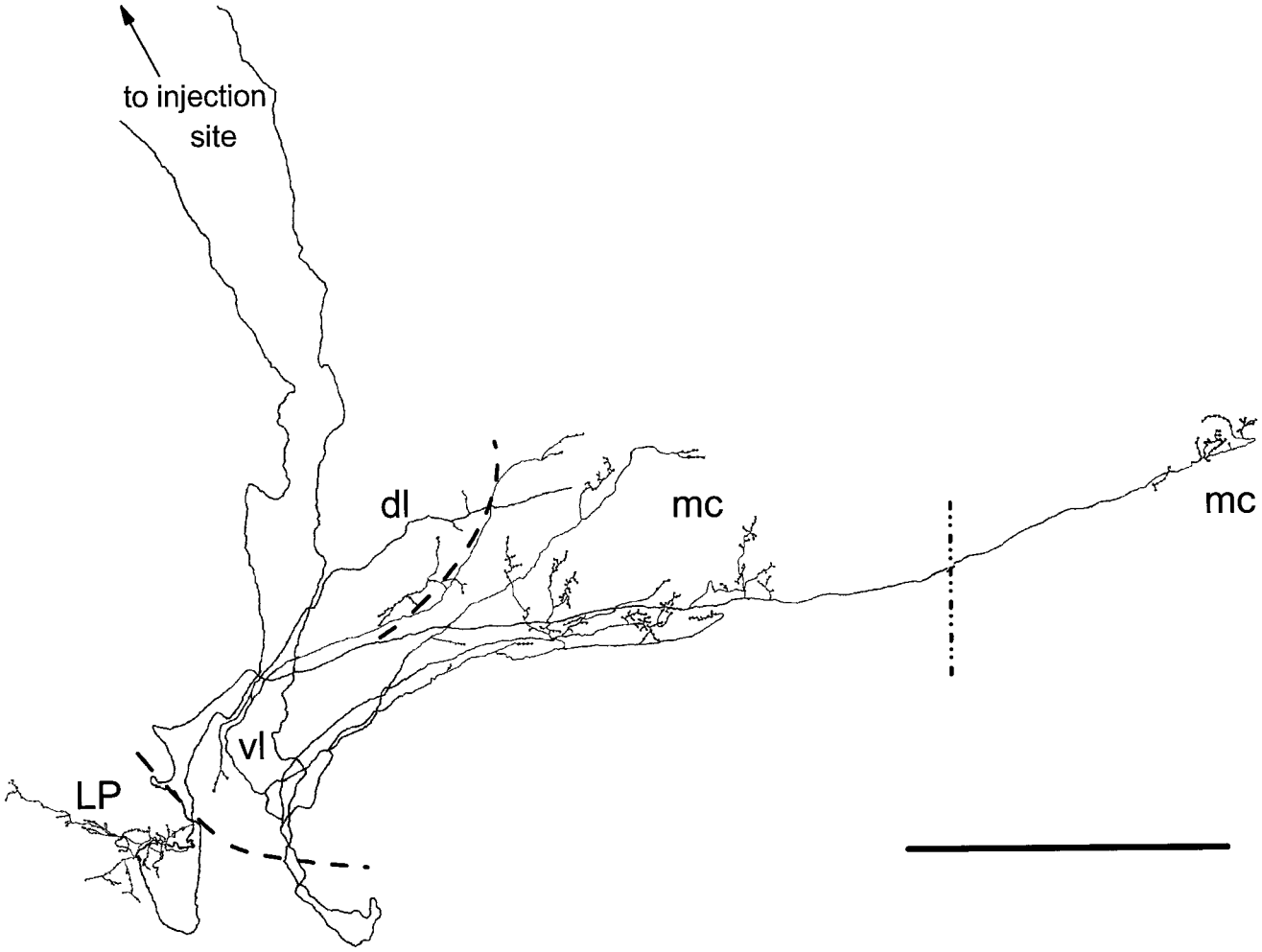


Fig. 6. Projections from nBOR to the pontine nuclei and the inferior olive (IO). Two fibers reconstructed from serial sections are shown (case 2). Both fibers terminated extensively in the ipsilateral medial column (mc) of the IO. Note that one of the fibers terminated bilaterally in the mc and gave off a collateral to the lateral pontine nucleus (LP). The dashed vertical line represents the midline. dl, dorsolateral subdivision of the inferior olive; vl, ventral subdivision of the inferior olive. Scale bar = 500 μm.

In none of the cases was terminal labelling seen in the Edinger-Westphal (EW), trochlear, or abducens nuclei. A few terminal fields were seen in the MLF adjacent to the OMC and IC in case 2 (ipsilateral) and in case 3 (ipsilateral and contralateral).

Projections to the accessory oculomotor and perirubral areas

In all cases, numerous terminal fields were seen bilaterally in the IC and the D, although labelling was heavier on the ipsilateral side (Fig. 9C,D). Heavy labelling was also apparent in the ipsilateral CtG (Fig. 9A,B), and, in case 3, some terminals were found in the contralateral CtG. Terminal fields were consistently observed in the ipsilateral Ru (Fig. 9F), although this termination could not be described as heavy, and, in cases 2 and 3, terminals were also seen in the contralateral Ru. Most terminal fields were observed in the rostral half of the Ru. A few terminals were seen in the stratum cellulare externum (SCE) and stratum cellulare internum (SCI) adjacent to the Ru, CtG, and IC in case 2 (ipsilateral) and in case 3 (bilateral; see Fig. 10). Figure 10 shows a reconstruction of two fibers from case 3 that projected to the accessory oculomotor and perirubral areas. One fiber left the nBOR dorsally, and a collateral terminated in the ipsilateral FRM. The parent fiber coursed dorsolaterally and entered the CtG. It then coursed ventrally, branched, (Fig. 9A,B), and terminal fields were seen in the CtG, D, IC (Fig. 9D), and SCE. The parent fiber eventually coursed laterally and terminated in the Ru (Fig. 9F). A few branchlets from this fiber crossed the midline and terminated in the contralateral CtG and SCE. The second fiber left the nBOR medially, and collaterals gave rise to terminals in the Ru. The parent fiber continued dorsally and crossed the midline. It continued dorsally, parallel to the midline, and then branched. Some branchlets coursed laterally, terminating in the contralateral CtG, D, and IC (Fig. 9C). Other branchlets travelled back across the midline, then coursed laterally, and terminated in the ipsilateral IC and CtG. It did not appear that fibers crossing the midline in the pc gave rise to terminal fields in the contralateral accessory oculomotor or perirubral areas.

