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Afferent and Efferent Connections of the Caudolateral Neostriatum in the Pigeon (*Columba livia*): A Retro- and Anterograde Pathway Tracing Study

SVEN KRÖNER* AND ONUR GÜNTÜRKÜN
AE Biopsychologie, Fakultät für Psychologie, Ruhr-Universität Bochum, 44780 Bochum, Germany

ABSTRACT

The avian caudolateral neostriatum (NCL) was first identified on the basis of its dense dopaminergic innervation. This fact and data from lesion studies have led to the notion that NCL might be the avian equivalent of prefrontal cortex (PFC). A key feature of the PFC is the ability to integrate information from all modalities needed for the generation of motor plans. By using antero- and retrograde pathway tracing techniques, we investigated the organization of sensory afferents to the NCL and the connections with limbic and somatomotor centers in the basal ganglia and archistriatum. Data from all tracing experiments were compared with the distribution of tyrosine-hydroxylase (TH)-immunoreactive fibers, serving as a marker of dopaminergic innervation. The results show that NCL is reciprocally connected with the secondary sensory areas of all modalities and with at least two parasensory areas. Retrograde tracing also demonstrated further afferents from the deep layers of the Wulst and from the frontolateral neostriatum as well as the sources of thalamic input. Efferents of NCL project onto parts of the avian basal ganglia considered to serve somatomotor or limbic functions. Projections to the archistriatum are mainly directed to the somatomotor part of the intermediate archistriatum. In addition, cells in caudal NCL were found to be connected with the ventral and posterior archistriatum, which are considered avian equivalents of mammalian amygdala. All afferents and projection neurons were confined to the plexus of densest TH innervation. Our results show that the NCL is positioned to amalgamate information from all modalities and to exert control over limbic and somatomotor areas. This organization might comprise the neural basis for such complex behaviours as working memory or spatial orientation. J. Comp. Neurol. 407:228–260, 1999.

Indexing terms: parasensory cortex; sensorimotor integration; tyrosine hydroxylase; immunocytochemistry; basal ganglia; prefrontal cortex

The neostriatum caudolaterale (NCL) of the pigeon has been compared with the mammalian prefrontal cortex (PFC), due to its dense dopaminergic innervation (Divac et al., 1985, 1994; Divac and Mogensen, 1985; Waldmann and Güntürkün, 1993; Wynne and Güntürkün, 1995), and the behavioral deficits in working memory (Mogensen and Divac, 1982, 1993; Gagliardo et al., 1996, 1997; Güntürkün, 1997), reversal learning (Hartmann and Güntürkün, 1998), and go/no-go tasks (Güntürkün, 1997) that follow its ablation. Working memory tasks selectively target the control of reactions depending on past experiences and the ongoing stream of sensory information that is currently being experienced, which in mammals is a key feature of the PFC (Goldman-Rakic, 1987; Fuster, 1989). A clear prerequisite for a structure in nonmammalian species that can subserve such functions and may thus be regarded as an analogue of the PFC is the ability to integrate all available sensory information and to exert influence over motor and limbic structures.

A number of previous studies have demonstrated afferent input to the lateral neostriatum from visual (Ritchie, 1979; Shimizu et al., 1995), auditory (Wild et al., 1993) and

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*Correspondence to: Sven Kröner, AE Biopsychologie, Fakultät für Psychologie, Ruhr-Universität Bochum, 44780 Bochum, Germany.
E-mail: sven.kroener@ruhr-uni-bochum.de

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somatosensory (Shimizu et al., 1995) areas, as well as a projection from the multimodal thalamic nucleus dorsolateralis posterior (DLP; Waldmann and Güntürkün, 1993; Leutgeb et al., 1996). Based on cytoarchitectonic and hodological data, Rehkämper and Zilles (1991) have proposed that the complete posterior neostriatum, including its caudolateral aspect, might represent an area of multimodal integration. Furthermore, in a recent retrograde labeling study focused on the NCL (Leutgeb et al., 1996), it has been shown that the NCL is reached by afferents from all major secondary sensory areas within the pigeon brain. Until now, however, a detailed study of the termination pattern of these afferents and a possible functional segregation within the pigeon's NCL is still lacking. Retrograde tracing data from a very recent study in chicks (Metzger et al., 1998) revealed distinct and nonoverlapping termination zones for the trigeminal, tectofugal, and auditory systems within the NCL. Because retrograde tracing in pigeons (Leutgeb et al., 1996) suggested a substantially different organization of the NCL with largely overlapping sensory compartments, this report describes the afferent and efferent connections of the NCL as studied by retro- and anterograde pathway tracing and compares it with the distribution of tyrosine hydroxylase-immunoreactive fibers.

MATERIALS AND METHODS

Neuroanatomical pathway tracing experiments

Fifty-seven adult pigeons (*Columba livia*) from local stock provided the data presented here. Treatment of animals conformed to NIH guidelines and specifications of the German Animal Welfare Act. Accordingly, prior to surgery, the animals were deeply anesthetized with 0.33–0.4 ml Equithesin per 100 g body weight. Animals received pressure injections of either the sensitive antero- and retrograde tracer cholera toxin, subunit b (CTb, 1% in distilled water; List Labs, Campbell, CA) or biotynilated dextran amines as anterograde tracer (BDA, 10,000 molecular weight form, 10% in sodium phosphate buffer, pH 7.3; Molecular Probes, Leiden, The Netherlands). Tracer was delivered through glass micropipettes (tip diameter 15–20 μm) attached to a nanoliter injector (World Precision Instruments, Sarasota, FL). Because previous studies (Leutgeb et al., 1996; Metzger et al., 1998) and our own data have indicated that the majority of connections of the NCL are restricted to the ipsilateral hemisphere, most animals received bilateral injections to minimize the number of pigeons used (Table 1). Stereotaxic coordinates for the injections were determined by using the atlas of Karten and Hodos (1967). The afferent sources of the NCL were determined by injections of CTb (30 –54 nl) into medial and lateral parts of the NCL along its rostrocaudal extent, as well as into the directly adjacent neostriatum dorsale (Nd, Bonke et al., 1979; Wild et al., 1993; Wild, 1994). We included Nd in our analysis because the pattern of catecholaminergic innervation suggests that Nd is continuous with NCL (Fig. 1) and might constitute its auditory subcomponent. To study the areal pattern of afferent input to the NCL, injections of CTb (9–80 nl) and BDA (40–100 nl) were made into most of the telencephalic regions which by means of retrograde transport had been

Abbreviations

AC	nucleus accumbens
Ai	archistriatum intermedium, pars centrale
Aidd	archistriatum intermedium, pars dorsodorsale
Aidv	archistriatum intermedium, pars dorsoventrale
AL	ansa lenticularis
Am	archistriatum mediale
Ap	archistriatum posterior
APH	area parahippocampalis
Av	archistriatum intermedium, pars ventrale
AVT	area ventralis tegmentalis
Bas	nucleus basalis
BNST	bed nucleus of the stria terminalis
CDL	corticoidea dorsolateralis
CPi	cortex piriformis
DIP	nucleus dorsointermedius posterior thalami
DIVA	nucleus dorsalis intermedius ventralis anterior
DLL	nucleus dorsolateralis anterior thalami, pars lateralis
DLM	nucleus dorsolateralis anterior thalami, pars medialis
DLP	nucleus dorsolateralis posterior
DMA	nucleus dorsomedialis anterior thalami
DMP	nucleus dorsomedialis posterior thalami
E	ectostriatum
Ep	ectostriatal belt
FPL	fasciculus prosencephali lateralis
GLd	dorsolateral geniculate nuclei
HA	hyperstriatum accessorium
HD	hyperstriatum dorsale
HIS	hyperstriatum intercalatus superior
HOM	tractus occipitomesencephalicus, pars hypothalami
Hp	hippocampus
HV	hyperstriatum ventrale
HVdv	hyperstriatum ventrale dorso-ventrale
HVvv	hyperstriatum ventrale ventroventrale
ICo	nucleus intercollicularis
IHA	nucleus intercalatus of the hyperstriatum accessorium
IMHV	intermediate and medial part of the hyperstriatum ventrale
L1	field L1
L2	field L2
L3	field L3
LFS	lamina frontalis superior
LH	lamina hyperstriatica
LHy	nucleus lateralis hypothalami
LPO	lobus parolfactorius
NCL	neostriatum caudolaterale
NCm	neostriatum caudomediale
Nd	neostriatum dorsale
NFL	neostriatum frontolaterale
NFT	neostriatum fronto-trigeminale
NI	neostriatum intermedium
NIL	neostriatum intermedium laterale
NIM	neostriatum intermedium medialis
NIMl	neostriatum intermedium medialis, pars laterale
NIMm	neostriatum intermedium medialis, pars mediale
OM	tractus occipitomesencephalicus
Ov	nucleus ovoidalis
PA	paleostriatum augmentatum
PP	paleostriatum primitivum
PT	nucleus pretectalis
Rt	nucleus rotundus
SAC	stratum album centrale
SCI	stratum cellulare internum
SGC	stratum griseum centrale
SGP	substantia grisea et fibrosa periventricularis
SPC	nucleus tractus septomesencephalici
SPL	nucleus spiriformis lateralis
SRt	nucleus subrotundus
T	nucleus triangularis
Tn	nucleus taeniae
TO	optic tectum
TPc	nucleus tegmenti pedunculopontinus, pars compacta
TPO	area temporo-parieto-occcipitalis
TSM	tractus septomesencephalicus
Va	vallecula
VIA	ventrointermediate area of the thalamus
VIP	ventrointermediate area of the posterior nuclei

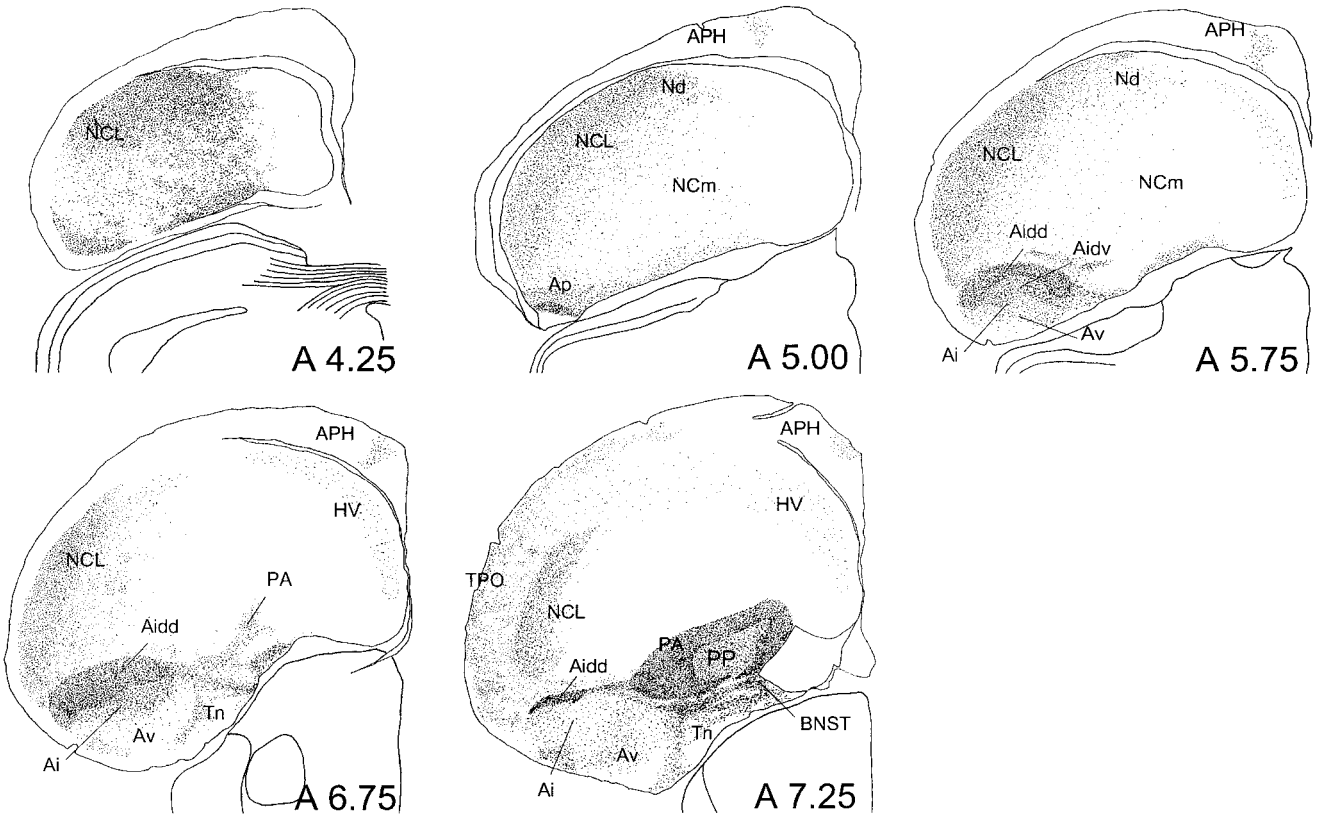

Fig. 1. Camera lucida drawing of tyrosine hydroxylase (TH)-immunoreactive fibers in the caudal telencephalon of the pigeon. Staining for TH produces a pattern very similar to that seen with an antibody against dopamine which has been previously used to define the neostriatum caudolaterale (NCL; Waldmann and Güntürkün, 1993; Wynne and Güntürkün, 1995; Metzger et al., 1996). For abbreviations, see list.

shown to constitute afferent sources of the NCL. Efferent connections of the NCL to motor and limbic structures were studied by placing injections into the somatomotor and limbic parts of the archistriatum (Zeier and Karten, 1971) as well as into parts of the avian basal ganglia that are comparable to parts of mammalian striatum.

Immunohistochemical procedures

Survival times were 3 days for CTb and 4–6 days for BDA. Fifteen minutes prior to perfusion, the animals were injected with 1,000 IU heparin and deeply anaesthetized with 0.4–0.5 ml Equithesin per 100 g body weight. Pigeons were then perfused transcardially with 200 ml 0.9% saline (40°C) followed by 1,000 ml of 4% paraformaldehyde in 0.12 M phosphate buffer (PB; 4°C, pH 7.4). After perfusion, brains were dissected and postfixed in the same fixative to which 30% sucrose was added, and then transferred to 30% sucrose in phosphate buffer containing 0.9% NaCl (PBS; pH 7.4) for approximately 18 hours at 4°C. Brains were cut in frontal slices of 40 µm on a freezing microtome and collected in PBS containing 0.01% NaN_3 as a preservative. Representative sections were then processed for the avidin-biotin-conjugate technique (ABC).

Immunohistochemical labeling for Cholera Toxin b

Endogeneous peroxidases were blocked by preincubating slices in a solution of 0.5% H_2O_2. Slices were washed and for immunohistochemistry of CTb free-floating sections were incubated overnight at 4°C in anti-CTb from goat (Jackson, West Grove, PA; 1:20,000) in PBS containing 0.3% Triton X-100 (Sigma, Deisenhofen, Germany). The following steps were carried out at room temperature, separated by three washes in PBS of 10 minutes each. After washing, slices were first incubated for 1 hour in biotinylated donkey anti-goat (Jackson,1:500 in 0.3% Triton X-100 PBS) for 1 hour and then in the avidin-biotin complex (ABC Elite, Vector Labs, Burlingame, CA; 1:100 in PBS with 0.3% Triton X-100) for 1 hour. Washes in PBS were followed by two additional washes in 0.12 M acetate buffer (pH 6). Staining was achieved by the 3,3'-diaminobenzidine (DAB) technique with heavy metal amplification (modified from Adams, 1981) by adding $H_8N_2NiO_8S_2$ (2.5 g/100 ml), NH_4Cl, and $CoCl_2$ (both 40 mg/100 ml). After 15 minutes of preincubation, the reaction was catalyzed with a solution of 0.5% H_2O_2. The reaction was stopped by rinsing the tissue in 0.12 M acetate buffer and PBS. Slices were then mounted, dehydrated, and coverslipped.

Labeling for BDA

Visualization of BDA was identical to that of CTb, except that primary and secondary antibodies could be omitted and slices were directly incubated in ABC, followed by the staining procedure described above. Selected series labeled for BDA or CTb were counterstained with cresyl violet.

Immunohistochemical labeling for tyrosine hydroxylase

To compare the distribution of afferent fibers and retrogradely labeled neurons within NCL with the distribution of putative dopaminergic fibers, several sections were processed for tyrosine hydroxylase (TH). Therefore, additional sections stained for CTb or BDA were either double-labeled with TH, or occasionally, sections adjacent to these were single-labeled for TH. The same basic procedure as for immunohistochemistry of CTb was applied for labeling of TH: After blocking of endogeneous peroxidases and thorough washing, free-floating sections were incubated overnight at 4°C in monoclonal mouse anti-TH (Boehringer, Mannheim, Germany) diluted 1:200 in PBS containing 0.3% Triton X. Slices were then incubated at room temperature in biotinylated rabbit anti-mouse (Chemicon, Temecula, CA; 1:200 in 0.3% Triton PBS) for 1 hour and finally in ABC for 1 hour. Staining was achieved using the DAB-technique as described for CTb. In those cases that were double-labeled, enhancement of the DAB staining by nickel ammonium sulfate was ommitted, resulting in a light brown signal for TH which could be clearly distinguished from the black reaction product of the tracers.

TABLE 1. Experimental Parameters[1]

Injection site	Number of animals	Number of cases	Tracer: BDA L	Tracer: BDA R	Tracer: CTb L	Tracer: CTb R
NCL	7	11	—	—	6	5
Nd	3	4	—	—	2	2
Field L	3	6	1	—	2	3
Ep	6	10	—	1	5	4
NFT	3	5	—	—	2	3
Rostral HA	3	5	1	—	2	2
Caudal HA	4	6	1	1	2	2
NIMm	4	6	1	—	3	2
NIMl	6	10	—	—	5	5
Ai and Av	6	10	—	3	2	5
Ap	3	5	—	1	2	2
LPO	5	8	—	—	4	4
PA	4	6	—	1	3	2

[1]R, right side; L, left side; for other abbreviations, see list.