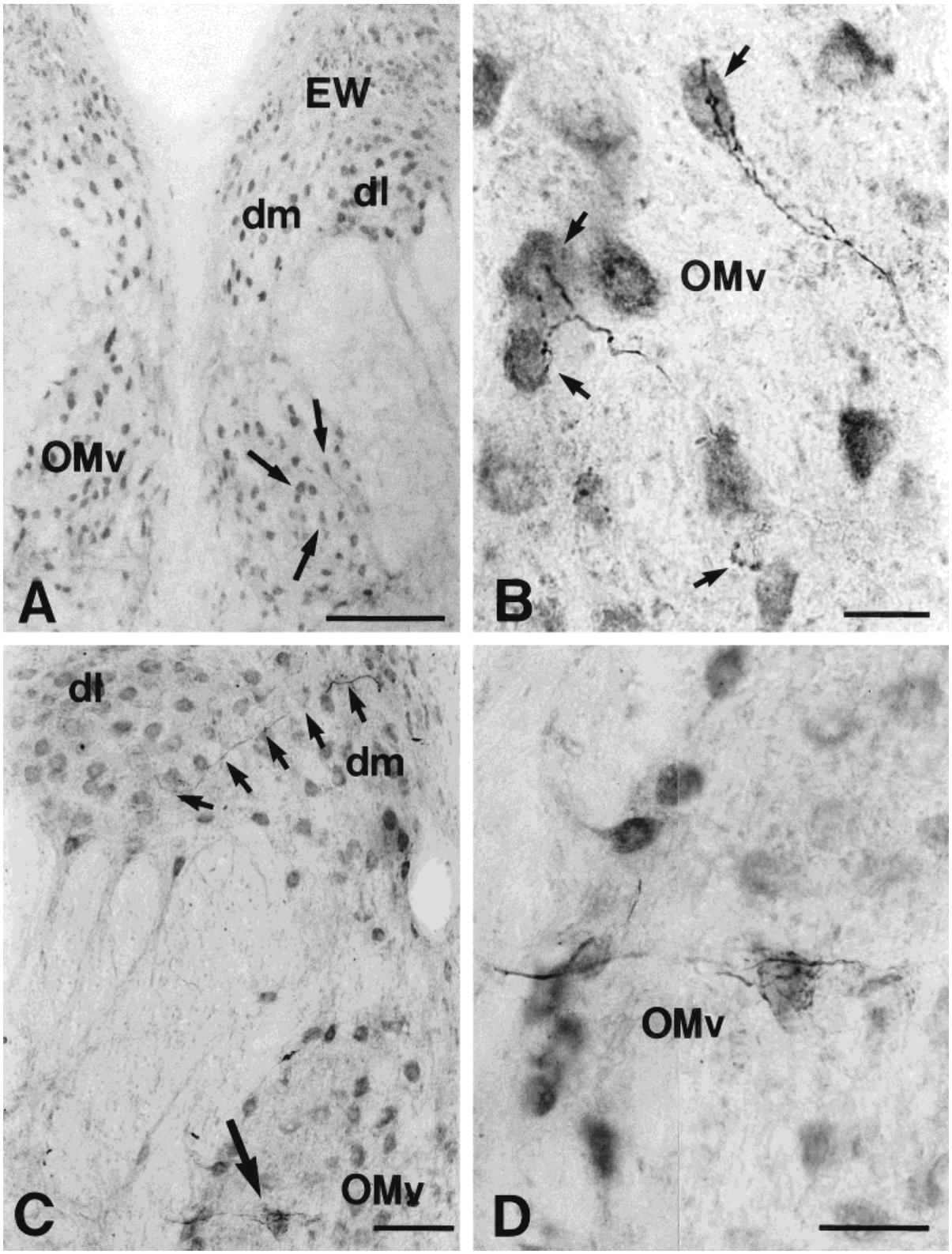


Fig. 7. **A–D:** Terminal labelling in the OMC. A: The four distinct divisions of the OMC. B: Illustration of large cells, which are indicated by the arrows apposed to terminal boutons (case 2). These cells were located in the lateral part of the (contralateral) ventral subdivision of the OMC (OMv), as indicated by the arrows in A. D: A cell in the contralateral OMv encased in terminal boutons (case 3). This cell, as indicated by the large arrow in C, was in the dorsolateral (dl) part of the OMv. The small arrows in C highlight a fiber traversing the dl and the dorsomedial (dm) subdivisions of the OMC. Terminals from this fiber were seen in both the dl and the dm (not shown). EW, Edinger-Westphal nucleus. Scale bars = 250 μm in A, 25 μm in B, 100 μm in C, 50 μm in D.

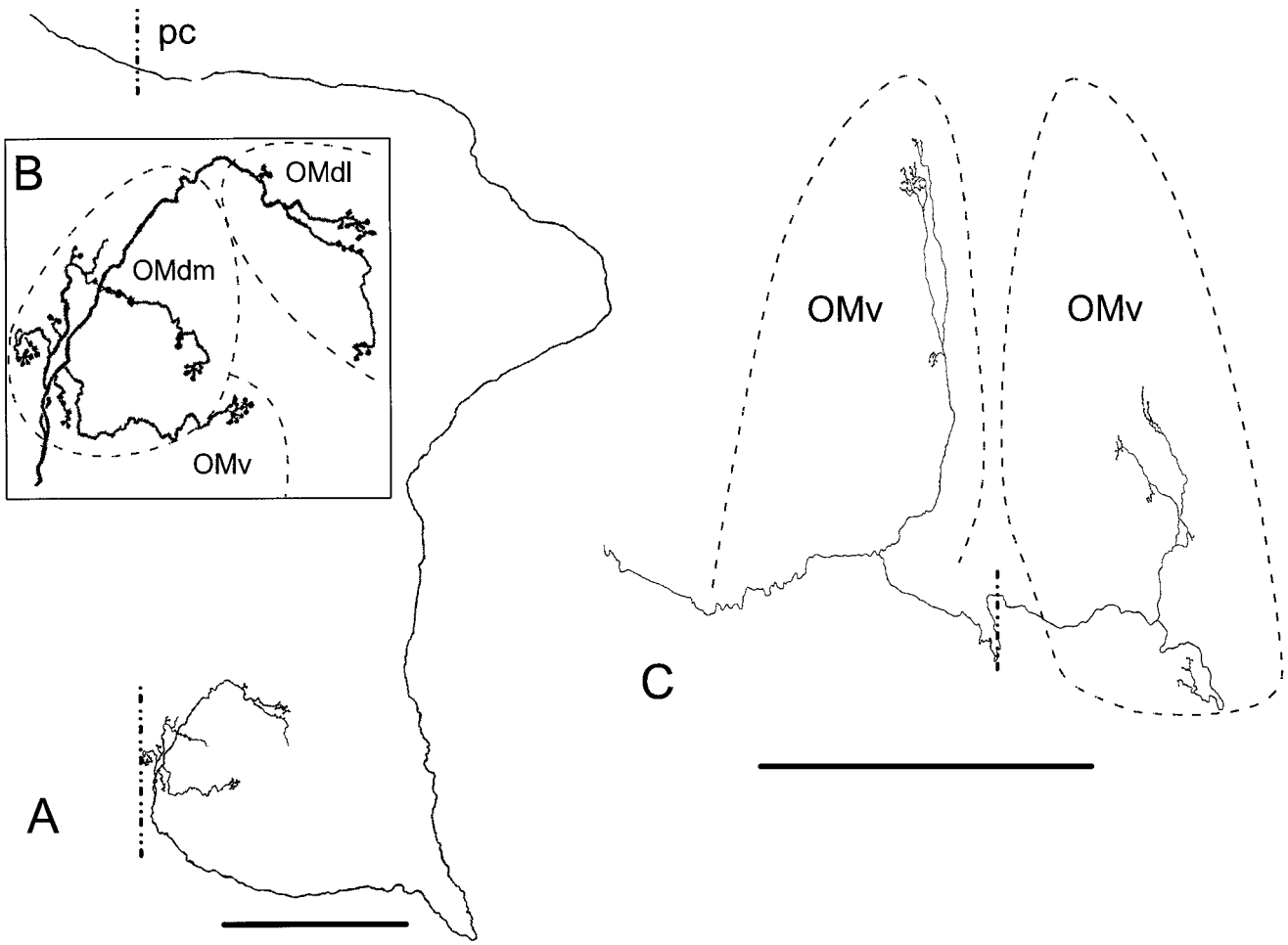


Fig. 8. **A–C:** Projections from the nBOR to the OMC. A shows a fiber from case 1 that crossed the midline via the posterior commissure (pc) and descended to the contralateral OMC. This fiber, as shown by the magnification in B, terminated largely in the OMdm and, to a lesser degree, in the OMdl, and one branchlet contacted a cell in the most rostrodorsal margin of the OMv. C shows a fiber from case 2 that terminated bilaterally in the OMv. Terminals were seen in the dorsomedial and ventrolateral margins of the OMv on the ipsilateral and contralateral sides, respectively. The dashed vertical line represents the midline. Scale bars = 500 μm in A and C.

Projections to the contralateral nBOR

In cases 1 and 3, several axons that crossed the midline via the pc descended and terminated in the caudal and dorsal aspects of the nBOR complex (see Fig. 11). Thus, it appears that most of these terminals were in the nBORd. In case 3, some terminal fields also extended into the nBORl. Before reaching the nBORd, most axons gave off collaterals that terminated in the FRM and/or FRL and the AVT (see Fig. 11). Figure 12 shows four fibers that were reconstructed from serial sections from case 1. All fibers crossed the midline in the pc and descended through the FRM. Two fibers terminated extensively in the caudal portion of the nBORd. Note that these fibers gave off collaterals to the FRM and the AVT. In case 2, no terminal labelling was seen in the contralateral nBOR.

Projections to the pretectum and dorsolateral thalamus

In pigeons, the pretectum consists of numerous nuclei, the borders of which are difficult to define. We have adopted the description by Gamlin and Cohen (1988). In their description, the LM consists of two subnuclei: LM pars lateralis (LMl) and LM pars medialis (LMm). Medial to the LMm is a strip of small cells, the laminaris precommisuralis (LPC), which appears to be contiguous with the internal lamina of the ventral lateral geniculate nucleus (GLv). Medial to the LPC is the nucleus principalis precommisuralis (PPC), which resides lateral to the nucleus rotundus (Rt). Ventrally, the LMm, LMl, and LPC course ventral to nucleus subpretectalis (SP) and posterior to the GLv. The LMm and LMl continue medially as a strip of cells as far as the nBORl. In this area, ventral to the SP and continuous with the nBORl, we find it difficult to distinguish the LMm, LMl, and LPC.

The pretectum received an extremely heavy projection that was similar in all cases. The terminal labelling in the LMl described below would represent, by far, the heaviest of the efferent projections of the nBOR. Dozens of fibers left the nBOR laterally and travelled through the nBORl, where numerous terminals were observed. These fibers continued laterally in the strip of cells ventral to the SP and posterior to the GLv. In this area, the terminal

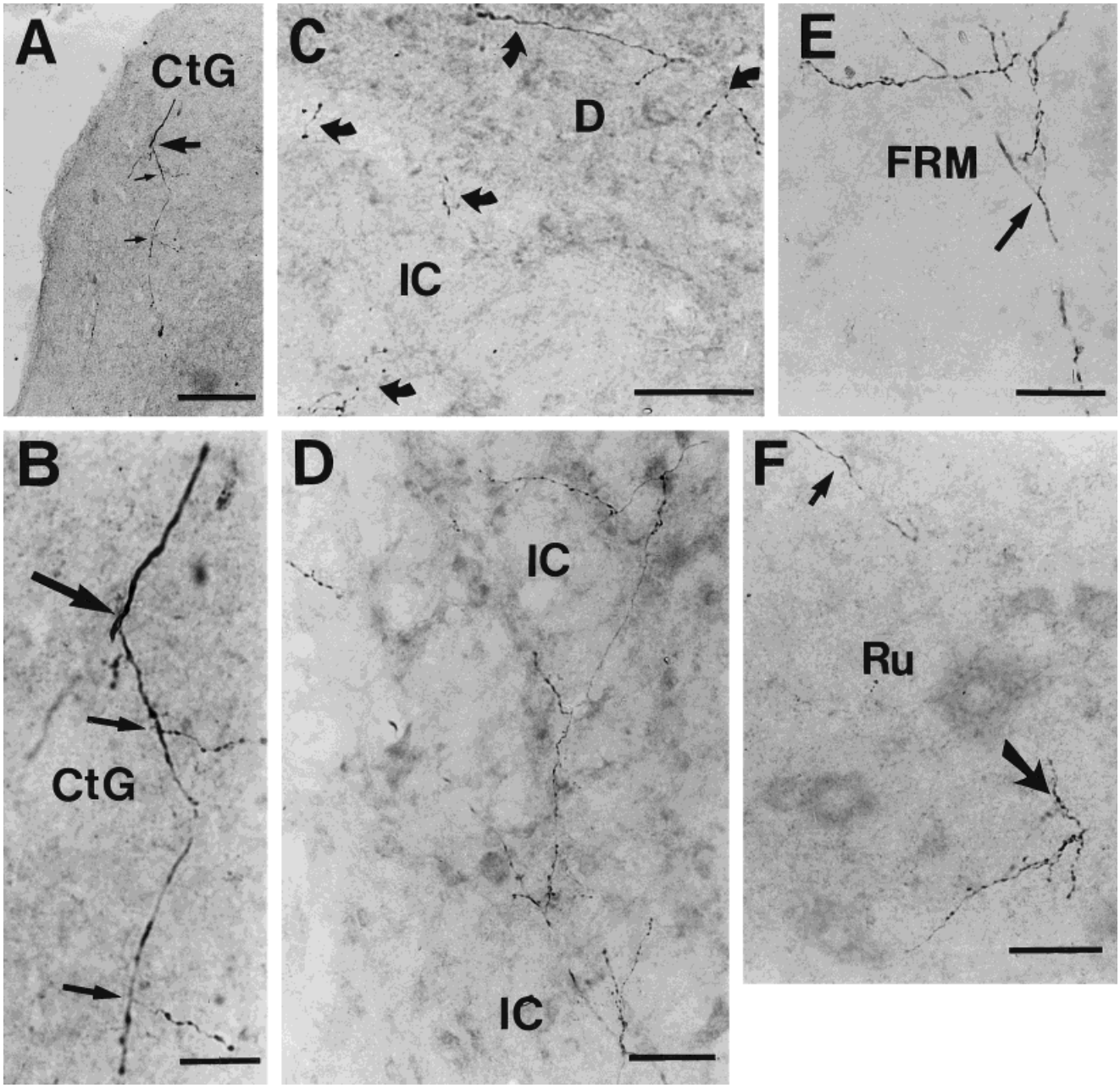


Fig. 9. Terminal labelling in the accessory oculomotor and perirubral areas. **A,B:** Terminal fields in the ipsilateral central gray (CtG; case 3). In both A and B, the large arrow indicates the branch from the parent fiber, whereas the small arrows indicate branchlets that give rise to terminal boutons. **C:** Terminal labelling in the ipsilateral interstitial nucleus of Cajal (IC; clockwise arrows) and the adjacent nucleus Darkshewitsch (D; counterclockwise arrows; case 3). **D:** An extensive terminal field in the ipsilateral IC (case 3). **E:** An axonal collateral terminating in the ipsilateral medial mesencephalic reticular formation (FRM; case 3). The branch point is indicated by the arrow. The parent fiber continued and terminated in the IC (not shown). **F:** A terminal field in the ipsilateral nucleus ruber (Ru; large arrow). The parent fiber (indicated by the small arrow) also gave off collaterals to the ipsilateral CtG, the stratum cellulare externum (SCE), and the IC (see Fig. 10). Scale bars = 100 μm in A, 25 μm in B, 50 μm in C, D, and F, 100 μm in E.

labelling was quite dense in the LMm and LMl, and some terminals were seen in the LPC (see Fig. 13A,B). (More rostrally, a few terminals were seen in the GLv). The fibers turned dorsally, and the LMl was extensively labelled (see Fig. 13C). Fewer fibers and terminals were seen in the LMm and LPC. Some fibers also coursed dorsally through the PPC, and a few terminals were seen. A few collaterals from fibers coursing through the LM terminated in the tectum, the tectal gray, the SOp, and the tractus opticus (TrO).