RESULTS

Retrograde tracing of afferent sources of the NCL

Our injections of CTb into medial and lateral parts of NCL generally replicated the results of an earlier study (Leutgeb et al., 1996). All injections were confined to NCL as defined by TH and dopamine (DA)-like immunoreactivity (Waldmann and Güntürkün, 1993; Wynne and Güntürkün, 1995; present study), and extended from the caudal tip of the telencephalon at approximately anterior (A) 4.25 to rostral A 7.00.

Telencephalic afferents to NCL. Areas that were found to project to the NCL included the medial aspect of the hyperstriatum accessorium (HA) throughout its visual (Karten et al., 1973; Shimizu et al., 1995) and somatosensory part (Delius and Benetto, 1972; Wild, 1987b; Funke, 1989; but see Deng and Wang, 1992, 1993), the ectostriatal belt (Ep) surrounding the ectostriatum dorsally and laterally (Karten and Hodos, 1970) and the adjoining lateral neostriatum, the anterior neostriatum overlying the nucleus basalis (neostriatum fronto-trigeminale, NFT, of Wild et al., 1985), and field L1 and L3 of the auditory field L complex. A large number of cells were labeled in the medial part of the intermediate neostriatum (NIM of Veenman et al., 1995b) and the overlying intermediate and medial parts of the hyperstriatum ventrale (HV): part of these neurons probably correspond to the previously described parasensory area in the intermediate neostriatum, situated between the rostral pole of field L and the caudomedial border of the visual ectostriatum, that receives multimodal input via the DLP (Gamlin and Cohen, 1986; Wild, 1987a, 1994; Funke, 1989; Korzeniewska and Güntürkün, 1990). These cells were predominantly labeled if injections were made into more rostral and medial (including Nd) parts of the NCL. After injections into caudal NCL, a distinct cell group occupying the remaining medialmost aspect of the NIM between approximately A 8.50 and A 12.50 was labeled. Cells within this area also extended across the lamina hyperstriatica (LH) into the intermediate and medial parts of the HV. These two cell groups roughly followed the cytoarchitectonic borders of the regions Ne 9 or Ne 8 and Ne 3, respectively, as described by Rehkämper et al. (1985). For the reason of simplicity, we will refer to them as the medial part of the NIM (NIMm) and the lateral part of the NIM (NIMl), respectively.

In the caudomedial neostriatum (NCm), scattered cells were found dorsal to the lamina medullaris dorsalis (LMD). Another band of cells stretched along the border between the hyperstriatum dorsale (HD) and the dorsal division of the ventral hyperstriatum (HVdv). These cells could be found in most cases, irrespective of the injection site within NCL. In cases that were centered more medially or caudally within NCL, this band of cells also extended into a small triangular-shaped zone within the vallecula. Finally, in several cases a number of cells were observed in the frontolateral part of the neostriatum (NFL). Injections of CTb into this area did indeed confirm a reciprocal connection with the ventrolateral part of the NCL (data not shown). The large majority of fibers from this part of the anterior neostriatum, however, terminated within the area corticoidea dorsolateralis (CDL) and the area temporo-parieto-occcipitalis (TPO) overlying the NCL. Therefore, we cannot fully exclude that part of the labeling within NFL was attributable to tracer spread into CDL.

In addition to labeling in sensory areas, retrograde transport revealed a number of labeled neurons in the dorsal and ventral parts of the intermediate archistriatum. Cells in the ventral archistriatum were the only telencephalic connection found to project bilaterally onto the NCL. In contrast to Leutgeb et al. (1996), we never observed any labeling within the nucleus taeniae (Tn). Furthermore, a few cells within the ventral striatum just dorsal to the fasciculus prosencephali lateralis (FPL) were also found to project to the NCL.

In general, injections into NCL resulted in a similar pattern of retrograde labeling, but regional differences exist. With respect to a mediolateral topography, our results resemble those of Leutgeb et al. (1996) and are thus not described in detail here. However, we found a strong rostrocaudal topography in the organization of afferent and efferent connections of the NCL. The nature of this topography was further elucidated in anterograde tracing experiments. Figure 2 illustrates the results after two injections into the far caudal and rostral aspects of NCL.

Subtelencephalic sources of afferent input to NCL were observed in the thalamus, midbrain, and tegmentum. In the lower brainstem, the avian equivalent of the substan-

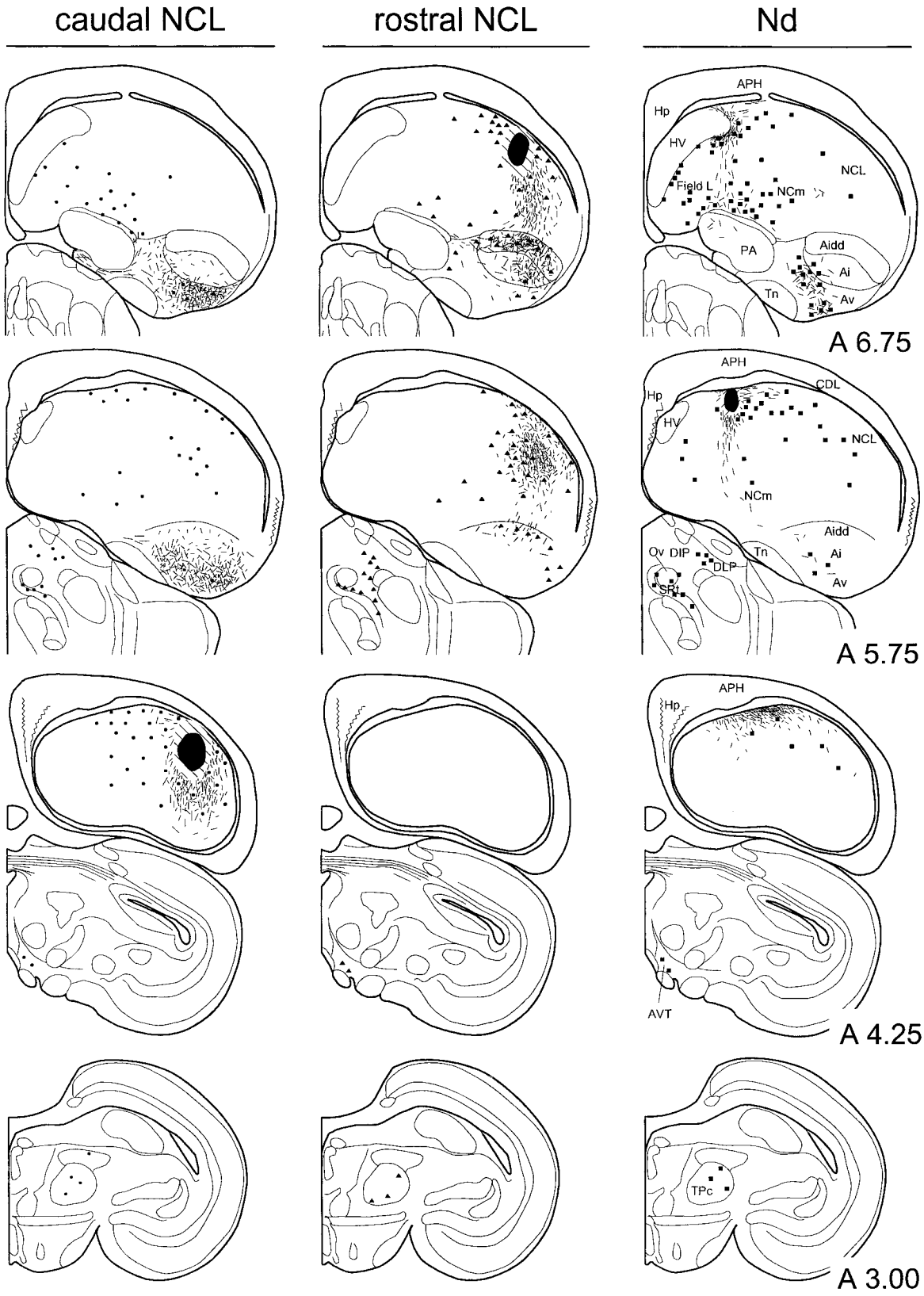

Fig. 2. Schematic representation of retro- and anterograde labeling following injections of Cholera Toxin b (CTb) into various locations within neostriatum caudolaterale (NCL). Retrogradely labeled cells are represented by filled symbols (dots, triangles, or squares for the different injection sites) and anterogradely labeled fibers and terminals are represented by short lines. Anterograde labeling is shown only for selected regions. The left and middle columns illustrate the topographic ordering of NCL afferents and efferents after injections into the caudalmost NCL (left column) or the far rostral NCL (middle column), respectively. The right column shows an example of an injection into neostriatum dorsale (Nd). Labeling after Nd injections was very similar to that observed after tracer deposits into medial NCL. In this and all following figures, medial is to the left and dorsal is at the top. For abbreviations, see list.

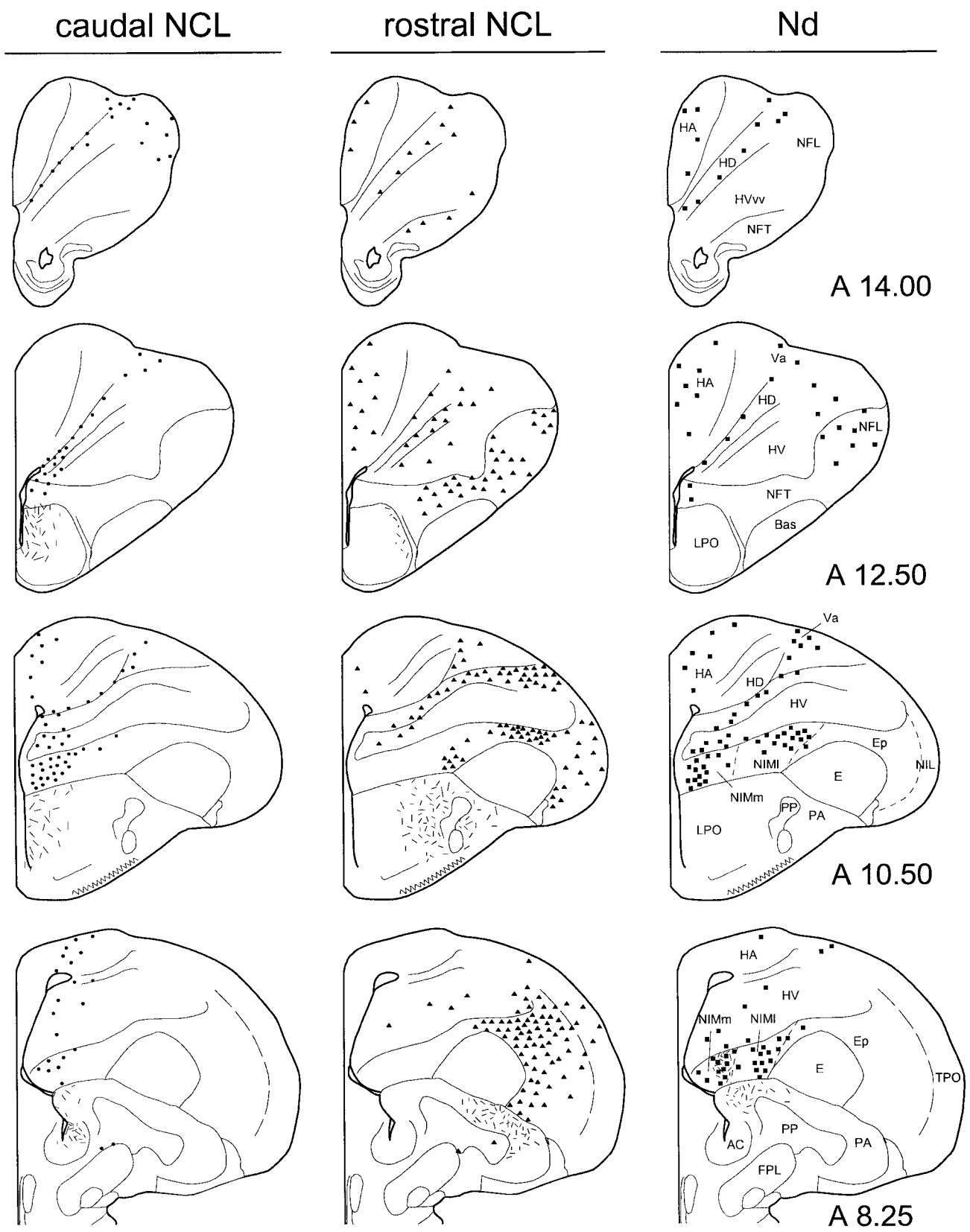

Figure 2 (Continued)

tia nigra, the nucleus tegmenti pedunculopontinus, pars compacta (TPc), the locus coeruleus (LoC), and the area ventralis tegmentalis (AVT) were labeled. These cell groups have been shown to be immunoreactive for TH and dopamine and contain the sources of dopaminergic afferents to the telencephalon (Waldmann and Güntürkün, 1993; Metzger et al., 1996; present study). The projection from the LoC and some cells in the formatio reticularis was bilaterally organized. In the thalamus, retrogradely labeled cells were mainly found in the nucleus subrotundus (SRt) and the DLP. Yet, we also found a projection from the n. dorsointermedius posterior thalami (DIP) and a band of cells that seemed to intersperse between DLP and DIP and also extended ventral to the latter two. Therefore, we termed these cells collectively the ventrointermediate area of the posterior nuclei (VIP). Figure 3 shows examples of retrogradely labeled neurons from sensory forebrain areas (Fig. 3A–F) and the sources of thalamic input to NCL following injections of CTb into NCL.

Anterograde labeling of efferents of the NCL. The pattern of anterograde labeling resulting from injections into NCL was studied within the basal ganglia and the archistriatum. Fibers showing terminal-like varicosities were found throughout most parts of the archistriatum. For the description of archistriatal subdivisions, we adopted the terminology of Wynne and Güntürkün (1995). Injections into the very caudal aspect of NCL predominantly labeled fibers in parts of the central (Ai) and ventral parts (Av) of the intermediate archistriatum and in some cases also in the posterior archistriatum (Ap). Injections into more rostral NCL resulted in terminal labeling that was confined to the dorsal and central parts of the intermediate archistriatum. After injections into the caudal NCL, we observed terminal-like labeling in the medial lobus parolfactorius (LPO) and the ventral striatum, i.e., the nucleus accumbens (AC) and the bed nucleus of the stria terminalis (BNST), which was not attributable to tracer spread into the piriform cortex (CPi) or the caudal archistriatum. Injections into rostral NCL, on the other hand, resulted in dense terminal labeling in the lateral aspects of LPO and large parts of the paleostriatum augmentatum (PA). Labeling in the PA was most abundant in its caudal extent. Both termination patterns within the archistriatum and the basal ganglia thus suggest that the anterior NCL may be connected to areas concerned with somatomotor functions, i.e., the dorsal and lateral striatum (Veenman et al., 1995a,b), as well as the dorsal and central archistriatum (Zeier and Karten, 1971), whereas the caudal aspect of NCL might project to limbic parts of the striatum (Veenman et al., 1995b) and the presumed avian homologue of the amygdala, e.g., the ventral and caudal archistriatum (Zeier and Karten, 1971; Dubbeldam et al., 1997). Figure 4 shows examples of anterograde labeling in the basal ganglia and the archistriatum following injections of CTb into NCL.

Labeling after Nd injections. Labeling after CTb injections into Nd largely paralled the results after medial NCL injections. A large number of retrogradely labeled cell bodies and fibers could be observed throughout the NIM, which seemed to cluster in two distinct cell groups as also observed after injections into the NCL. Strong labeling was also present in the caudomedial neostriatum and areas L1 and L3 of the field L complex. Furthermore, cells were found in the medial HV and along the border of HV and HD, the caudal and rostral aspects of HA, the valleculla (Va), and the NFL. Finally, somata and terminal-like labeling could be observed in the ventromedial archistriatum and lateral parts of the NCL. Terminal-like labeling in the basal ganglia after Nd injections was restricted to the medial and central parts of the caudal PA. In the thalamus, labeling was most prominent in the SRt and DLP. A number of cells was also found within the shell of the nucleus ovoidalis (Ov) and the nucleus semilunaris parovoidalis. In the midbrain AVT, TPc and LoC contained labeled cell bodies. The results following an injection into Nd are summarized schematically in Figure 2 (right column).

Anterograde tracing experiments

Injections into the ectostriatal belt. After injections into the dorsal and lateral ectostriatal belt and the adjoining neostriatum intermedium (NI) underneath the external pallium (Veenman et al., 1995b), a massive projection of labeled fibers was observed to move caudally through the NI and to innervate the anterior and lateral NCL. This projection seemed to be topographically organized and extended in the case of caudal injections posteriorly to about A 5.00. In addition to terminals, a number of retrogradely labeled cell bodies also were found, indicating a reciprocal connection between the NCL and the ectostriatal belt region. As shown in Figure 5, a massive reciprocal connection of the Ep exists with the deeper hyperstriatal layers, especially with the lateral part of HV. Cells within HV and the NI or NFL, respectively, were distributed up to far rostrally within the hemisphere. Relatively few cells and fibers were found within the outer rind of the pallium, i.e., the lateral NI (NIL), TPO, and CDL, the larger portion of them remaining underneath the border that separates the NI and anterior NCL from the overlying external pallium. Furthermore, in the dorsal and ventral aspects of the rostral archistriatum, small clusters of cells were labeled, as well as a number of somata in the paleostriatum primitivum (PP). Within the ectostriatal core, labeled cells were found in a narrow area below the injection site. In the thalamus, large numbers of neurons were labeled in nucleus rotundus which probably are due to tracer spread into the ectostriatal core.