Many fibers continued dorsally, coursed medially, and entered the dorsolateral thalamus. Numerous terminals were seen in the anterior dorsolateral thalamus (DLA; see Fig 13D,E), and many terminals were seen relatively posterior, in an area referred to in the atlas of Karten and Hodos (1967) as the DLA. Adjacent to these, many termi-

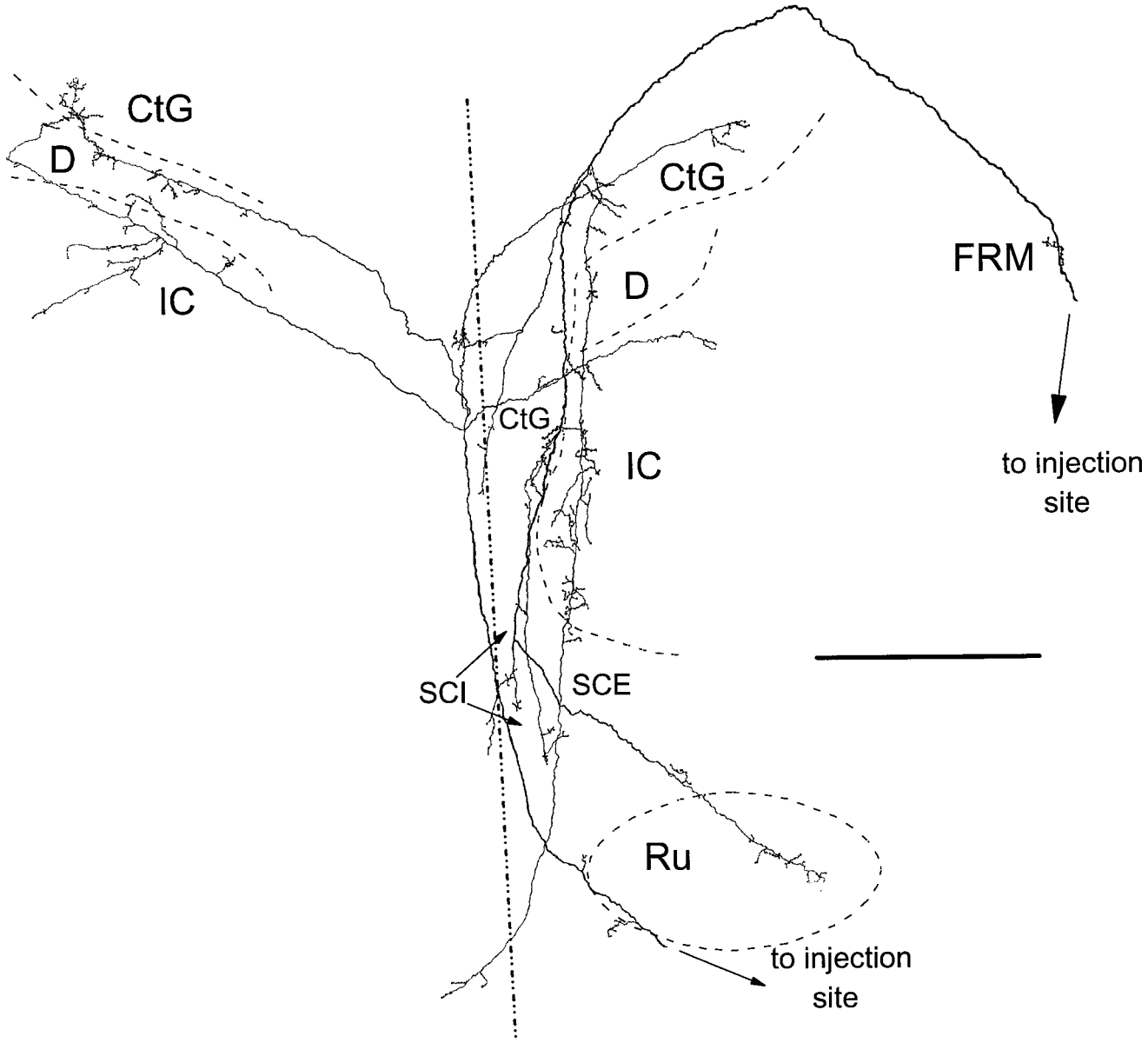


Fig. 10. Projections from the nBOR to the accessory oculomotor and perirubral areas. Two fibers, which were reconstructed from serial sections, are shown (case 3). See text for detailed description. The dashed vertical line represents the midline. SCI, stratum cellulare internum. Scale bar = 500 μm.

nals were also seen in the medial subdivision of the anterior dorsolateral thalamus (DLM). More rostrally, numerous terminals were seen in the lateral subdivision of the DLA (DLL). A few terminals were also found in the posterior subdivision of the DLA (DLP) and in the magnocellular DLA (DLAmc). Figure 14 shows a fiber from case 3 that coursed through the pretectum and terminated in both the DLL and the DLM. A collateral from that fiber terminated in the PPC. In the pretectal and thalamic regions, a few terminals were also seen in the SP, the nucleus interstitiopretectosubpretectalis (IPS), the nucleus pretectalis (PT), the nucleus intercollicularis (ICo), the lateral mesencephalic nucleus pars ventralis (MLv), the nucleus pretectalis medialis (PTM), the nucleus periventricularis (PV), the tractus pretectosubpretectalis (PST), the nucleus triangularis (T), and the Rt.

Locations of other terminal fields

In case 3, a single, isolated terminal field was seen in the medial lemniscus. In case 1, a single fiber travelled quite caudally and terminated in the nucleus et tractus descendens nervi trigemini (TTD), the nucleus solitarius, and the external cuneate nucleus.

DISCUSSION

In this study, we used the anterograde tracer BDA to determine the projections of the nBOR in pigeons. We have confirmed and extended the previous studies by Karten and colleagues (Brauth and Karten, 1977; Brecha and Karten, 1979; Brecha et al., 1980). This discussion will consider each projection area in turn, noting differences