Injections into field L. In accordance with previous reports (Bonke et al., 1979; Wild et al., 1993), tracer deposits into the auditory field L complex which were mainly centered on the secondary sensory field L1 lead to massive terminal-like labeling in Nd. Yet, injections of CTb revealed a diffuse projection that also extended further laterally in caudal NCL (Fig. 6). In the medioventral aspect of NCL also a small number of retrogradely labeled cells could be observed. Field L injections also resulted in retrograde labeling of neurons throughout the HA, NIM, and HV, as well as in ventral and intermediate archistriatum. Diencephalic neurons were labeled within shell and core regions of n. ovoidalis and the n. semilunaris parovoidalis.

Injections into the hyperstriatum accessorium. After injections into the Wulst that were centered on the medial aspect of the dorsal hyperstriatum accessorium, fibers were found to travel through the lamina frontalis superior (LFS) and further laterally along the border that separates the anterior NCL from the overlying LPO and CDL. Fibers showing terminal-like varicosities remained in close apposition to the ventricle as they moved further caudally through NCL. Neurons that project back to the injected site generally followed the distribution of terminating fibers but extended somewhat ventrally to these.

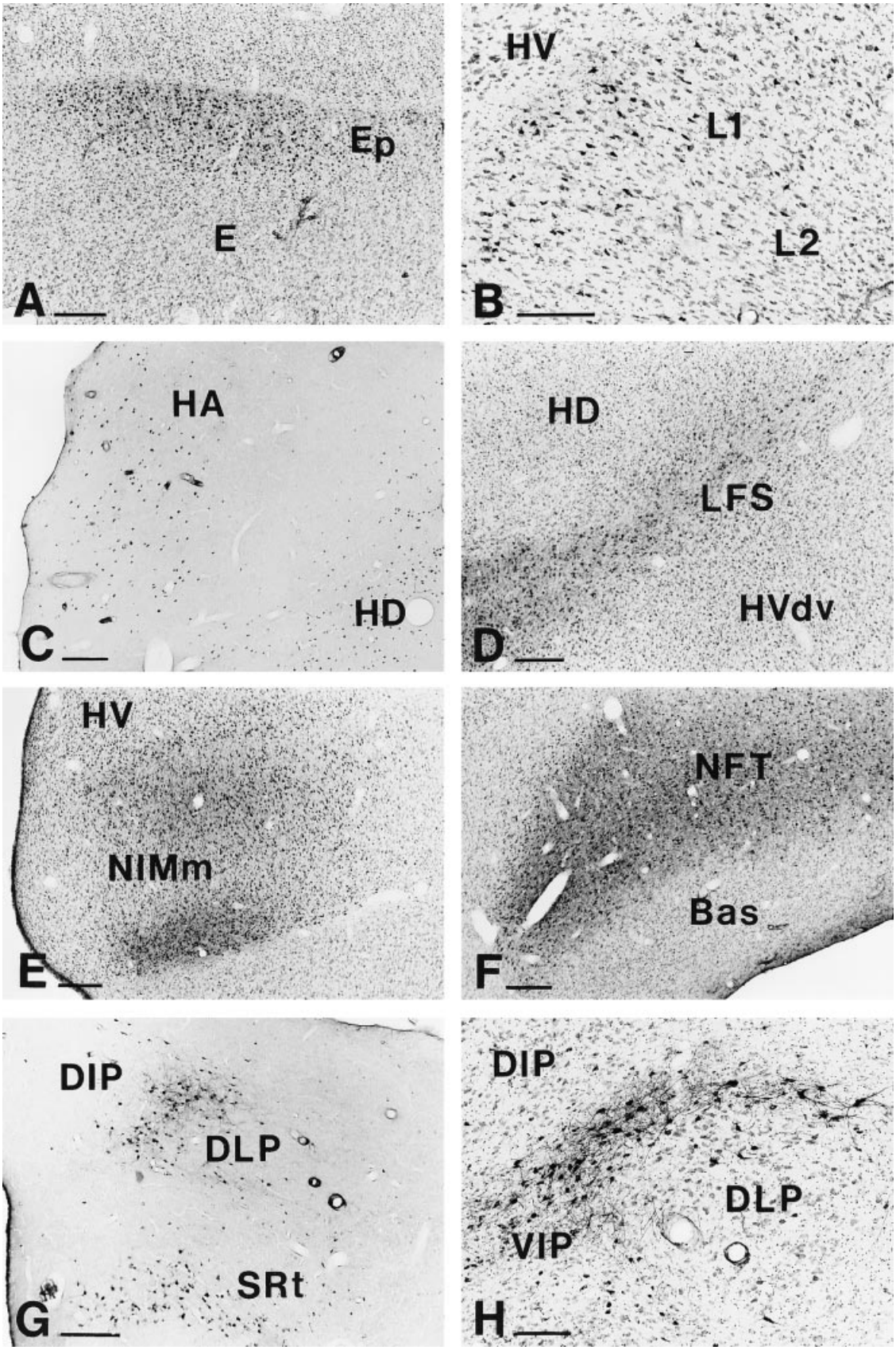

Fig. 3. Photomicrographs of retrogradely labeled cells resulting from injections of Cholera Toxin b (CTb) into the neostriatum caudolaterale (NCL) similar to those shown in Figure 2. Afferents arise from secondary sensory "belt" regions adjacent to primary thalamorecipient areas. See text for details. Retrogradely labeled cells in the telencephalon include the ectostriatal belt (**A**), field L 1 (**B**), HA and HD (**C**), the border between HD and HVdv (**D**), the presumed parasensory area NIMm (**E**), and the NFT (**F**). Labeling in the thalamus was most abundant in the DLP and SRt (**G**). **H:** Cells in the ventrointermediate area of the posterior nuclei (VIP) labeled after an injection into far lateral NCL. Scale bars = 100 µm in B, H; and 250 µm for A, C – G. For abbreviations, see list.

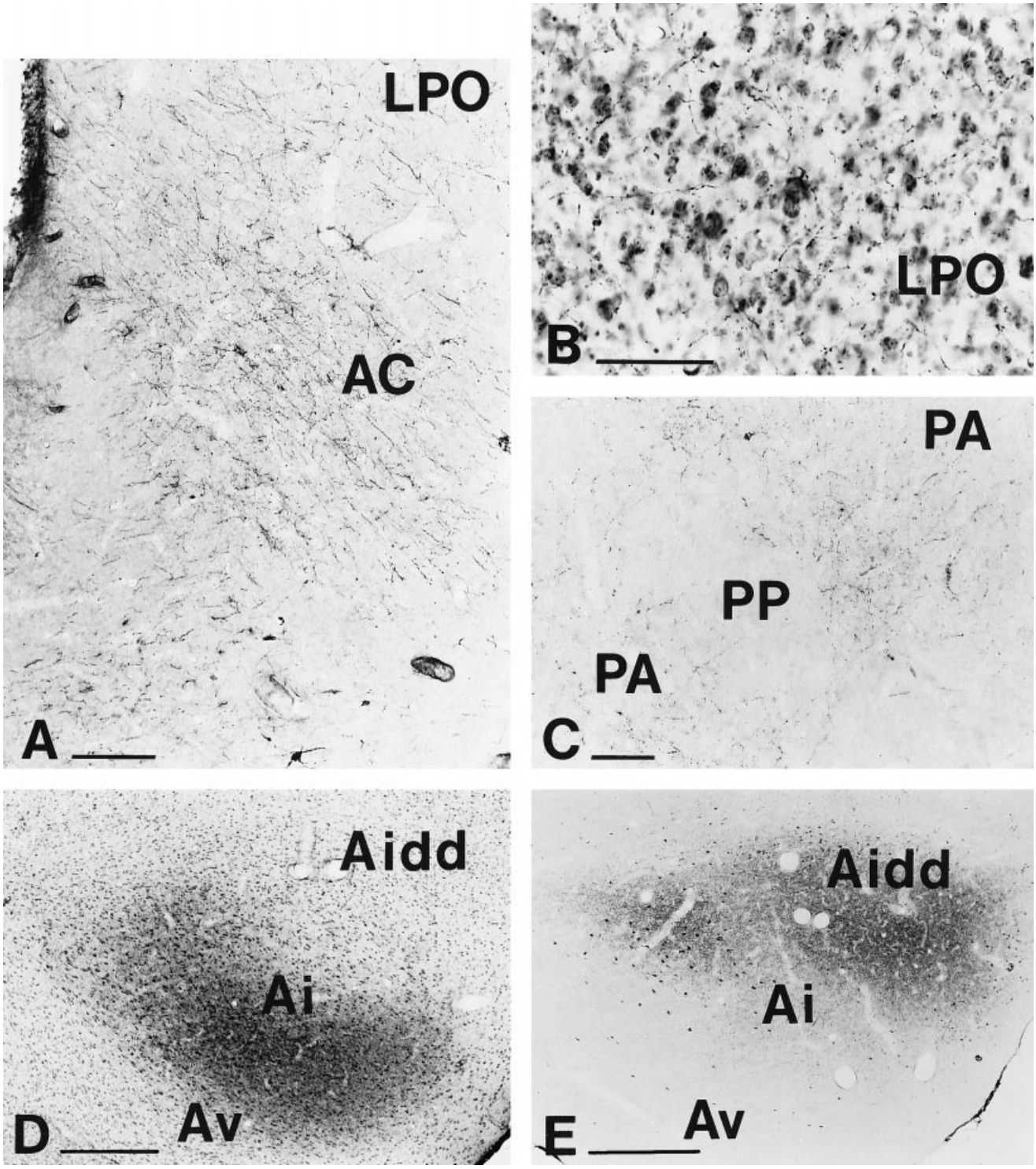

Fig. 4. Photomicrographs of anterograde labeling of neostriatum caudolaterale (NCL) efferents to the basal ganglia and archistriatum. **A:** Labeled fibers in the presumed "limbic" parts of the avian striatum (i.e., nucleus accumbens and medial lobus parolfactorius, LPO) after an injection of Cholera Toxin b (CTb) into far caudal NCL. **B** and **C:** Labeling in the presumed "somatomotor" parts of the basal ganglia, the lateral LPO (B) and central paleostriatum augmentatum (PA; C). **D** and **E:** Labeled fibers and somata in somatomotor and limbic parts of the archistriatum. Injections into the most caudal NCL label numerous fibers in the central part of the intermediate archistriatum, but also extend into the ventral archistriatum which forms part of the avian amygdala (D). In contrast, injections into the rostral NCL lead to labeling in the dorsal and central parts of the intermediate archistriatum which are considered somatomotoric in function. Cells from most parts of the archistriatum project back to the NCL. The projection from archistriatum intermedium, pars ventrale (Av) is the only bilaterally organized connection of the NCL. Aidd, archistriatum intermedium, pars dorsodorsale; Ai, architriatum intermedium, pars centrale. For abbreviations, see list. Scale bars = 250 µm for A; 50 µm for B; 100 µm for C; and 500 µm for D, E.

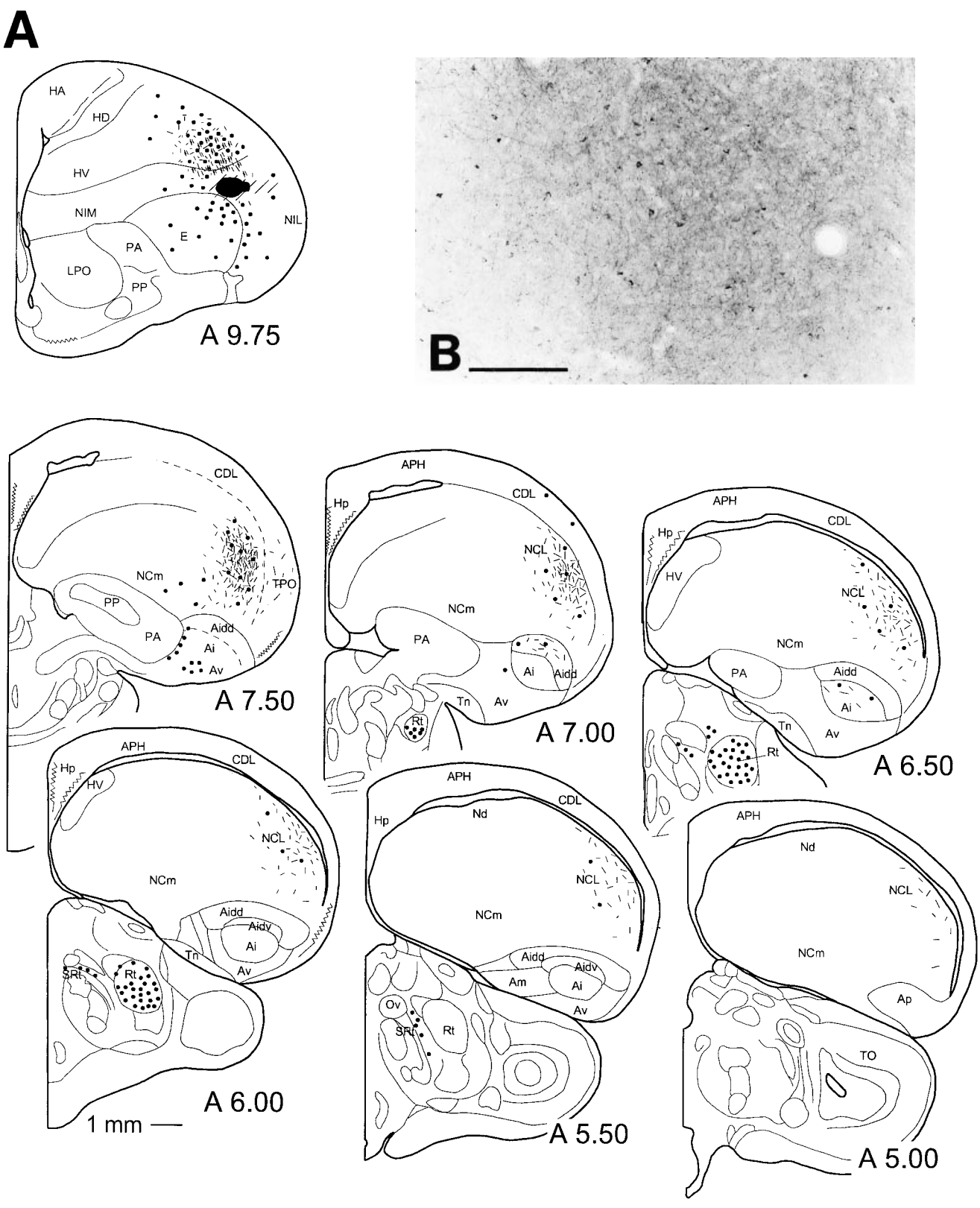

Fig. 5. Results of a 15-nl Cholera Toxin b (CTb) injection into the ectostriatal belt region, which receives afferents from the ectostriatum, the primary visual forebrain area of the tectofugal pathway. **A:** Schematic representation of labeling witin the caudal telencephalon. **B:** Photomicrograph showing the innervation of the anterior neostriatum caudolaterale (NCL) and retrogradely labeled cell bodies at about anterior 7.00. For abbreviations, see list. Scale bar = 200 µm.

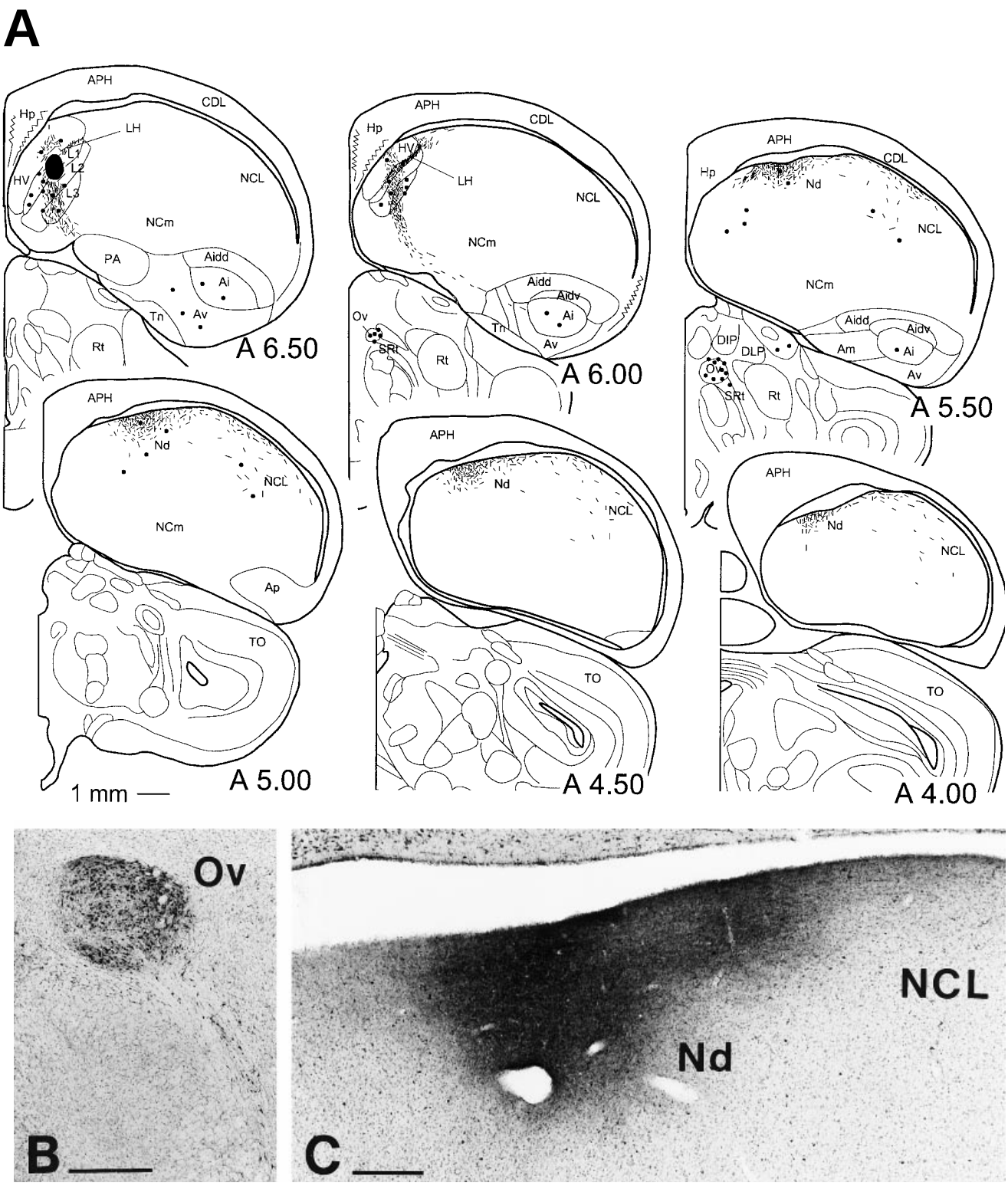

Fig. 6. Results of a 9.2-nl Cholera Toxin b (CTb) injection centered onto the secondary sensory field L1 of the auditory field L complex with slight tracer spread into the hyperstriatum ventrale (HV). **A:** Schematic representation of labeling within neostriatum dorsale (Nd) and the adjoining parts of neostriatum caudolaterale (NCL). **B:** Retrogradely labeled neurons in the nucleus ovoidalis, the main thalamic relay of auditory input to the telencephalon, resulting probably from tracer spread into the primary field L2. Ov, nucleus ovoidalis. **C:** Photomicrograph of labeled fibers in Nd and NCL. For abbreviations, see list. Scale bars = 500 µm for B; and 250 µm for C.

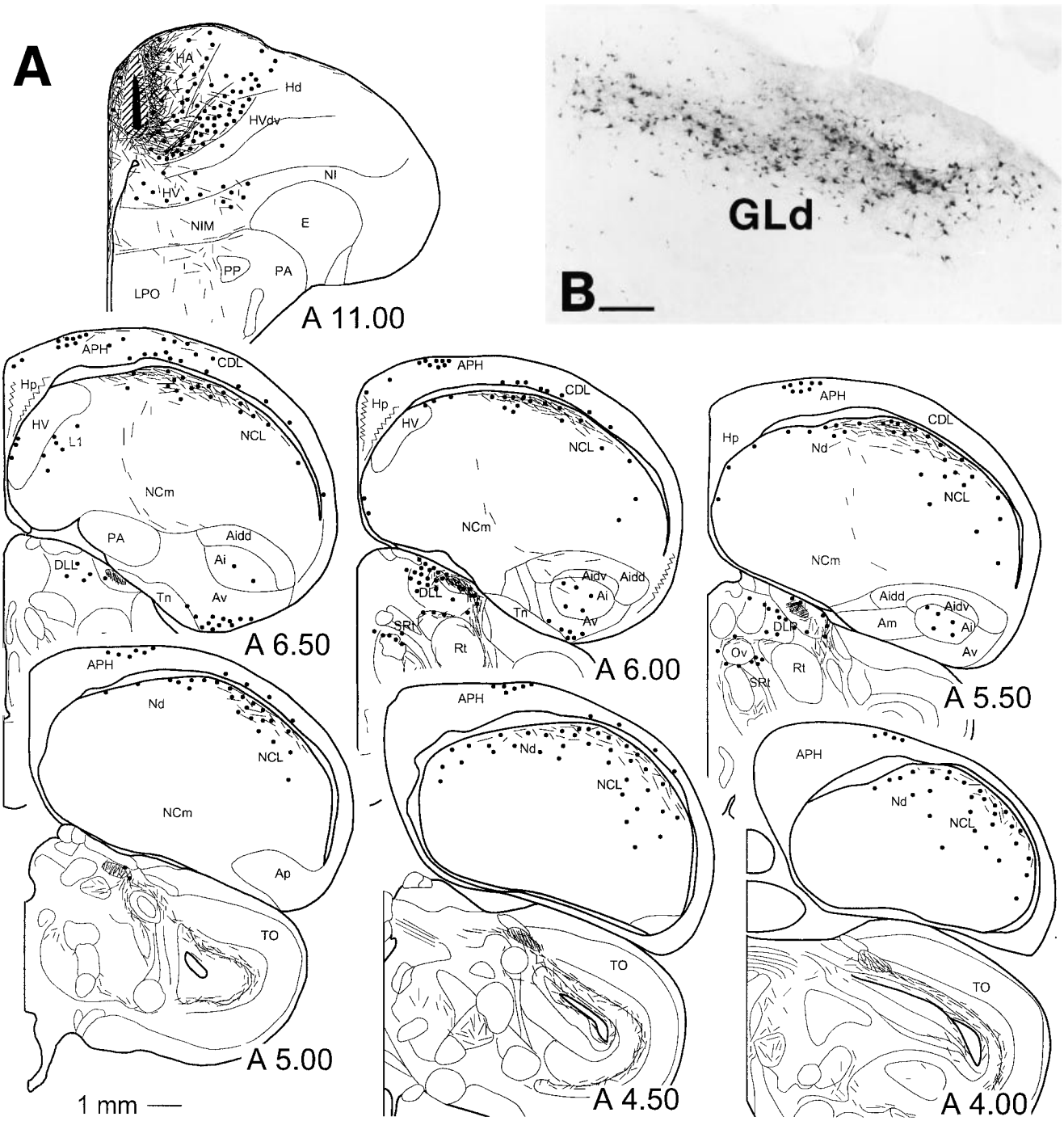

Fig. 7. Labeling observed after a 40-nl injection of Cholera Toxin b (CTb) into the caudal hyperstriatum accessorium (HA). **A:** Schematic representation of labeled fibers and cell bodies in the dorsal neostriatum caudolaterale (NCL). Injections of biotynilated dextran amines (BDA) revealed a similar amount of anterogradely labeled fibers but only very few retrogradely labeled cells. **B:** Photomicrograph showing retrogradely labeled cells in the nuclei of the dorsolateral geniculate complex (GLd), as could be observed in some cases in which the injection site involved the thalamorecipient intercalated nucleus of the HA. For abbreviations, see list. Scale bar = 200 µm.

Injections along the complete rostrocaudal extent of the Wulst revealed a topographic pattern of termination within NCL with more caudal injections leading to stronger labeling in the posterior NCL, whereas afferents from most rostral HA were confined to more anterior aspects of the NCL. This termination pattern may thus reflect the previously described functional segregation of the Wulst into a caudal visual and a rostral somatosensory area. Yet, the projections from HA onto NCL were not restricted to separate termination fields but showed considerable overlap (compare Figs. 7 and 8).

Injections into all parts of the HA evinced retrogradely labeled cells in the HD, frontolateral neostriatum, field L1, external pallium (CDL and TPO), a caudomedial portion of

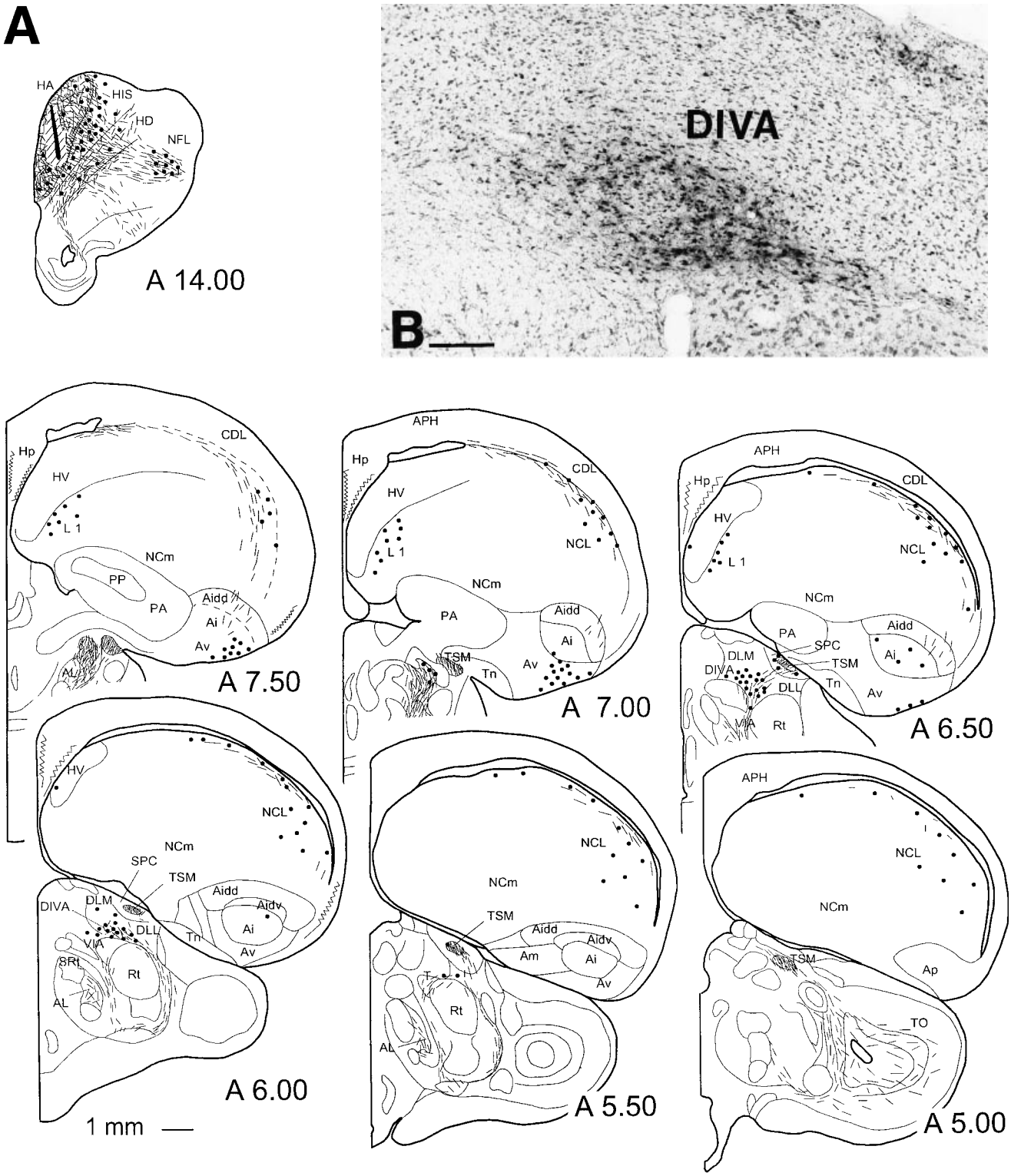

Fig. 8. Results following a 13.8-nl injection of Cholera Toxin b (CTb) into the rostral hyperstriatum accessorium (HA). **A:** Schematic representation of labeled fibers and cell bodies in the neostriatum caudolaterale (NCL). The projection from rostral HA is largely restricted to the anterior NCL. **B:** Photomicrograph showing retrogradely labeled cells in the somatosensory thalamic n. dorsalis intermedius ventralis anterior (DIVA) resulting from tracer spread into the intercalated nucleus of the HA. For abbreviations, see list. Scale bar = 200 µm.

the area parahippocampalis (APH), and the ventral and central archistriatum. Injections into rostral HA additionally labeled cells in the NIM. In several cases in which tracer spread occurred into the thalamorecipient granular layer of the intercalated nucleus of the HA (IHA), retrogradely labeled cells were observed in the thalamic relay stations of the thalamofugal visual and somatosensory system, respectively: deposits of tracer into the caudal Wulst evinced cells in the dorsal aspect of the lateral geniculate nuclei (GLd; Karten et al., 1973; Güntürkün et al., 1993). Injections into the rostral HA, on the other hand, predominatly labeled cells in the somatosensory nucleus dorsalis intermedius ventralis anterior (DIVA; Wild, 1987b; Funke, 1989; Medina et al., 1997).

Injections into the neostriatum frontotrigeminale. After injections into the NFT dorsal to the nucleus basalis (Bas), fibers gathered in the tractus fronto-archistriatalis and passed caudally until they terminated within the lateral part of the anterior archistriatum and the rostral and ventral part of NCL. As can be seen in Figure 9, the terminal field of this projection occupied a large part of the anterior and lateral NCL and extended caudally up to about A 5.00. Within this dense terminal field, a comparatively small number of neurons were found to project back to the injection site. In those cases that showed no or minimal tracer spread into Bas, retrogradely labeled fibers and cells within Bas were restricted to the area directly ventral to the injection site. Furthermore, cells were labeled in the HV dorsal to the injection site, the anterior archistriatum, along the tractus fronto-archistriatalis, and in medial HA.

Injections into the neostriatum intermedium, pars medialis. Injections into the intermediate neostriatum attempted to evaluate whether two separate projections from this area onto NCL exist as indicated by the results from our retrograde tracing experiments reported above. Tracer deposits were thus aimed at the terminal field of the DLP just medially and caudally to the ectostriatum, termed NIMl here, and the medialmost aspect of NI, the NIMm, respectively.

Injections into NIMm consistently produced dense terminal labeling and a considerable number of retrogradely labeled cell bodies in the most caudal aspect of NCL. Fiber bundles left the injection site laterally and travelled caudally within the LH. They reached the caudal neostriatum at the rostral end of Nd where they made massive terminations. The remainder of labeled fibers coursed laterally and caudally within the periventricular roof of NCL. On their way towards the caudal pole of the hemisphere, they gradually fanned out towards the midline until they occupied a large proportion of the hemisphere (Fig. 10).

Small injections that were entirely confined to NIMl resulted in anterograde labeling that was largely restricted to Nd and the dorsal roof of the medial NCL. Labeling in these cases was virtually identical to that seen after field L injections (compare Fig. 6). However, labeling within the NCL varied considerably with the amount of tracer used. Larger NIMl injections that also extended into one of the adjacent areas, HV, NIMm, or Ep, led to a much higher number of labeled fibers and somata within NCL, whereas at the same time, the terminal field also expanded further lateral and medial (Fig. 11). However, the distribution of these fibers did not resemble the terminal fields resulting from injections into NIMm or Ep. In addition, all of these cases showed a similar labeling in the thalamus that was distinct from the pattern observed after NIMm injections (below).

Deposits of CTb into the medialmost NI yielded numerous neurons within the medial HV, dorsal to the injection site, HA, HD, in Ai and Av. Retrogradely labeled cells from Av were also found on the contralateral side. Massive anterograde labeling was seen in medial LPO. Injections into lateral NIM resulted in a similar pattern of labeling which included the somatosensory and visual Wulst, medial HV dorsal to the injection site, as well as Av and Ai. In addition, cells were labeled in field L1 and L3, as well as in large aspects of the caudomedial neostriatum. In these cases, labeled fibers were seen in the PA ventral to the injection site, but not within LPO. Labeling in the thalamus further strengthened the notion of two distinct subareas within NIM: injections into the NIMl confirmed the projection from DLP (Kitt and Brauth, 1982; Gamlin and Cohen, 1986; Wild, 1994) and in addition labeled cells in SRt, the shell of Ov and DIP. In contrast, after tracer deposits into the medialmost NI with slight spread into the overlying HV, but not into PA or LPO, a large number of retrogradely cells were found in the medial part of the dorsal thalamus, namely the n. dorsomedialis posterior thalami (DMP) and DIP, and only very few within DLP.

Injections into the archistriatum. One of the most intriguing results of our retrograde labeling experiments was the extremely high number of cells seen in the NCL that project to the archistriatum, and the close match between the distribution of these cells and the distribution of TH-immunoreactive fibers (Fig. 12). After injections of CTb into the anterior two-thirds of the archistriatum that involved the central and ventral parts of the intermediate archistriatum, cells along the whole rostrocaudal extent of the NCL were labeled (Fig. 13). These cells clustered underneath the dorsal roof of the NCL and gradually fanned out towards the medial neostriatum. This distribution thus follows closely the original description of the NCL based on the distribution of dopaminergic and catecholaminergic fibers (Waldmann and Güntürkün, 1993; Wynne and Güntürkün, 1995; Metzger et al., 1996; present study) and it thus seems that all parts of the NCL, including Nd, project upon the archistriatum.

According to the injection site within the archistriatum, this projection showed an anterior to posterior gradient with more rostral archistriatal injections labeling relatively more cells in anterior NCL. Yet, in general, the highest absolute number of cells was seen in the caudalmost aspect of NCL where labeled cells extend far medially and ventrally. There might exist a further parcellation with respect to dorsal and ventral subdivisions of the archistriatum as suggested from the anterograde tracing experiments, yet with our injections which always involved various subdivisions of the intermediate archistriatum, we could not confirm this.