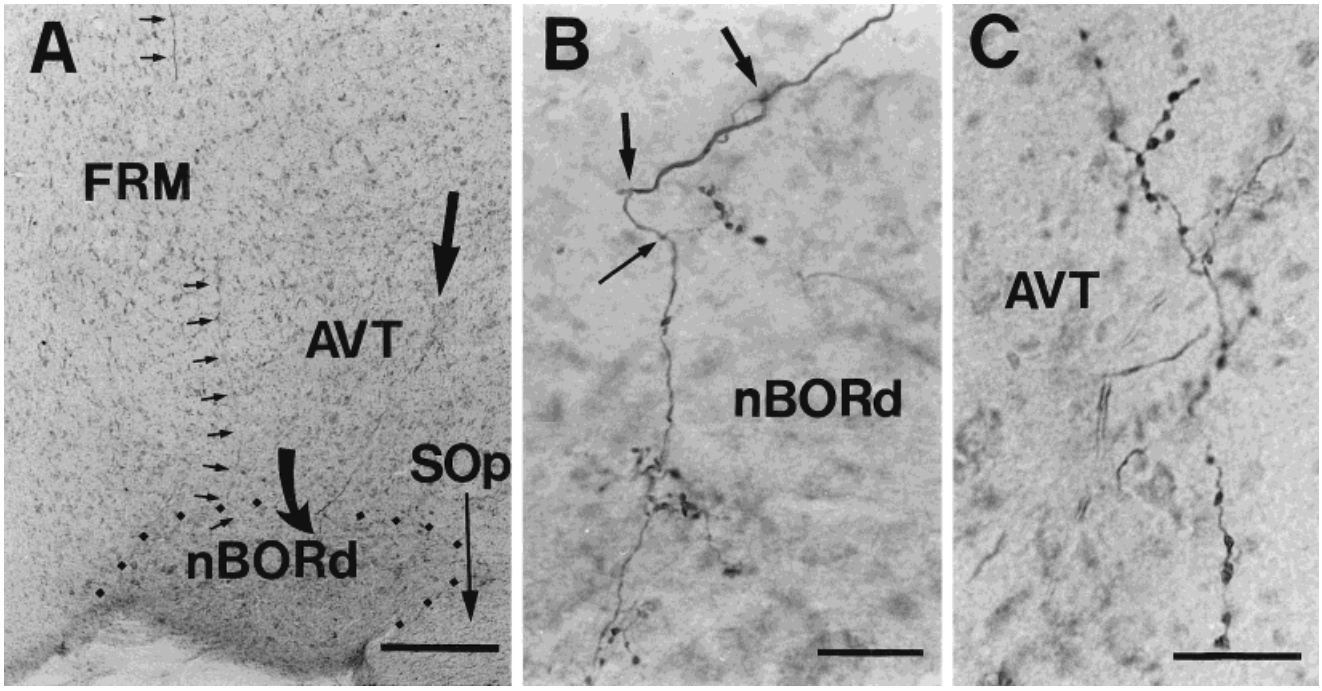


Fig. 11. **A–C:** Terminal labelling in the contralateral nBOR and the adjacent AVT. A shows a transverse section in the caudal portion of the nBOR complex (case 1). At this caudal level, only the nBOR dorsalis (nBORd) is present. The dotted line indicates the border of the nBORd. The thick straight arrow and the curved arrow in A indicate the terminals in the AVT and the nBORd that are shown in B and C, respectively. Both terminal fields arose from the same fiber (see Fig. 12). The short thin arrows in A highlight a second fiber that also terminated in the nBORd (not shown). The thick arrows in B indicate two branch points from the parent fiber, and the thin arrow in B indicates an additional branchlet. Scale bars = 250 μm in A, 25 μm in B,C.

from those previous studies. The results of the present study will also be compared with the projections of the pigeon LM (Clarke, 1977; Gamlin and Cohen, 1988), because the LM has been shown to be functionally similar to the nBOR. The main difference in the physiology between the LM and the nBOR is that, whereas most neurons in the LM (and the nBORl; McKenna and Wallman, 1981, 1985) respond best to optokinetic stimuli (OKS) moving forward (temporal to nasal) in the visual field (Winterson and Brauth, 1985; Wylie and Frost, 1996), neurons in the nBOR (excluding the nBORl) respond best to OKS moving either upward, downward, or backward (Wylie and Frost, 1990a). We will also compare the results of the present study with the projections of the AOS in mammals (Giolli et al., 1984, 1985, 1988; Blanks et al., 1995). In this case, only the medial and lateral terminal nuclei (MTN/LTN) will be considered, because the dorsal terminal nucleus is functionally more similar to the nucleus of the optic tract, which is the homolog of the avian LM (Simpson, 1984; Simpson et al., 1988a). The major difference in the physiology between the nBOR and the MTN/LTN is that, in the latter, neurons are responsive to OKS moving either upward or downward, but not backward. Finally, the function of the newly identified projections will be considered.

Projections to the cerebellar cortex, cerebellar nuclei, and vestibular nuclei

We confirmed that MFs from the nBOR project bilaterally to the cerebellum, as shown by Karten and colleagues (Brauth and Karten, 1977; Brecha and Karten, 1979; Brecha et al., 1980). Indeed, we have shown that individual fibers project bilaterally to the VbC (Wylie and Linkenhoker, 1996). According to those previous studies and the present study, the projection is largely to folium IXc,d. Gamlin and Cohen (1988) found that the LMm and LMl project bilaterally, although predominantly contralaterally, upon folia VI–X. Most of the terminal labelling was in folia IXc,d and VIc (see also Clarke, 1977). It is somewhat surprising that the MF projection from the LM and the nBOR does not include folium X, because Purkinje cells in folium IXc,d and X have similar complex spike activity in response to OKS, (i.e., they receive similar climbing fiber input; Wylie and Frost, 1991; Wylie et al., 1993). It is noteworthy that the primary vestibular projection to the VbC is largely to folium X and, to a lesser extent, the ventral lamella of IXc,d (Schwarz and Schwarz, 1983). In mammals, a direct projection from the AOS to the vestibulocerebellum has been reported in the chinchilla (Winfield et al., 1978) but not other mammalian species (see Simpson et al., 1988a).

In the present study, we showed that the MFs gave off collaterals to the cerebellar and, to a lesser extent, the vestibular nuclei. These are areas that receive input from Purkinje cells in the VbC (Arends and Zeigler, 1991a; for a further discussion of the MF projection from the nBOR to the VbC, see Wylie and Linkenhoker, 1996).

Projections to the cerebellar and vestibular nuclei from the nBOR have not been reported previously, and such a projection from the pigeon LM was not found (Clarke, 1977; Gamlin and Cohen, 1988). In mammals, there is an extensive, predominantly contralateral connection from the AOS to the superior and lateral vestibular nuclei (Giolli et al., 1984, 1985, 1988; Blanks et al., 1995).