A different pattern was seen after injections into the posterior archistriatum which is the source of the tractus occipitomesencephalicus, pars hypothalami (HOM) and which together with parts of the ventromedial archistriatum has been suggested to constitute the avian homologue of the amygdala (Zeier and Karten, 1971; Dubbeldam et al., 1997; Davies et al., 1997). In these cases, a small numer of retrogradely labeled cells could be observed in the periventricular rim of the NCL and Nd (Fig. 14). Their number increased towards the caudal tip of the hemisphere, supporting the notion that the most caudal NCL projects to the limbic/amygdaloid part of the archistria-

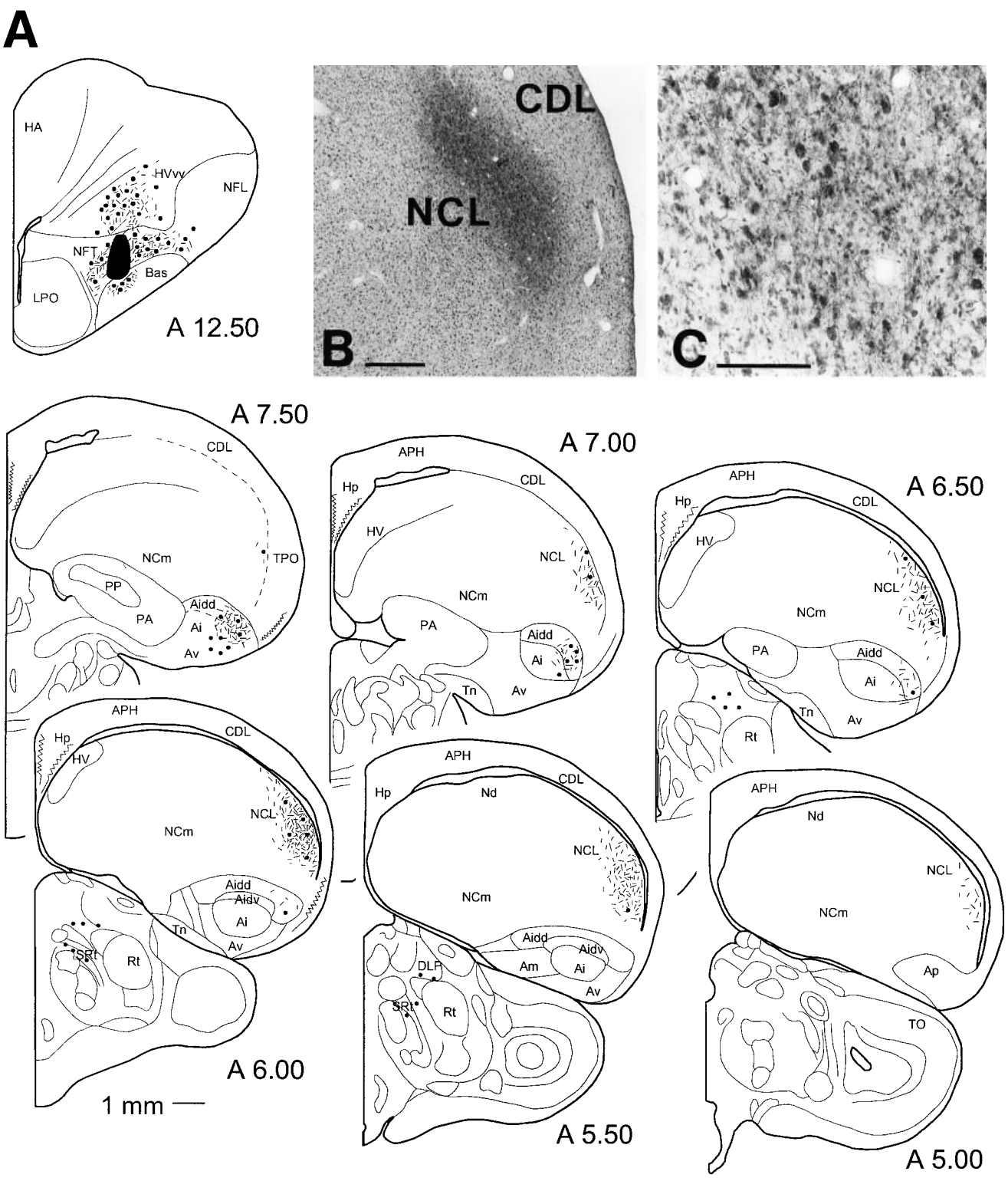

Fig. 9. (**A–C**) Results of a 13.8-nl Cholera Toxin b (CTb) injection into the neostriatum frontotrigeminale overlying the n. basalis. B: Photomicrograph showing the dense anterograde labeling in the rostral and lateral aspects of neostriatum caudolaterale (NCL). CDL, corticoidea dorsolateralis. C: Detail from B showing the border between NCL and the adjacent medial neostriatum. For abbreviations, see list. Scale bars = 500 µm for B; and 100 µm for C.

tum. A very large number of cells, however, was labeled in the ventralmost neostriatum surrounding the archistriatum dorsally and caudally.

After injections into the central and ventral archistriatum, a large number of retrogradely labeled cells was seen in the ventral hyperstriatum and the intermediate neostria-

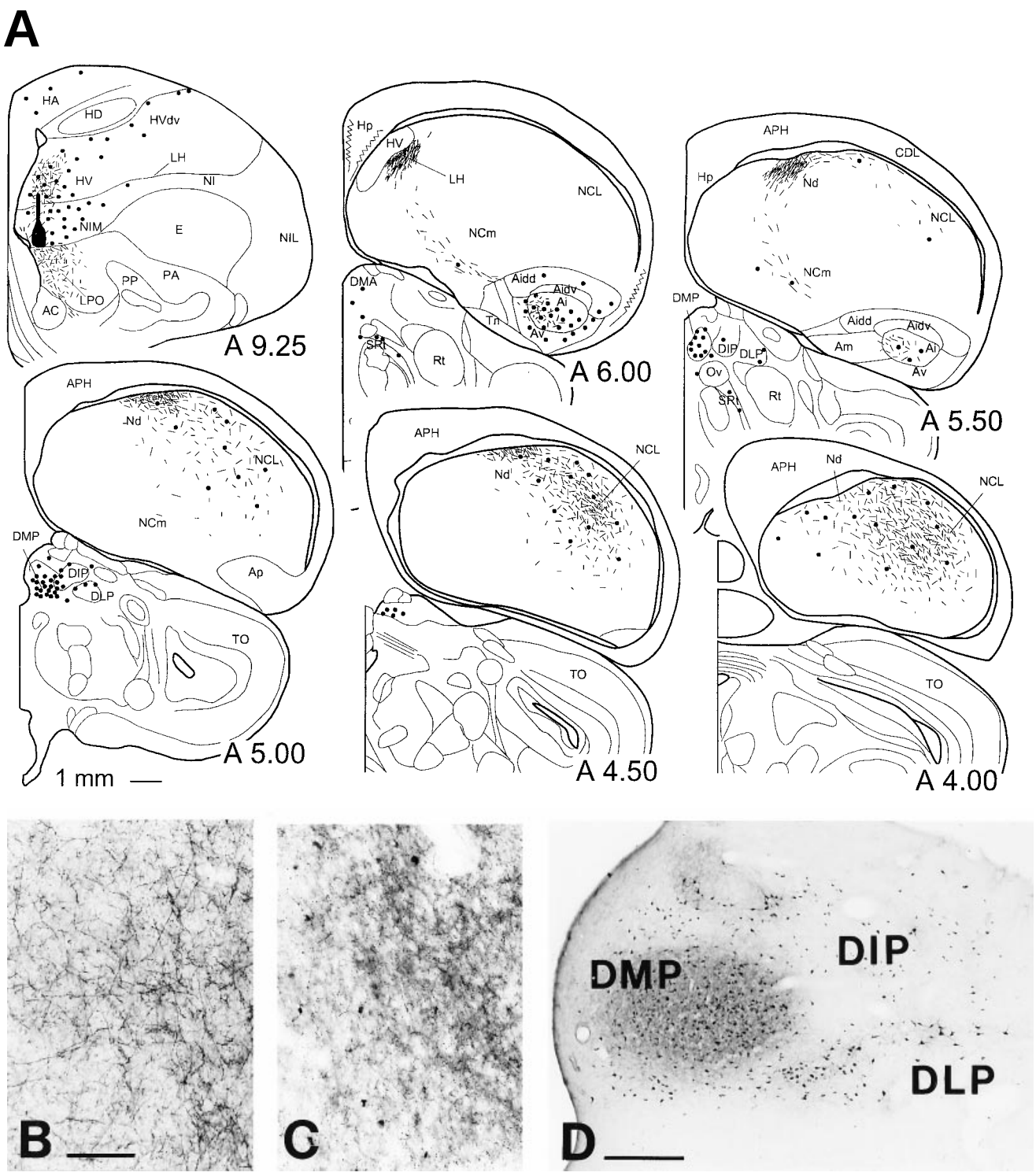

Fig. 10. Pattern of labeling observed after a 11.5-nl injection into the medialmost neostriatum intermedium medialis (NIM). As shown in **A,** fibers travel from the injection site in a compact bundle caudally within the lamina hyperstriatica until they reach the medialmost neostriatum caudolaterale (NCL) from where they gradually fan out to diffusely innervate the caudalmost part of NCL. **B, C:** Photomicrographs showing the abundant distribution of anterogradely labeled fibers and retrogradely labeled cells in the caudalmost NCL, following injections of biotinylated dextran amine (B) and Cholera Toxin b (CTb; C) into the medialmost NIM. **D:** Retrogradely labeled cells in the posterior thalamus, specifically in nucleus doarsomedialis posterior thalami (DMP). DIP, nucleus dorsointermedialis posterior thalami; DLP, nucleus dorsolateralis posterior. In B and C, dorsal is to the right. For abbreviations, see list. Scale bars = 100 μm for B, C; and 300 μm for D.

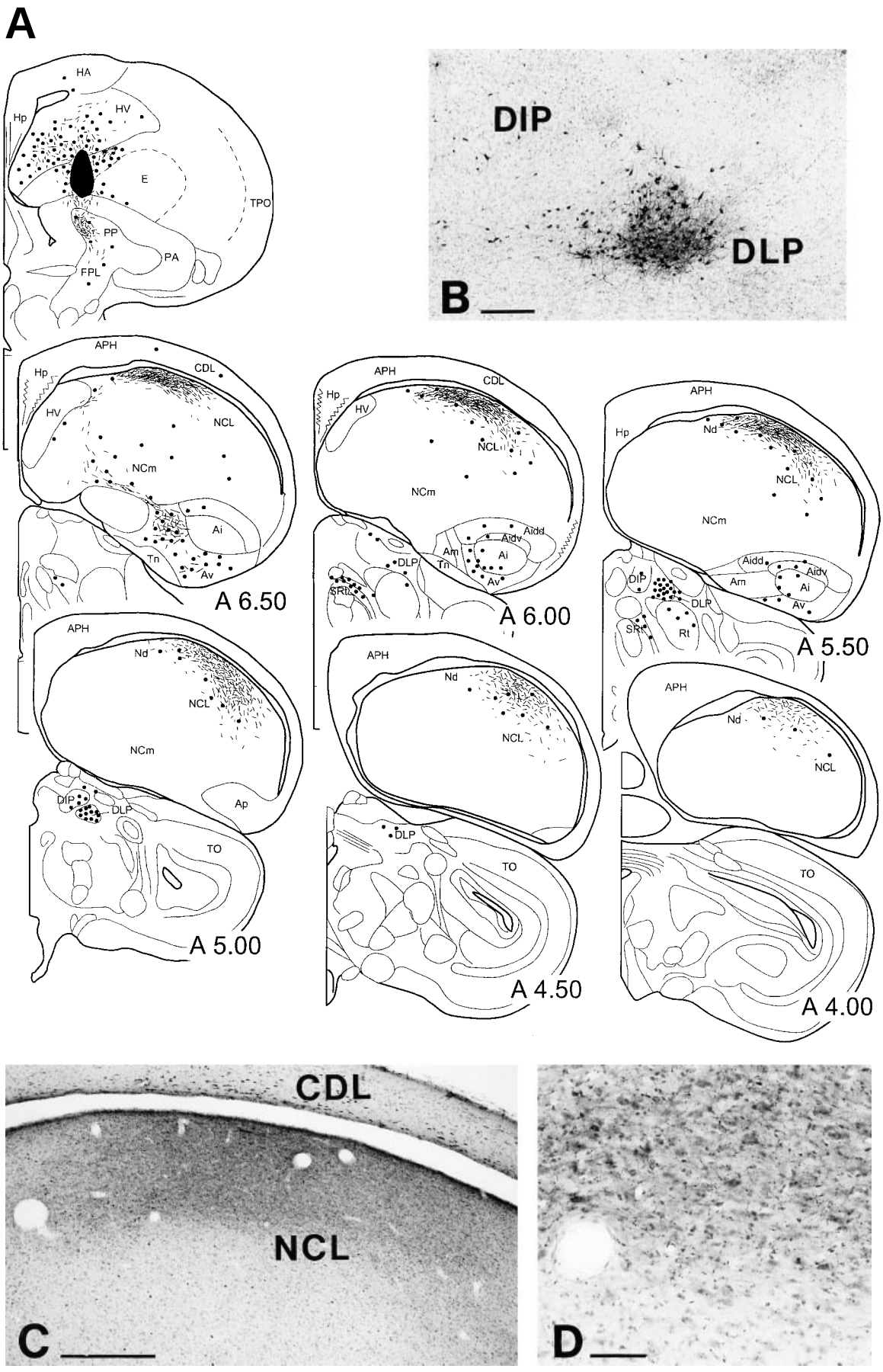
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Figure 11

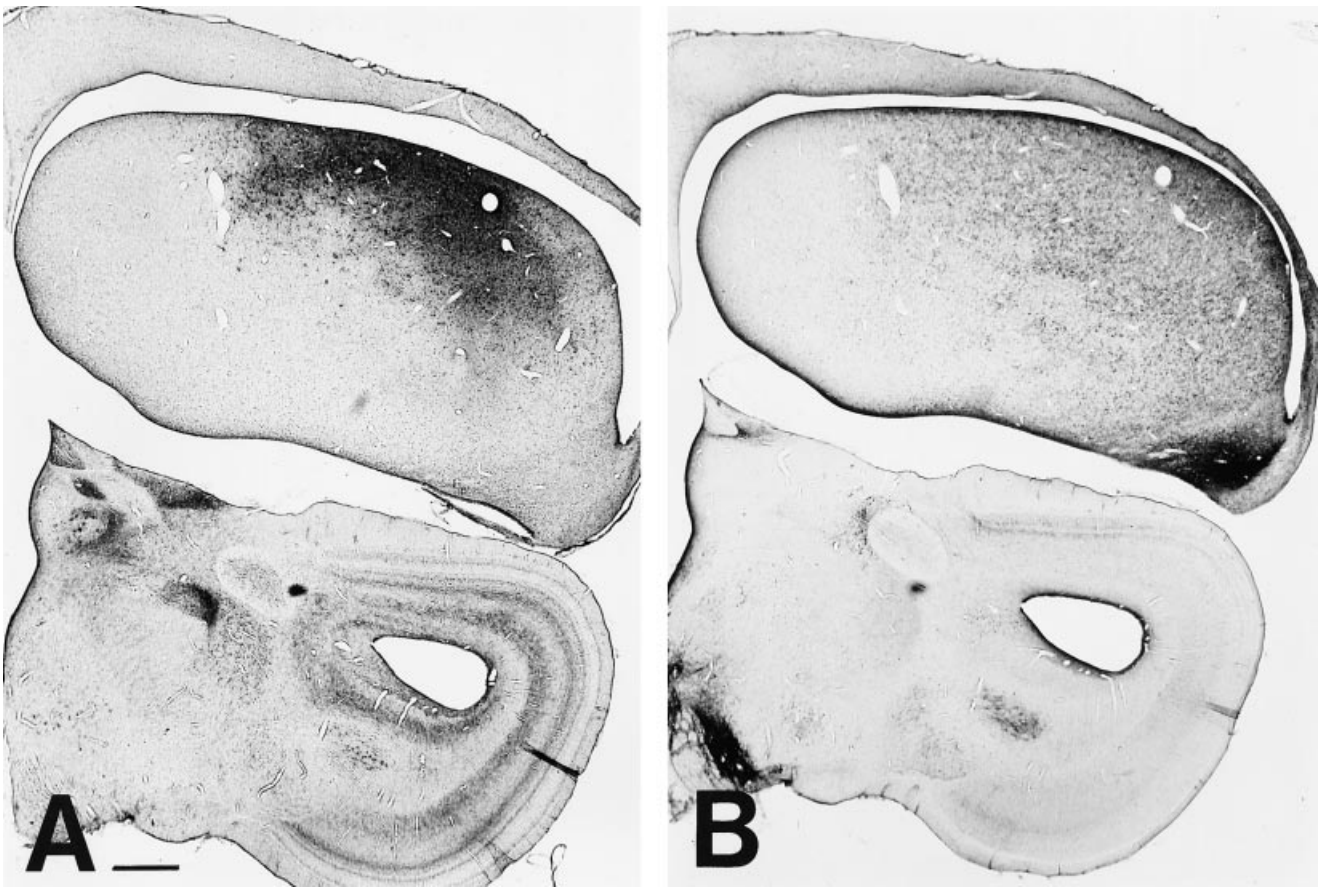

Fig. 12. Photomicrographs illustrating the close correspondence between neostriatum caudolaterale (NCL) projection neurons to the archistriatum and the catecholaminergic innervation of the caudal telencephalon. Cells in **A** were retrogradely labeled after a Cholera Toxin b (CTb) injection into the intermediate archistriatum similar to that shown in Figure 13. **B** shows an adjacent slice from the same animal processed for tyrosine hydroxylase (TH) immunoreactivity. Scale bar = 1 mm.

tum. Other areas that project to the central archistriatum include the caudomedial neostriatum, medial HA, rostral HD and the vallecula, the field L complex as well as cells within NFT and NFL. Strong terminal-like labeling was seen in LPO and medial PA as well as in HV. Descending fibers leave the intermediate archistriatum through the tractus occipitomesencephalicus (OM), from which they eventually split off to provide massive input to the deep layers of the optic tectum. Terminal-like labeling was furthermore seen in the dorsal thalamus, predominantly in the posterior thalamic nuclei DLP, DIP, and SRt, all three of which also contained labeled cell bodies, as well as in the nucleus spiriformis medialis (SPm) and the nucleus intercollicularis (ICo). At midbrain level, terminal-like labeling and retrogradely labelled neurons could be observed in TPc, AVT, and LoC. The OM further descended onto various nuclei in the brainstem (see Zeier and Karten, 1971; Dubbeldam et al., 1997; Davies et al., 1997).

Injections into the posterior archistriatum labeled somata in the mediodorsal HV and along the LFS. The Ap seemed to be reciprocally connected with cells in CDL and APH, as well as the n. accumbens. Within the archistriatal complex, cells in the "limbic" subcomponents, i.e., the nucleus taeniae and Av, were labeled. The Ap was also found to project heavily onto the BNST and tuberculum olfactorium. Descending fibers of the HOM terminated mainly within the lateral hypothalamus (lHy). In the diencephalon, cell bodies were observed in SRt and along the whole track of the HOM. At the level of the midbrain, cells could be found within TPc, AVT, and LoC.