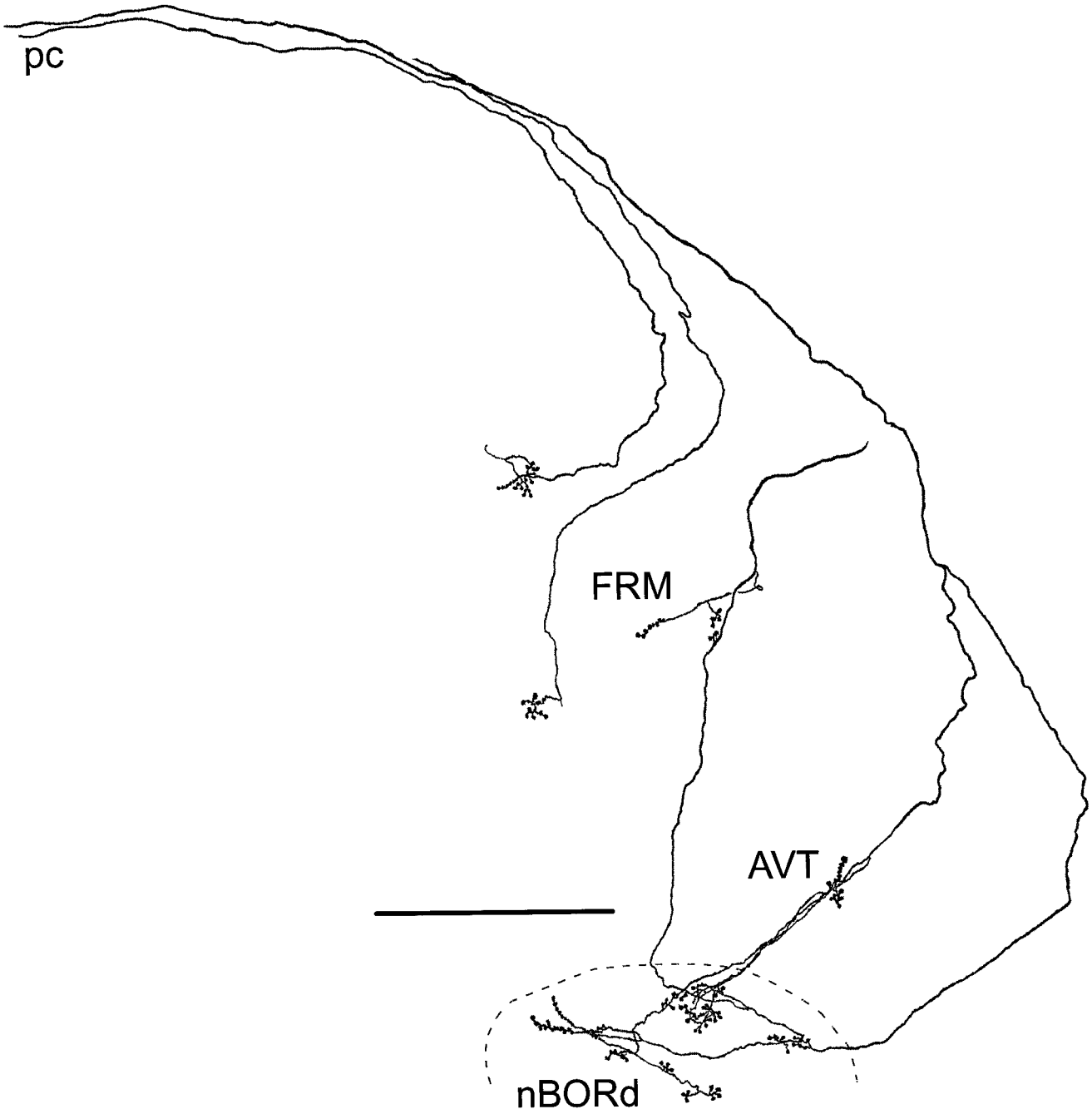


Fig. 12. Projections from the nBOR to the contralateral nBOR and the adjacent mesencephalic reticular formation. Four fibers that crossed the midline via the posterior commissure (pc) are shown (case 1). Two fibers terminated in the FRM. The third fiber gave off a collateral to the FRM, but the parent fiber continued ventrally and terminated in the nBORd. The fourth fiber terminated in both the AVT and the nBORd (see Fig. 11). Scale bar = 500 μm.

Although we found some terminals in the SVN, MVN, and Ta, the projection to the vestibular nuclei could hardly be considered extensive.

Projections to the inferior olivary complex and pontine nuclei

In case 2, a bilateral projection to the IO was found, although terminal labelling was more prevalent on the ipsilateral side. Using the nomenclature of Arends and Voogd (1989), most of the terminals were localized to the mc and to the medial extreme of the vl. Brecha et al. (1980) also found that the nBOR projected to this area of the IO and, by using retrograde transport of HRP, they showed that the projection was from the nBORd and from a few small cells scattered in the nBORp. Thus, it is not surprising that we found terminal labelling only in the IO from case 2, which involved the nBORd. Brecha et al. (1980) found that those fibers projecting to the contralateral side

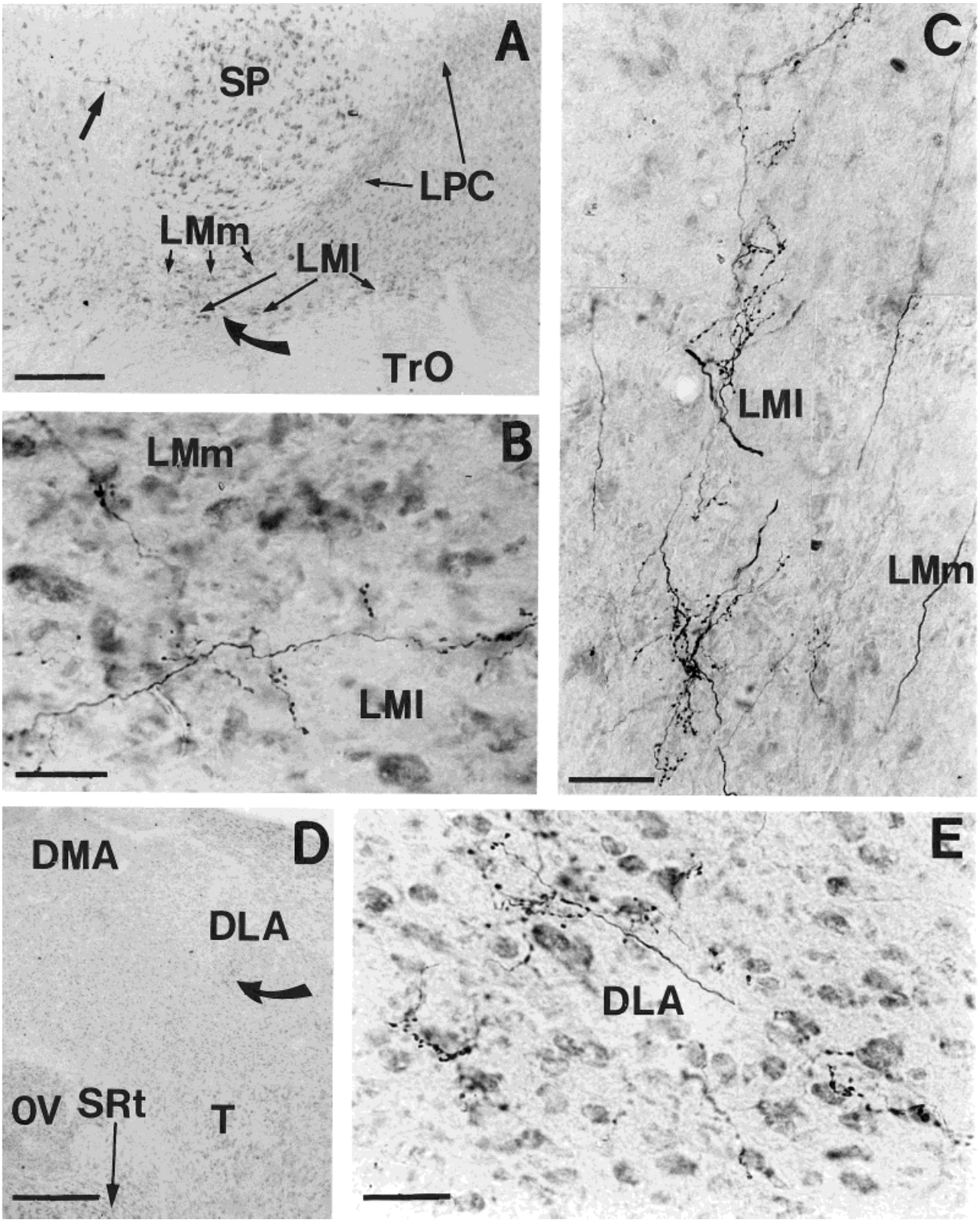


Fig. 13. **A–E:** Terminal labelling in the pretectum and the dorsal thalamus. The curved arrow in A indicates the terminal field shown in B (case 3). This terminal field was found in the group of cells ventral to the SP and posterior to the ventral lateral geniculate nucleus (GLv), and it appeared to transverse both the medial and the lateral subdivisions of nucleus lentiformis mesencephali (LMm and LMl, respectively). The thick straight arrow in A indicates a terminal field that was found just medial to the SP. C shows terminal fields from fibers travelling dorsally through the LMl (case 1). The fibers on the right were in the LMm. The curved arrow in D indicates the location (anterior dorsolateral thalamus; DLA) of the terminal fields shown in E (case 3). Other arrows refer to indicated areas. DMA, anterior dorsomedial thalamus. For other abbreviations, see list. Scale bars = 250 μm in A, 25 μm in B,E, 50 μm in C, 400 μm in D.