Injections into the paleostriatum augmentatum. Injections into medial and central parts of the paleostriatum augmentatum between A 7.75 and A 9.00 labeled neurons along the complete rostrocaudal extent of NCL and Nd. As illustrated in Figure 15, these cells could be found throughout the whole depth of the NCL, although their number seemed to be highest within or just medially of the tractus archistriatalis dorsalis, at the medial border of the TH-rich caudal neostriatum. A large number of retrogradely labeled cells was seen in the dorsal part of the archistriatum. A smaller bilateral projection furthermore seemed to originate from portions of the anterior archistriatum. In addi-

Fig. 11. Results of a comparatively large (23 nl) Cholera Toxin b (CTb) injection into lateral neostriatum intermedium lmedialis (NIM) which also extended slightly into hyperstriatum ventrale (HV) as shown in **A**. See text for details. **B:** Photomicrograph of retrogradely labeled cells in the thalamus. DLP, nucleus dorsolateralis posterior. **C:** Labeled fibers and cells in the dorsal neostriatum caudolaterale (NCL) at about A 6.00. CDL, corticoidea dorsolateralis. **D:** Detail showing the border of the densest innervation. For abbreviations, see list. Scale bars = 200 μm for B; 500 μm for C; and 50 μm for D.

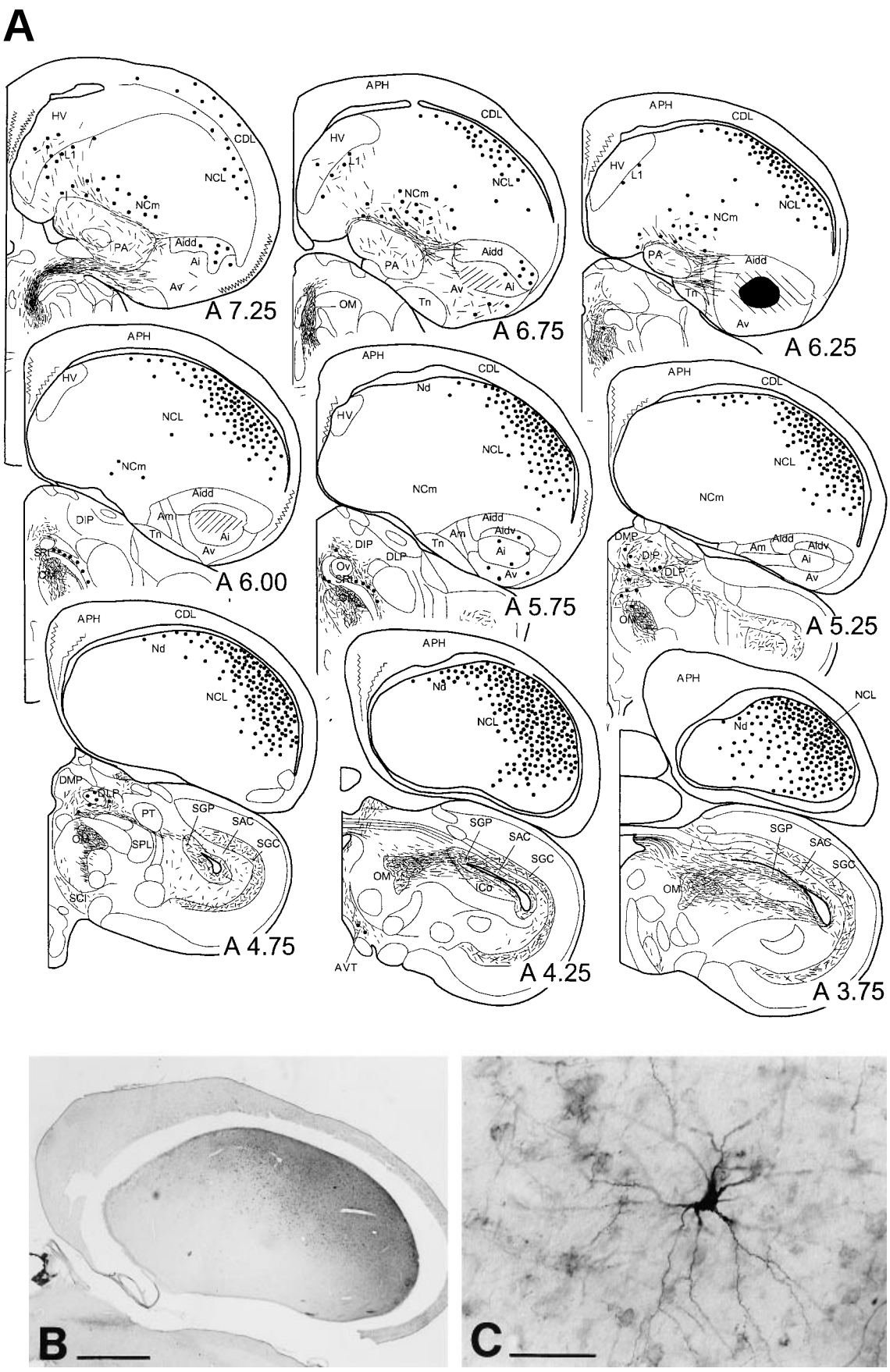

Fig. 13. Results from a large (81 nl) injection of Cholera Toxin b (CTb) into the archistriatum which involved parts of the central and ventral intermediate archistriatum. **A:** Diagrammatic representation of retrogradely labeled projection cells within neostriatum caudolaterale (NCL). **B:** Photomicrograph showing cells in the far caudal NCL. **C:** Retrogradely labeled cell in the NCL following a biotynilated dextran amines (BDA) injection in the intermediate archistriatum colocalized with tyrosine hydroxylase (TH)-immunoreactive fibers. For abbreviations, see list. Scale bars = 1 mm for B; and 50 µm for C.

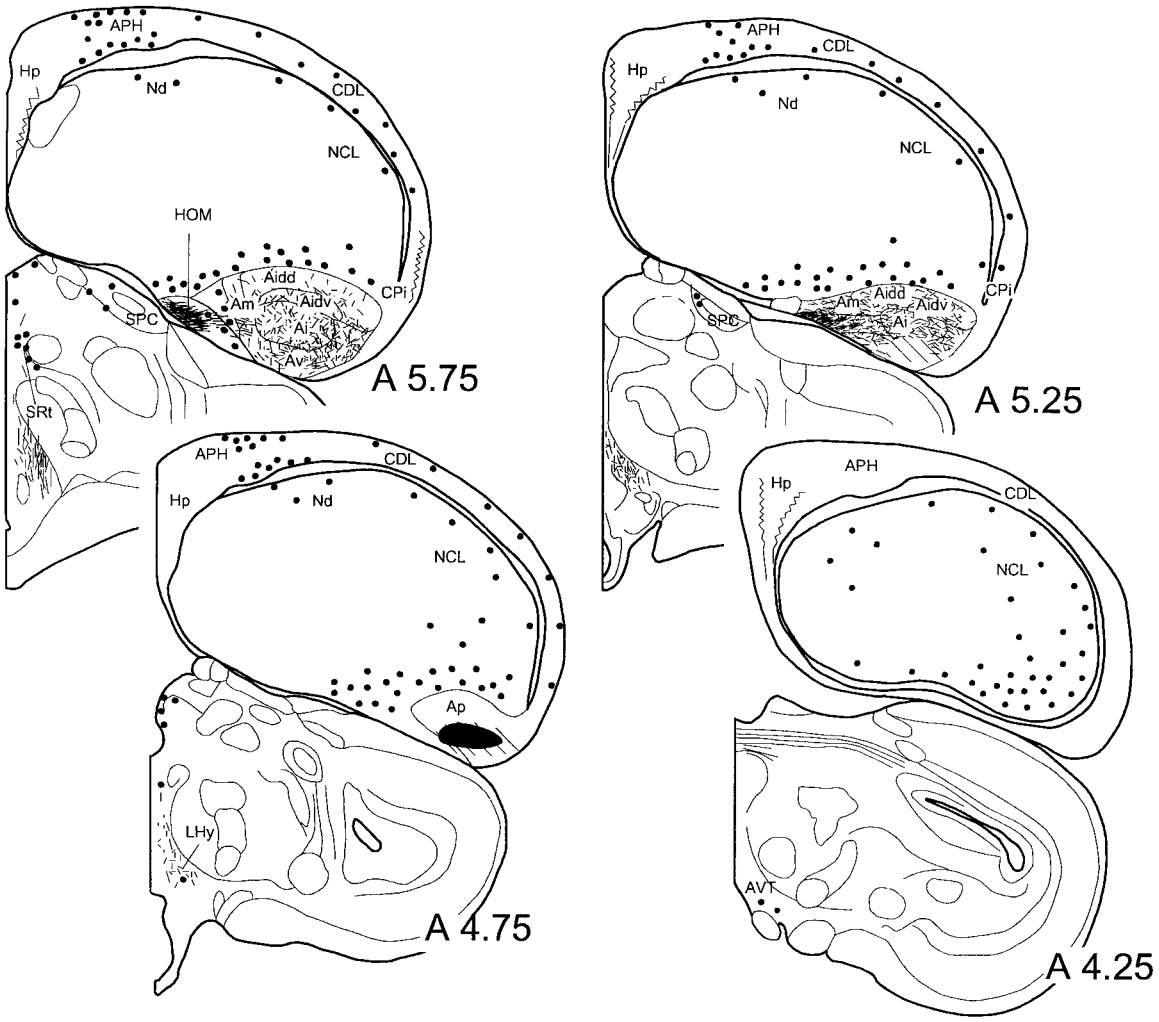

Fig. 14. Schematic representation of labeling in the caudal telencephalon after a deposit of 15 nl Cholera Toxin b (CTb) into the posterior archistriatum. All injections into the archistriatum were placed using a lateral approach. Cells within neostriatum caudolaterale (NCL) project only relative sparsely onto archistriatum posterior (Ap). Their number increases towards the caudal pole of the hemisphere. A strong projection arises from cells immediately dorsal of the archistriatum. This area seems to intersperse between NCL and archistriatum; in contrast to the latter two, it also labels considerably weaker for tyrosine hydroxylase (TH; compare also Fig. 1). For abbreviations, see list.

tion, our injections into PA labeled cells in HV, lateral HD, and the caudal pallium (e.g., NIL, TPO, and CDL). A few cells were also seen along the needletrack in NI, the caudomedial HV, and the NCm. In the thalamus, cells were labeled within the lateral "somatic" area of the dorsal thalamic zone, namely DIP, VIP, and to a lesser extent in DLP, SRt, n. suprarotundus (SpRt), and nuclei of the ansa lenticularis. Sometimes marked neurons were also observed within the ventrointermediate area of the thalamus (VIA) and n. rotundus (Rt) as well as n. triangularis (T). Although labeling within VIA was most likely due to tracer spread into the dorsal pallidum, i.e., PP (Medina and Reiner, 1997), labeling in Rt and T derived from tracer spread into the ectostriatum (Benowitz and Karten, 1976). At the level of the midbrain, AVT and TPc also contained a number of labeled cells.

Injections into the medial lobus parolfactorius. Labeling within NCL after deposits of CTb into medial LPO between A 9.50 and A 11.50 was very similar to that observed after PA injections. Again, retrogradely labeled neurons were distributed diffusely along the medioventral and rostrocaudal extension of NCL, yet cells were predominantly located along the medial border (Fig. 16). This was also true for two cases in which the injection accidentally was centered onto lateral LPO and PA. Regarding a possible rostrocaudal topography of NCL projections to the basal ganglia, we found a relatively larger number of retrogradely labeled neurons projecting to the LPO in caudal NCL, whereas neurons projecting to the PA tended to be located more rostrally and medially. However, as noted above, these projections largely overlapped. Labeling in other areas of the telencephalon included the NIM and HV dorsal to the injection site, medial HA and HD, and the area prehippocampalis (APrH). Many cells were also seen in TPO, CDL, and up to far rostral levels within NFL, but only few in NIL. In the archistriatum, large parts of the Av and Ai were labeled. The projection from the Av seemed to be bilaterally organized. We found that in the thalamus, CTb injections which were centered on medial LPO yielded numerous neurons within n. dorsomedialis

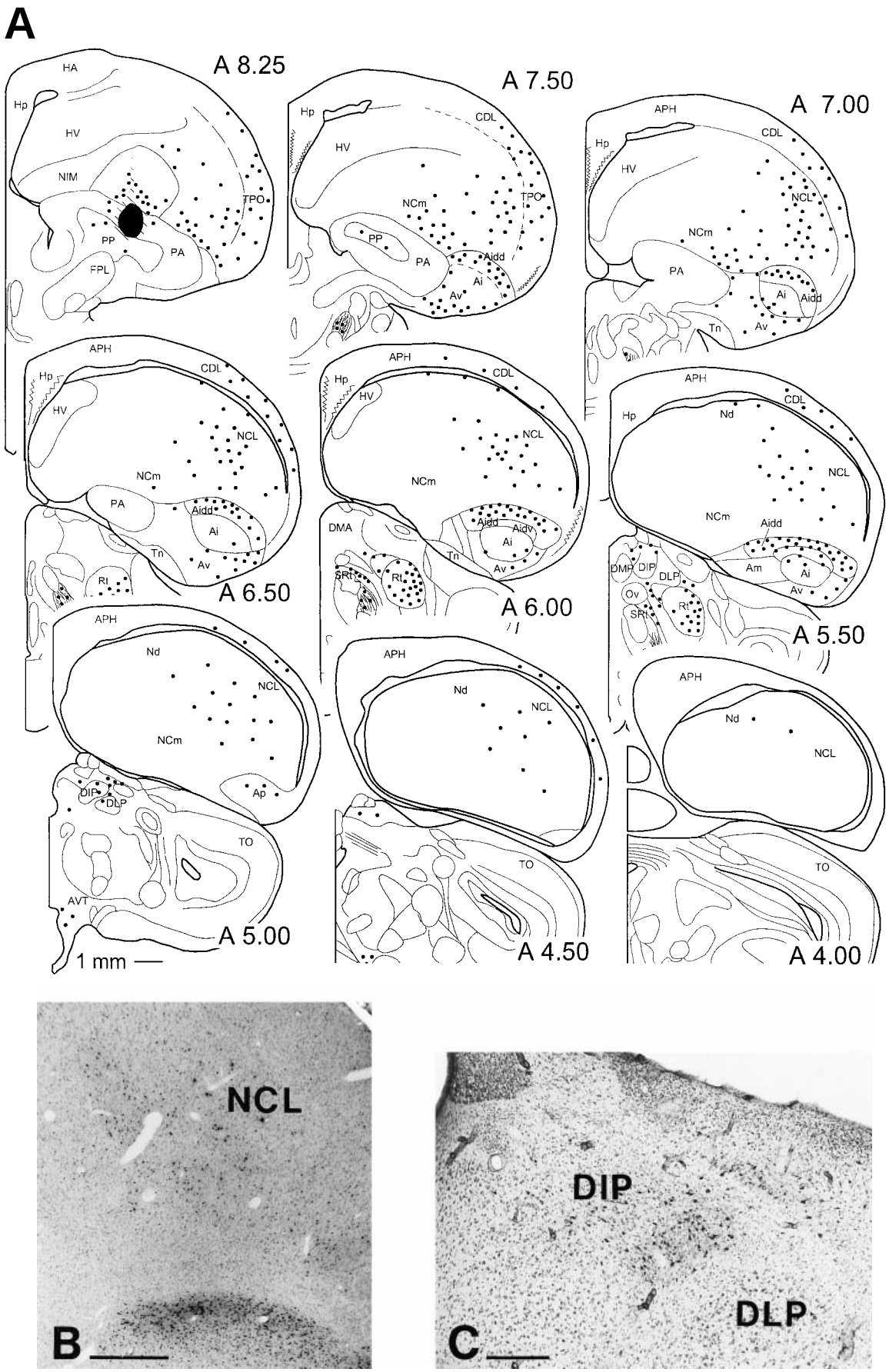
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Figure 15

anterior thalami (DMA) and DMP, and to a lesser extent also in the n. subhabenularis (SHL) and DIP. In the mesencephalon, cells were found in AVT, TPc, and LoC.

DISCUSSION

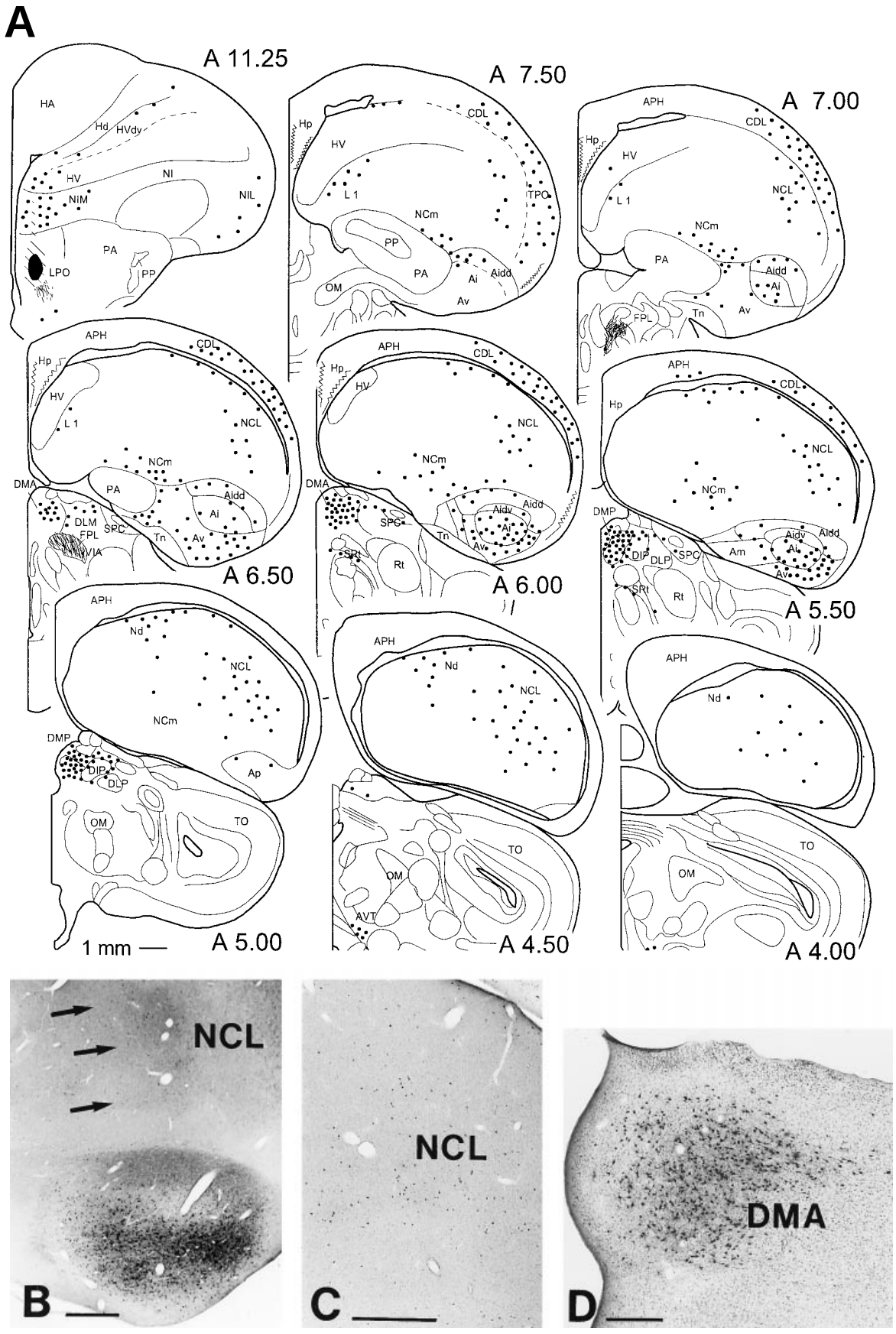
The main results of this study can be summarized as follows: the NCL has reciprocal connections with the secondary sensory areas of all modalities, as well with at least two parasensory areas in the NIM and the deep layers of HV. The afferents from these areas have diffuse and largely overlapping termination fields within NCL (see Fig. 17). These connections are restricted to the plexus of the densest innervation by catecholaminergic and presumably dopaminergic fibers as demonstrated here by TH immunoreactivity. Furthermore, all parts of the so defined NCL project onto the basal ganglia and the archistriatum. The importance of these findings for sensorimotor integration in the avian telencephalon and their possible relevance for the evolution of cortex-equivalent structures will be discussed separately in detail below.

Sensory integration within NCL

All five secondary sensory areas were found to project to NCL. The organization of these pathways conforms with a general pattern of sensory processing in the avian telencephalon (summarized in Veenman et al., 1995b): the primary receptive fields of subtelencephalic input relay the information to adjacent secondary sensory structures, which in turn project to areas of the external pallium. In the case of the tectofugal visual pathway, the ectostriatum is the primary sensory structure (Kondo, 1933; Benowitz and Karten, 1976). From there, intratelencephalic projections lead to the ectostriatal belt (Karten and Hodos, 1970; Watanabe et al., 1985). The present study demonstrates in accordance with Leutgeb et al. (1996) that the NCL is the tertiary telencephalic component of the tectofugal complex. This pattern also holds for the other sensory systems. Caudal IHA and the caudolateral component of HD are the primary sensory areas of the thalamofugal visual pathway (Karten et al., 1973), from where projections lead to HA (Shimizu et al., 1995), which by itself projects to NCL (Shimizu et al., 1995; Leutgeb et al., 1996). More rostrally, somatosensory thalamic fibers terminate in HD/hyperstriatum intercalatus superior (HIS) and IHA (Delius and Bennetto, 1972; Funke, 1989; Wild, 1997) which in turn project to rostral HA (Wild, 1987b). Field L2 is the primary telencephalic area of the auditory system (Wild et al., 1993), which projects to L1 and L3, from where efferents lead to Nd/NCL (Bonke et al., 1979; Wild et al., 1993; Leutgeb et al., 1996). N. basalis is the primary telencephalic area of the trigeminal system (Schall et al., 1986), which projects to NFT (Wild et al., 1985; Wild and Farabaugh, 1996), from where efferents lead to NCL (Wild et al., 1985; Schall et al., 1986; Wild and Farabaugh, 1996). Thus, the NCL is the tertiary telencephalic component of all sensory modalities examined in the present study. Due to this multimodal input and the broad overlap of terminations, the NCL is a true associative forebrain structure. Additionally, parts of the caudal neostriatum may also have access to olfactory information: after injections into the posterior archistriatum, we found a large number of cells in the ventralmost neostriatum overlying the archistriatum. This region has been suggested to be reciprocally connected with the avian piriform cortex and olfactory bulb, which, as their mammalian counterparts, process olfactory information (Reiner and Karten, 1985; Haberly and Bower, 1989; Bingman et al., 1994). In concert with the CPi and limbic archistriatum, this area might thus be concerned with viscerolimbic functions. However, from our combined immunocytochemical and pathway tracing data, it seems that this part of the NC is not a genuine subdivision of the NCL, although it might be ventrally continuous with it. Olfactory information can reach the NCL, nevertheless, via its connections with the HD. In addition to afferents from the visual dorsolateral thalamus (Karten et al., 1973; Güntürkün and Karten, 1991; Güntürkün et al., 1993) and nonspecific input from the mediodorsal thalamus (Bagnoli and Burkhalter, 1983), the HD is also reciprocally connected with the hippocampal formation and the CPi (Casini et al., 1986; Bingman et al., 1994; Shimizu et al., 1995).

The pattern of afferents within NCL might provide clues to the functional architecture of the pigeon's nervous system. The only two pathways which show no or little overlap within NCL are those from the auditory and the trigeminal systems. Indeed, conditioning paradigms have shown that pigeons have severe constraints to associate auditory signals with food reward in an appetitive learning paradigm in which pecks on a key serve as an operant (LoLordo and Furrow, 1976; Delius and Emmerton, 1978). The same animals are rapidly able to associate in a classical conditioning paradigm the very same auditory signals with a mild shock applied to the body (Delius and Emmerton, 1978). Delius and Emmerton (1978) speculated that a granivorous animal such as a pigeon is simply not in need of associating acoustic cues with food objects because grains are mostly silent. However, grains can be quite noisy during pecking due to the direct auditory feedback generated by the impact of the beak on the substrate. Indeed, Delius (1985) could show that pigeons are easily able to learn an auditory tone discrimination in an appetitive paradigm if the acoustic signals are generated by the pecks. Yet, delaying the acoustic feedback by more than 0.5 seconds abolishes learning. Because the n. basalis not only receives trigeminal projections but also some auditory afferents from the lemniscal nuclei (Delius et al., 1979; Schall et al., 1986; Arends and Zeigler, 1986; Wild and Farabaugh, 1996), it is likely that the specialized auditory-trigeminal associations occurring during pecking are directly processed within the basalis system. Indeed, lesions of the n. basalis eliminate the ability to discriminate acoustic signals generated by the animals' own pecks (Schall and Delius, 1991). Thus, it is conceivable that the separation of auditory and trigeminal afferents within NCL is related to the severe constraints of pigeons in associating acoustic and trigeminal stimuli.

Fig. 15. Results following an injection of 28 nl Cholera Toxin b (CTb) into the "somatic" central paleostriatum augmentatum (PA). **A:** Schematic representation of retrogradely labeled cells in the caudal telencephalon. The most abundant labeling can be seen in the dorsal part of the archistriatum and the rostral neostriatum caudolaterale (NCL). See text for details. **B:** Photomicrograph illustrating the location of projection neurons at the medial border of the NCL and within the archistriatum intermedium, pars dorsodorsale (Aidd). **C:** Photomicrograph of labeling in the posterior dorsal thalamus. In addition to labeled neurons within nucleus dorsointermedialis posterior thalami (DIP), cells could often be observed in the ventrointermediate area of the posterior nuclei (VIP), nucleus dorsolateralis posterior (DLP), and nucleus subrotundus (SRt). For abbreviations, see list. Scale bars = 500 μm for B; and 200 μm for C.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AVT
B
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D
NCL
NCL
DMA

Figure 16

Both the tectofugal and the thalamofugal systems project to NCL, but their common area of termination seems limited. This fact might be related to differences in visual field representations between the thalamo- and the tectofugal pathway. The retina of pigeons has two areas of enhanced vision (Galifret, 1968; Binggeli and Paule, 1969). One is the central fovea which looks into the monocular lateral field. The other is the so-called "red field" in the dorsotemporal retina with which the animal views stimuli in the inferior frontal visual field (Güntürkün, 1998). The representation of the red field within the GLd of the thalamofugal pathway is extremly sparse, whereas the central fovea is heavily represented (Remy and Güntürkün, 1991). Thus, the thalamofugal pathway mainly processes stimuli from the lateral rather than the frontal visual field. Accordingly, thalamofugal lesions produce minor deficits when tested with frontal stimuli, but severe deficits when tested with lateral stimuli (Güntürkün and Hahmann, 1998). Contrarily, there is evidence that tectofugal rotundus lesions impair frontal acuity while leaving lateral acuity intact (Güntürkün and Hahmann, 1998). This in turn may be due to the fact that ventral tectal cells, which represent the lower frontal visual field, project heavily onto rotundus, whereas the contribution of dorsal tectal cells to the tectofugal pathway is limited (Hellmann and Güntürkün, 1997). Thus, thalamo- and tectofugal visual pathways in pigeons seem to differentially represent lateral and frontal vision, respectively. Their largely complementary representation within NCL might thus be related to their differential representation of the visual field. Despite the small overlap of the tecto- and the thalamofugal visual fields within NCL, these domains extensively overlap with the trigeminal and the auditory projections, respectively. The large common territory of the tectofugal visual and the trigeminal system might be related to the specialization of the tectofugal pathway to the lower and frontal visual field (Hellmann and Güntürkün, 1997; Güntürkün and Hahmann, 1998), which within the egocentric space overlaps with trigeminal inputs from the beak. Thus, a common sensory focus of both systems could create a need for common coding which might be accomplished by extensive areas of terminal overlap in an associative structure such as NCL. The large overlap between thalamofugal visual and auditory domains might be similarly interpreted. As outlined above, the thalamofugal pathway in pigeons is oriented laterally (Remy and Güntürkün, 1991; Güntürkün and Hahmann, 1998). Like most other birds, pigeons fixate distant objects laterally with their central fovea (Blough, 1971; Martinoya et al., 1981; Bischof, 1988), because their lateral monocular acuity is about twice as high as their frontal monocular one (Hahmann and Güntürkün, 1993; Güntürkün and Hahmann, 1994). Thus, the thalamofugal visual system is more related to distant visual objects and might therefore need common processing with audition, which also is a distance sense.

Connections of the NCL with the NIM and ventral hyperstriatum

Our retrograde and anterograde tracing experiments have suggested the existence of two different, albeit continuous, sources of afferents from NIM to NCL. Whereas the NIMl projection innervates the Nd region and the laterally adjacent parts of the NCL, afferents from NIMm terminate abundantly throughout the caudalmost NCL. Both areas receive differential input from the dorsal thalamus (Kitt and Brauth, 1982; Gamlin and Cohen, 1986; Wild, 1987a, 1994; Metzger et al., 1996; present study) and differ in their cytoarchitectonic characteristics (Rehkämper et al., 1985). The NIMl has been shown to receive visual and somatosensory information from telencephalic areas (Funke, 1989; Wild, 1987b, 1994; Shimizu et al., 1995; present study). Because we found retrogradely labeled cells in L1 and L3 after injections into NIMl, this structure probably also integrates auditory information. In addition, polysensory input reaches the NIMl via DLP (Kitt and Brauth, 1982; Gamlin and Cohen, 1986; Korzeniewska and Güntürkün, 1990; present study).

The NIMm, as defined here, resembles in its location and connectivity the mediorostral neostriatum/hyperstriatum ventrale (MNH) of the chick, which has been extensively studied in the context of imprinting (e.g., Metzger et al., 1996; Gruss and Braun, 1996; Bredenkötter and Braun, 1997; for review: Scheich, 1987). Injections into NCL which labeled cells in NIMm also always produced cells in the overlying HV, suggesting a similar translaminar organization of this area in the pigeon, as is characteristic for the MNH. Data on the connections of either the MNH or NIMm with telencephalic regions are very limited (Metzger et al., 1996). Our results indicate that the NIMm, like the NIMl, might also receive input from the visual and somatosensory areas of the Wulst. Thalamic input to NIMm originates mainly in the DMP and to a much lesser extent in the DMA, a situation which is reversed for the MNH of chicks (Kitt and Brauth, 1982; Wild, 1987a; Metzger et al., 1996; present study). The sensory properties of these afferents are not entirely clear, but the nuclei of the dorsomedial thalamus receive input from the hypothalamus and tractus solitarius (Berk and Butler, 1981; Berk and Hawkin, 1985; Arends et al., 1988; Wild et al., 1990) and in turn project to the viscerolimbic striatum and CPi (Kitt and Brauth, 1982; Wild, 1987a; Bingman et al., 1994; Veenman et al., 1995a, 1997; Metzger et al., 1996). Furthermore, the NIMm and to a lesser extent also the NCL of pigeons display strong immunoreactivity for the calcium-binding protein parvalbumin (S. Kröner, unpublished observations), as has previously been shown for the MNH of chicks (Braun et al., 1991a). Parvalbumin is associated with fast spiking gamma aminobutyric acid (GABA)ergic neurons (DeFelipe et al., 1989; Kawaguchi and Kubota, 1993), and in songbirds it is characteristic of nuclei displaying high metabolic activity, notably all nuclei of the vocal motor system (Braun et al., 1985, 1991b). As outlined above, both areas of the NIM appear capable of multisensory processing. This draws attention to our observation that their afferents terminate predominantly

Fig. 16. Projections to the limbic medial striatum. **A:** Results of a 22-nl injection of Cholera Toxin b (CTb) into the medial lobus parolfactorius (LPO) with no obvious tracer spread into nucleus accumbens (AC) or lateral LPO. Labeling in the caudal telencephalon was complementary to that observed after injections into the somatic parts of the basal ganglia. Most abundant labeling was seen in the ventral part of the intermediate archistriatum and the caudal neostriatum caudolaterale (NCL). **B:** Photomicrograph showing the location of NCL projection neurons (arrows) at the medial border of the tractus archistriatalis dorsalis as well as in architriatum intermedium, pars centrale (Ai) and archistriatum intermedium, pars ventrale (Av) in a slice double-labeled for tyrosine hydroxylase (TH). **C:** Retrogradely labeled cells in the posterior neostriatum cluster at the medial extent of the NCL. **D:** Photomicrograph of retrogradely labeled thalamic neurons within nucleus dorsomedialis anterior thalami (DMA). For abbreviations, see list. Scale bars = 500 μm for B, C; 200 μm for D.

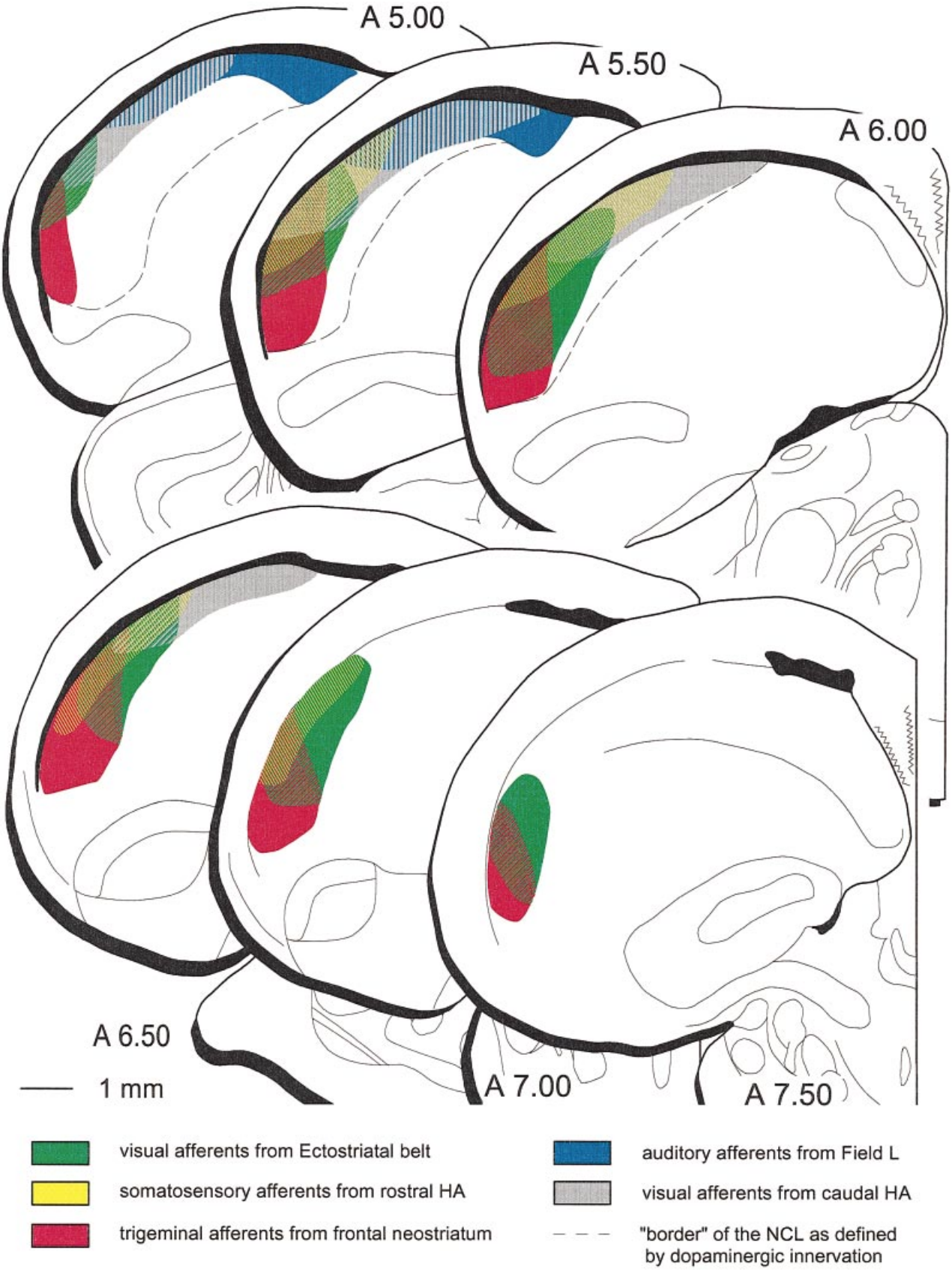

Fig. 17. Schematic representation of terminal fields within neostriatum caudolaterale (NCL) showing the large overlap of afferents from secondary sensory areas. Note that the afferents from the presumed parasensory areas within neostriatum intermedium medialis (NIM), which occupy large parts of the caudalmost NCL are not included in this figure. See text for details.

in those aspects of the NCL which receive relatively little input from secondary sensory regions (compare Fig. 17). Although it is possible that other telencephalic areas which send projections to NCL (e.g., HA or NFT) are also parasensory in nature (Schall et al., 1986; Deng and Wang, 1992, 1993; Wild and Farabaugh, 1996), the nuclei within NIM clearly are a step progressed in an assumed hierarchy of stimulus processing, as they, like the NCL, receive their afferents from secondary sensory structures. It thus seems that parasensory inputs from NIM to the NCL complement the pattern of multimodal integration.