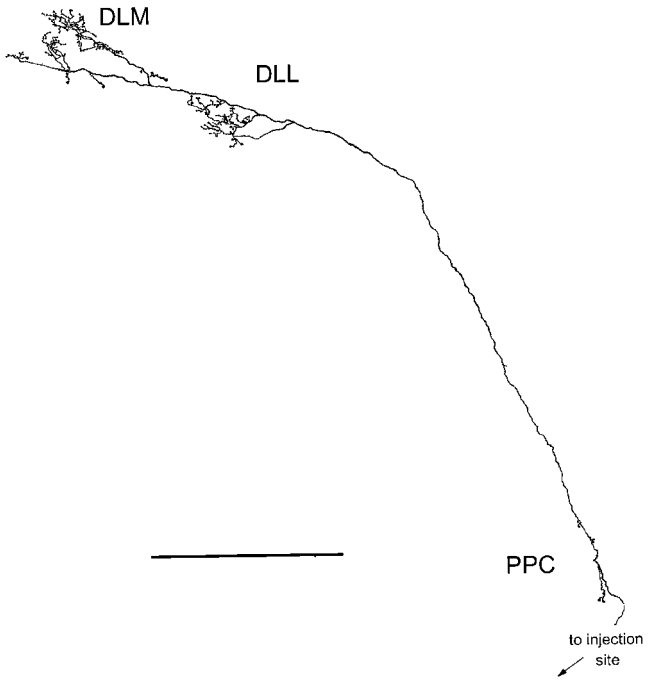


Fig. 14. Projections from the nBOR to the pretectum and the dorsal thalamus. This fiber was reconstructed from serial sections and was located more rostrally than most of the fibers in the pretectum. The fiber travelled through the rostrolateral margin of the nucleus principalis precommisuralis (PPC), which is contiguous with the LM in more caudal sections. A collateral gave rise to a terminal field in the PPC. The parent fiber continued dorsally, then coursed medially, and terminated in both the medial and the lateral subdivisions of the anterior dorsolateral thalamus (DLM, DLL). Scale bar = 500 μm.

crossed the midline in the decussationis brachiorum conjunctivorum. We did not confirm this pathway. Instead, we found that these fibers crossed the midline ventral to nucleus raphes (R) and that individual fibers could project to both the ipsilateral and the contralateral mc.

It has been shown that the pigeon LM projects ipsilaterally to the mc as well (Clarke, 1977; Gamlin and Cohen, 1988). These IO-projecting cells form a thin band that resides on the LMl/LMm border (Gamlin and Cohen, 1988). The mc of the IO provides climbing fiber input to the VbC (Arends and Voogd, 1989), where Purkinje cells are responsive to either translational or rotational OKS (Wylie and Frost, 1991, 1993; Wylie et al., 1993). In mammals, the AOS projects bilaterally, but predominantly ipsilaterally, to the dorsal cap and the ventrolateral outgrowth of the IO (Giolli et al., 1984, 1985, 1988; Blanks et al., 1995), which, in turn, project to the VbC (Alley et at., 1975; Gerrits and Voogd, 1982; Ruigrok et al., 1992; Tan et al., 1995). Interestingly, Simpson et al. (1988a) noted that the neurons providing input to the IO are predominantly in the ventral tegmental relay zone (VTRZ), which is in the AVT adjacent to the MTN. Below, we suggest that the nBORd is functionally equivalent to the mammalian VTRZ.

We also noted that some IO-projecting fibers gave off collaterals to the pontine nuclei and that other fibers terminated in the pontine nuclei. The projection was predominantly ipsilateral, included both the MP and the LP, but was heavier to the MP. Brecha et al. (1980) noted the presence of fibers passing through the pontine nuclei but did not report any terminal labelling. Previous studies have noted that the LM in pigeons projects to the ipsilateral MP and LP (Clarke, 1977; Gamlin and Cohen, 1988), and the projection was heavier to the LP (Clarke, 1977). In mammals, it has been shown that the AOS projects to the ipsilateral dorsolateral nucleus of the basilar pontine complex and the nucleus reticularis tegmenti pontis (Giolli et al., 1984, 1985, 1988; Blanks et al., 1995).

Projections to the FR

In the present study, we found a substantial number of terminal fields throughout the FRL and FRM on both the ipsilateral and contralateral sides. Some of these came from collaterals of fibers that terminated in the accessory oculomotor area and the contralateral nBOR. A projection to the FR from the pigeon nBOR has not been reported previously; however, Gamlin and Cohen (1988) noted a sparse projection from the LM to the contralateral FR. It was not stated whether this was to the pontine reticular formation or to the FR. In mammals, the AOS has been shown to project to the ipsilateral FR but to project sparsely to the pontine reticular formation (Giolli et al., 1984; Blanks et al., 1995).

Projections to the OMC

In this report, we have shown that the nBOR complex projects bilaterally upon all subdivisions of the OMC. Injections confined to the nBORp (cases 2 and 3) resulted in labelling in the contralateral OMdl, OMdm, and OMv. Serial reconstructions showed that individual fibers could terminate in all three subdivisions (Fig. 8B). The injection that included the nBORd (case 2) resulted in bilateral labelling in the OMv, and serial reconstructions showed that some individual fibers terminated bilaterally in the OMv (Fig. 8B).

With respect to this projection, our findings are slightly different from those reported by Brecha et al. (1980) in several ways. First, Brecha et al. reported a sparse bilateral projection to the trochlear nucleus, whereas we found none. Second, they reported that the projection was heavy to the ipsilateral OMv and the contralateral OMdl, sparse to the ipsilateral OMdl and the contralateral OMv, but no labelling was found in the OMdm. Furthermore, they reported that the axons crossed the midline ventral to the OMC to reach the contralateral side. Although we did confirm this pathway, we found that many fibers reached the contralateral OMC via the pc. Based on retrograde transport of HRP, Brecha et al. concluded that the ipsilateral and contralateral projections to the OMC were from the nBORd and the nBORp, respectively. With the use of serial reconstructions, we found that at least some cells in the nBORd project bilaterally to the OMC. This is consistent with electrophysiological studies, in that, whereas neurons in the nBORp have monocular receptive fields, Wylie and Frost (1990b) found that neurons in the nBORd have binocular receptive fields (see below). The LM does not project to the OMC in pigeons (Gamlin and Cohen, 1988), and the AOS in mammals does not project directly to the OMC (Simpson, 1984; Simpson et al., 1988a).

Projections to the accessory oculomotor and perirubral areas

Brecha et al. (1980) found a bilateral projection from the nBOR to the IC. We have confirmed this but have also found bilateral projections to the adjacent D and CtG. Some terminal fields were found in the rostral Ru, and a few were found in the SCE and SCI. Serial reconstructions

showed that some individual neurons project to all of these structures, and some project bilaterally. After injections into the LM, Gamlin and Cohen (1988) found a few terminals in the SCE and the rostrolateral Ru, but no terminals were seen in the IC, D, or CtG. In mammals, bilateral AOS projections to the IC, D, and CtG have been shown (Giolli et al., 1984, 1985, 1988; Blanks et al., 1995).

A projection to the IC from the nBOR, but not from the LM, is consistent with the physiological literature. Based on the direction preferences of the LM and nBOR neurons outlined above, the LM is involved primarily in the control of horizontal eye movements, whereas the nBOR is involved in the control of vertical and horizontal eye movements. Recent studies have implicated the IC in the control of vertical eye movements (see, e.g., Fukushima and Kaneko, 1995).

Projections to the contralateral nBORd: Is the nBORd analogous to the mammalian VTRZ?

With anterograde tracing methods, Brecha et al. (1980) found a projection from the nBOR to the contralateral nBORd. With retrograde methods, they determined that this projection was from cells in the nBORp and the nBORl. The results of the present study confirm these findings. Terminals were seen in the contralateral nBORd in cases 1 and 3, which were confined to the nBORp, but not in case 2, which included the nBORd. This is also consistent with electrophysiological studies showing that neurons in the nBORd have binocular receptive fields (Wylie and Frost, 1990b). The LM also projects to the nBORd (Gamlin and Cohen, 1988).

In mammals, the AOS projects to a small group of neurons in the AVT (Giolli et al., 1984, 1985; Blanks et al., 1995) that has been designated the VTRZ. Like the pigeon nBORd, it projects to the subdivisions of the IO that provide input to the optokinetic zones in the VbC (for review, see Simpson et al., 1988a). Physiologically, neurons in the LTN/MTN and the nBORp have simpler receptive field properties than neurons in the VTRZ and the nBORd. Neurons in the MTN/LTN and the nBORp respond to OKS moving in a particular direction in the contralateral eye (see, e.g., Simpson, 1984; Wylie and Frost, 1990a). However, second-order neurons in the VTRZ have more complex receptive fields that respond best to rotational OKS around one of three axes corresponding to the three axes of the semicircular canals (Simpson et al., 1988b). VTRZ neurons often have binocular receptive fields. In the nBORd, second-order neurons have binocular receptive fields and respond best to rotational or translational OKS (Wylie and Frost, 1990b). For these reasons, we suggest that the nBORd is to the nBORp as the VTRZ is to the MTN and LTN.

Projections to the pretectum and thalamus

The pretectum received a massive projection from the nBOR in all three cases. The bulk of this projection was to the LMl. These fibers exited the nBOR and travelled laterally, giving off numerous terminals into the nBORl and the ventral margins of the LMm and LMl. The fibers then coursed dorsally, mostly through the LMl, where numerous terminals were seen, and eventually terminated in the dorsal thalamus. The LMl must be regarded as the primary projection site of the nBOR based on the density of terminal labelling. Some fibers reached the dorsal thalamus through the LMm, and fewer reached the dorsal thalamus through the LPC and PPC. A few terminals from collaterals were seen in the LMm, LPC, and PPC. Some collaterals also terminated in the tectum, SOp, TrO, and GLv. In the dorsal thalamus, numerous terminals were seen in the DLL, DLM, and DLA. It should be noted that the few terminals seen in the PPC were in the rostrolateral margin, not in the main caudolateral margin of the PPC.

Brecha et al. (1980) also noted a heavy projection to the LM. By using the existing nomenclature, they described the area as the magnocellular LM, but an examination of their drawings suggests that the bulk of the terminal labelling was in the LMl according to the current nomenclature. In mammals, the AOS projects heavily to the nucleus of the optic tract (homolog of the avian LM; Giolli et al., 1984, 1985, 1988; Blanks et al., 1995). A projection to the dorsal thalamus was not described by Brecha et al. (1980), and such a projection does not have a mammalian equivalent (Simpson et al., 1988a). The DLL and DLAmc are two of the three components of the nucleus opticus principalis thalami (OPT) described by Karten et al. (1973). The third component, the nucleus lateralis anterior (LA), did not receive a projection from the nBOR. The three components of the OPT receive retinal inputs, and the DLL projects bilaterally to the visual wulst of the telencephalon (Karten et al., 1973). Thus, the OPT and the visual wulst, respectively, are considered to be equivalent to the lateral geniculate nucleus and the primary visual cortex of mammals. The DLM also projects to the telencephalon, but to an area ventral to the retinal recipient neurons in the wulst (Karten et al., 1973). Neurons in OPT have small receptive fields and respond to small moving or stationary stimuli (Britto et al., 1975).

AOS: Beyond oculomotor control

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., 1988a). Thus, investigation has focused on those subsystems concerned with oculomotor control, namely, the AOS-olivocerebellar pathway, the vestibular nuclei, and, to a lesser extent, the pontine nuclei (see Simpson, 1984; Simpson et al., 1988a). However, one should considered the AOS in its broader sense: a system that is dedicated to the analysis of the visual consequences of self-motion (Simpson et al., 1988a; Frost et al., 1990; 1994; Grasse and Cynader, 1990). There is an abundance of information available in the optic flow field as one moves through the environment, as emphasized by Gibson (1954, 1958). 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 and one's orientation relative to the environment (see also Nakayama, 1985). We would like to consider the various projections of the nBOR in light of the numerous possible functions of the system.

Oculomotor control. The contribution of the AOS to oculomotor control has been well documented in numerous species. In the present study, we found projections from the nBOR to numerous structures that are known to contribute to oculomotor control in various species. These include the OMC, the vestibular nuclei (birds: Arends et al., 1991), the cerebellar nuclei (see, e.g., Gruart and Delgado-Garcia, 1994), the LM (McKenna and Wallman, 1981, 1985; Gioanni et al., 1983b), the IO (birds: Arends and Voogd, 1989; for reviews, see Simpson, 1984), the

pontine nuclei (see, e.g., Mustari al., 1988), and the IC (see, e.g., Fukushima and Kaneko, 1995).

Head movement control. Friedman (1975) and Frost (1978) have shown that the characteristic head bobbing of pigeons is under visual control. Head bobbing as pigeons walk produces horizontal visual flow, but head bobbing also occurs when a pigeon executes a landing, which results in vertical visual flow (Davies and Green, 1988). Essentially, head bobbing can be considered to be gaze stabilization accomplished by compensatory head movements in response to optic flow. In the laboratory, under head-free conditions, much of the compensatory response by pigeons in response to rotating optokinetic stimuli is accomplished by head movements (Gioanni, 1988). Both lesion and electrophysiological studies have implicated the nBOR in the processing of vertical and horizontal visual flow and vertical and horizontal stabilizing eye and head movements (Fite et al., 1979; Lazar, 1983; Gioanni et al., 1983b, 1984; Wylie and Frost, 1990a). In the present study, we found projections from the nBOR to numerous nuclei that project to neurons in the upper cervical cord in birds. These include the IC, FRM, and Ru (Webster and Steeves, 1988). These data corroborate earlier lesion studies that implicated the nBOR in the visual control of head bobbing.

Control of posture and locomotion. Stabilization of optic flow fields can be accomplished with ambulatory limb movements as well. Because the visual world is normally stationary, one can maintain orientation by stabilizing motion of the entire visual world. Moreover, during locomotion, the optic flow field is a source of proprioceptive feedback, which is important for the control of self-motion. There is a wealth of psychophysical literature demonstrating that visual flow fields influence posture (e.g., Lee and Aronson, 1974) and participate in the control of locomotion (for review, see Owen, 1990). In either case, one might posit that neurons responsive to optic flow would influence structures that control limb movements. In the present study, we have shown that the nBOR projects to structures that provide input to the lumbar spinal cord in birds. These include the IC, FRM, FRL, and Ru (Wild et al., 1979; Cabot et al., 1982; Webster and Steeves, 1988; Arends et al., 1991; Wild, 1992). Moreover, both the D and the CtG receive afferent input from the lumbar and sacral regions of the spinal cord in some species (see, e.g., Kunzle, 1993).

Perception. Gibson emphasized that optic flow is important as a cue for two aspects of perception: perception of self-motion and perception of the three-dimensional layout of the environment (Gibson, 1954, 1958). Indeed, observers presented with optic flow stimulation encompassing large parts of the visual field 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 (see, e.g., Anderson, 1986). The three-dimensional layout of the environment can be constructed from optic flow because of motion parallax that results from translation through the environment: The images of objects nearer to the observer move faster in the flow field than the images of more distant objects; thus, "velocity edges" result, that is, differential motion in the optic flow field (Nakayama, 1985). An analysis of such information requires data about small moving stimuli relative to large moving stimuli. Neurons in the OPT respond to respond to small moving stimuli (Britto et al., 1975). It follows that OPT neurons receiving input from the nBOR might be important for analyzing motion parallax that occurs during translation through the environment, and this information may influence the perception of the three-dimensional layout of the environment.

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