It should be noted that our injections into NCL also labeled cells in the HV which, based on their location, resemble the intermediate and medial part of the hyperstriatum ventrale (IMHV), another area which in the chick has been extensively studied in the context of imprinting and memory formation (Bradley et al., 1985; Davies et al., 1988; review by Horn, 1998). Although we did not target these cells in the anterograde tracing experiments, results from the study of Shimizu et al. (1995) suggest that afferents from the HV also terminate abundantly throughout the caudalmost neostriatum (Shimizu et al., 1995).

Projections to the archistriatum

We found a continous band of cells in the NCL which project in a topographically ordered manner onto most parts of the intermediate archistriatum. In addition, the posterior archistriatum receives a weak projection from cells in the caudal- and dorsalmost aspects of the NCL. The connections with the intermediate archistriatum are reciprocally organized (Leutgeb et al., 1996; Davies et al., 1997; Metzger et al., 1998; present study) and bilaterally projecting cells in the Av provide a means of interhemispheric comparison (Wild and Farabaugh, 1996; Metzger et al., 1998; present study). Functionally, the avian archistriatum has generally been divided into two main subdivisions (Zeier and Karten, 1971; Davies et al., 1997; Dubbeldam et al., 1997). These are a somatic sensorimotor part which in the pigeon comprises parts of the anterior and intermediate archistriatum (Aa, Ai, Aidd, Aidv), and a viscerolimbic division that includes the posterior and medial archistriatum, as well as the ventral parts of the intermediate archistriatum (Ap, Am, Av). The sensorimotor archistriatum receives widespread afferent projections from higher order sensory areas of the telencephalon (e.g., Ritchie, 1979; Wild et al., 1985, 1993; Shimizu et al., 1995) and is involved in high-level motor control (Zeier, 1971; Knudsen et al., 1995) and memory function (Knudsen and Knudsen, 1996). Furthermore, via the OM, the archistriatum projects to premotor areas of the brainstem (e.g., reticular formation and lateral pontine nuclei) in all birds (Zeier and Karten, 1971; Wild et al., 1985, 1993; Davies et al., 1997; Dubbeldam et al., 1997; present study) and to some specific groups of brainstem motoneurons involved in respiration and vocalization in songbirds (Nottebohm et al., 1976; Wild, 1993). The limbic portion of the archistriatum, on the other hand, is considered homologous to the mammalian amygdala (Zeier and Karten, 1971; Davies et al., 1997; Dubbeldam et al., 1997). It seems to be crucially involved in such viscerolimbic functions as agonistic behavior and homeostasis. (e.g., Cohen, 1975; Ramirez and Delius, 1979; Lowndes and Davies, 1995). The archistriatum's functional segregation is reflected in the extratelencephalic projections via the OM or HOM, respectively (Zeier and Karten, 1971; Davies et al., 1997; Dubbeldam et al., 1997), and in its connections with limbic or somatic striatum (Veenman et al., 1995b; present study). Whereas the main output from the NCL might be directed to the sensorimotor part of the archistriatum (Leutgeb et al., 1996), especially the caudalmost NCL also appears to be capable of modulating the amygdaloid division of the archistriatum (present results). The very large number of neurons from NCL that project to the archistriatum, and the close correspondence between the position of these output neurons and the densest catecholaminergic innervation, underline the importance of this projection for an understanding of the functions of the NCL. In addition, we believe that the projection from the caudal neostriatum to the archistriatum might serve as a criterion for the delineation of NCL. Given the fact that injections into the archistriatum labeled a continuous band of cells that extended from the ventrolateral NCL up to Nd, we think it reasonable to consider Nd the "auditory subcomponent" of NCL. This view is also supported by the facts that the Nd shares afferents with the adjacent NCL from areas other than the field L complex, shows the same dense dopaminergic innervation, and shows a similar organization of efferent connections other than those to the archistriatum.

Projections to the basal ganglia

The connectivity, neurotransmitter content, and cytoarchitecture of the avian basal ganglia are highly similar to that in mammals (Karten and Dubbeldam, 1973; Reiner et al., 1984; Veenman and Reiner, 1994; Veenman et al., 1995b). In mammals, corticostriatal inputs from association, sensorimotor, and limbic cortices project in a segregated manner onto three distinct striatal regions referred to as associative, sensorimotor, and limbic striatal territories (Parent, 1990; Parent and Hazrati, 1995). These corticostriatal inputs provide the basal ganglia with exteroceptive sensory information as to the location of objects in space, interoceptive sensory information on relative body position in space, and neural feedback and feedforward information on ongoing and impending body movements (McGeorge and Faull, 1989; Alexander et al., 1990; Romo et al., 1992; Schultz et al., 1992; Aldridge and Berridge, 1998). Based on its palliostriatal connections, a similar functional segregation has recently been suggested for the avian striatum (Veenman et al., 1995b): ventral striatal structures such as the AC, the BNST, and olfactory tubercle constitute the "limbic" parts of the avian striatum. These "limbic" parts also include the medial LPO and lateralmost PA. The remaining dorsal striatal parts (lateral LPO, medial PA), on the other hand, are considered sensorimotor in nature. We show here that all parts of the NCL project to the ventral and dorsal aspects of the striatum. Our combined retro- and anterograde tracing experiments suggest a rostrocaudal topography of these projections, with caudal parts of NCL projecting predominantly onto limbic medial LPO, and more rostral parts of NCL projecting to lateral LPO and mainly medial PA (Fig. 18). The projection onto the limbic striatum had already been indicated by the study of Veenman et al. (1995b), but as their injections also involved the CPi and Ap (see their Fig. 18 and Discussion), which also project heavily onto the limbic parts of the avian basal ganglia (Bingman et al., 1994; Veenman et al., 1995b; present study), until now the existence of this connection from the NCL was not entirely clear. In addition to this direct pathway, the NCL is also capable of influencing the ventral basal ganglia via its connection with the limbic archistriatum. The ventral striatum of mammals receives input from limbic cortical

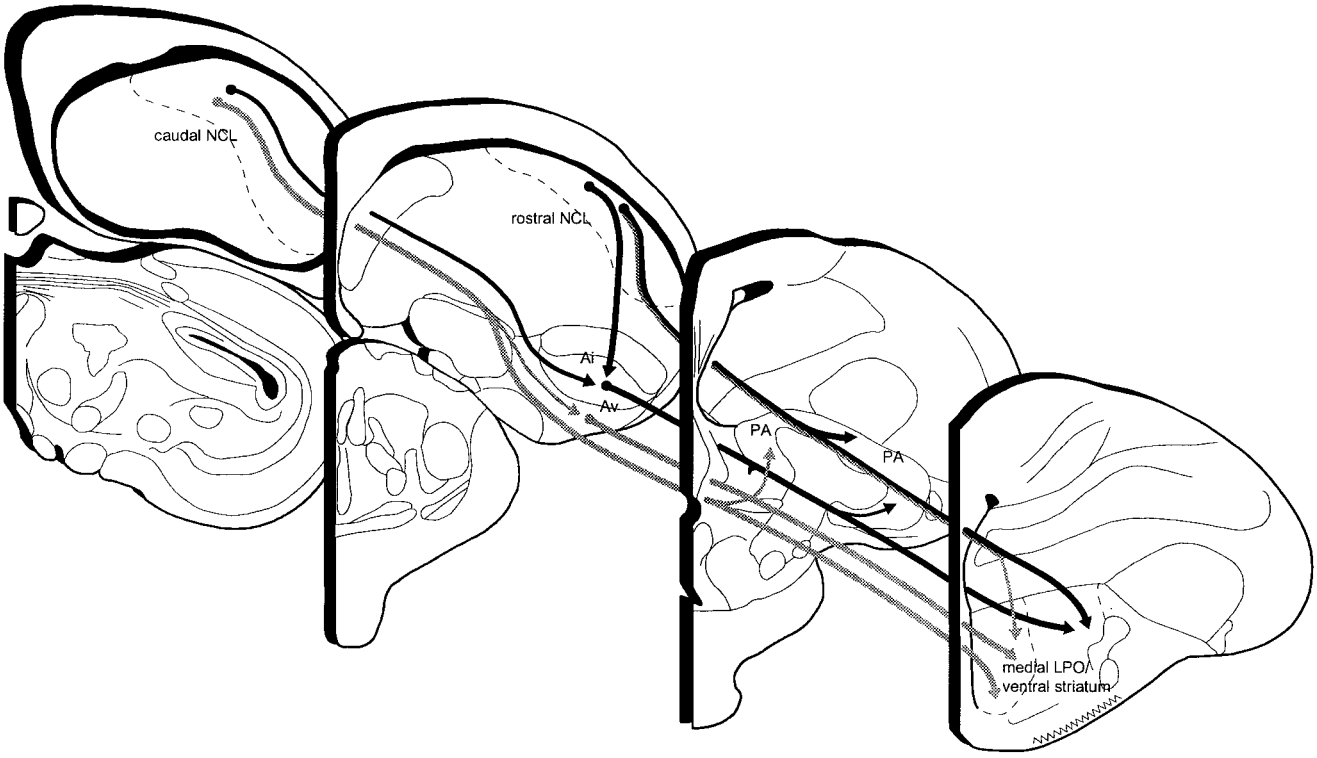

Fig. 18. Diagrammatic illustration of the organization of presumed "limbic" (grey) and "somatic" (black) pathways from the neostriatum caudolaterale (NCL) to the archistriatum and the basal ganglia. All parts of the NCL send projections to both limbic and somatomotor areas, but with a complementary rostral to caudal topography (see text for details and compare Figs. 15 and 16). The relative contribution of the caudal and rostral NCL to these pathways is indicated by the width of the arrows. In addition to direct connections, indirect pathways exist, as limbic and somatomotor parts of the archistriatum also project to corresponding areas within the basal ganglia. For abbreviations, see list.

regions such as hippocampus, cingulate cortex, amygdala, and piriform cortex (McGeorge and Faull, 1989; Alexander et al., 1990), and similar projections have been shown for the avian homologues of these structures (Bingman et al., 1994; Veenman et al., 1995b). In mammals, a further prominent input to the ventral striatum originates in the frontal cortex (Sesack et al., 1989; Alexander et al., 1990; Berendse et al., 1992), and particularly the prefronto-accumbal network plays a crucial role in motivated behavior (Apicella et al., 1991; Schultz et al., 1992; Floresco et al., 1997). The demonstration of a projection from caudal NCL onto the AC thus further strengthens the notion that the NCL might be functionally equivalent to the PFC (Veenman et al., 1995b; present study). As in mammals, this projection might provide the sensory information required, e.g., for the evaluation of appetitive and aversive stimuli. In addition to the projection upon limbic striatum, we found a prominent projection onto large parts of PA and lateral LPO which comprise the somatomotoric divisions of the avian striatum (Veenman et al., 1995b), providing the NCL with a further direct pathway for movement initiation. It is unclear why the projection from NCL to the somatic PA was not described by Veenman et al. (1995b), but it seems possible that this reflects differences in the sensitivity of the different tracers used, or, more likely, that their injections into PA were not centered on those regions in which we found the most abundant anterograde labeling, namely the caudal aspects of the central and lateral PA (compare their Figs. 5 and 6 with Figs. 2 and 15 of the present study).

The palliostriatal projections form asymmetric and probably excitatory synapses with spiny striatal neurons (Veenman and Reiner, 1996), a situation comparable to that in mammals (Dube et al., 1988). Based on these and similar findings, large parts of the external pallium, including the NCL and the archistriatum, have been compared with a subpopulation of corticostriatal projection neurons from layer III and V in the rat (Zeier and Karten, 1971; Akintunde and Buxton, 1992; Cowan and Wilson, 1994; Veenman et al., 1995b). In sum, the NCL is positioned to amalgamate sensory inputs from all modalities and to relay them to the sensorimotor division of the basal ganglia, providing the latter with information that has been further processed and integrated with input from other modalities.

Comparison with vocal control pathways in songbirds

In songbirds, much work has focused on the pathways that control the acquisition and production of learned song. Within oscines, the forebrain vocal system comprises two major pathways that converge on the same premotor nucleus of the archistriatum. The two pathways diverge from a nucleus in the caudolateral neostriatum, the "high vocal center" (HVC, Nottebohm et al., 1976, 1982). The main descending vocal motor pathway leads from the HVC to the robust nucleus of the archistriatum (RA), which in turn projects onto mesencephalic and medullary nuclei

involved in vocalization (Nottebohm et al., 1976, 1982; Bottjer et al., 1989; Vates et al., 1997). HVC also projects to RA by a second pathway that involves nuclei in the anterior forebrain. This circuit sequentially connects HVC, area X of the LPO, the dorsolateral thalamus, the magnocellular nucleus of the anterior neostriatum (MAN), and RA (Bottjer et al., 1989; Vates et al., 1997). Auditory input is thought to reach both major pathways of the vocal system via HVC and the adjacent "shelf" region, which receive auditory information from the field L complex and associated regions of the caudal forebrain (Kelley and Nottebohm, 1979; Fortune and Margoliash, 1995; Vates et al., 1996). In nonsongbirds, the projection from field L 1 and L3 to the Nd/NCL is similar to this ascending auditory pathway in oscine songbirds (Wild et al., 1993; present study), whereas the projection from NIMl to the Nd/NCL has been compared with another polysensory projection upon HVC which arises from the nucleus interfacialis (Nottebohm et al., 1982; Wild, 1994; Fortune and Margoliash, 1995). The present demonstration of a prominent input from NIMm to Nd/NCL suggests a correspondence of this pathway with yet another ascending projection onto HVC: in oscine songbirds, MAN shares a similar location in the intermediate neostriatum with the NIM. The MAN can also be divided into a lateral (lMAN) and a medial (mMAN) part which receive differential input from the medial portion of the dorsolateral thalamus (DLM) and the DMP, respectively (Bottjer et al., 1989; Johnson et al., 1995; Foster et al., 1997; Vates et al., 1997), thus resembling the thalamic projections to NIMl and NIMm (Kitt and Brauth, 1982; Wild, 1987a; present study). The mMAN then gives rise to a projection onto HVC and the adjacent "shelf" region (Nottebohm et al., 1982; Fortune and Margoliash, 1995; Vates et al., 1996, 1997; Foster et al., 1997). A similar recursive pathway through the anterior forebrain also exists in budgerigars: the central nucleus of the lateral neostriatum (NLc) integrates information from other forebrain nuclei and relays it to the premotor neurons of the archistriatum (Brauth et al., 1994; Striedter, 1994; Durand et al., 1997). It has previously been suggested that the HVC complex, as might be true for the NLc of parrots, is concerned not only with translating auditory signals into vocal output, but with the integration of multimodal inputs, and that the song system arose from an elaboration of pathways generally present in all birds (e.g., Wild, 1994; Margoliash et al., 1994). The fact that the shelf region adjacent to HVC shares the afferent inputs of HVC (Fortune and Margoliash, 1995; Vates et al., 1996; Foster et al., 1997) further strengthens the notion that HVC represents a specialized nucleus for the control of learned song, whereas neural populations in the adjacent neostriatum might be concerned with other aspects of multisensory integration and motor control. However, judging from the presently available data, important differences seem to exist: the HVC of Passeriformes, or NLc of parrots, respectively, do not receive similarly abundant sensory input as described for NCL (e.g., Hall et al., 1993; Brauth et al., 1994; Striedter, 1994; Fortune and Margoliash, 1995; Leutgeb et al., 1996; present study). Furthermore, in pigeons, the NCL and the archistriatum have direct reciprocal connections with all sensory and parasensory areas investigated here, and in addition both project onto the striatum (Veenman et al., 1995b; present study).

Comparison with mammalian prefrontal cortex

The PFC of mammals is actually not a single functional region but, rather, a group of anatomically and functionally heterogenous areas (e.g., Goldman-Rakic, 1987). It is commonly thought to involve the dorsolateral PFC, as well as the orbitofrontal and anterior cingulate cortices (Walker, 1940; Akert, 1964; discussed in Preuss, 1995; Condé et al., 1995). These areas participate to different extents in the complex cognitive, limbic, and premotor functions that the PFC subserves, depending on their respective afferent and efferent connections (Sesack et al., 1989; Pandya and Yeterian, 1990). Thus, in primates, deficits resulting from damage to the lateral frontal region involve mainly attentional, temporal, and integrative functions and are different from changes relating to emotion following orbitofrontal, and motivational changes following medial frontal damage (summarized in Fuster, 1989). Sensory input reaches the PFC via a set of interconnected pathways (for reviews: Jones and Powell, 1970; Pandya and Yeterian, 1990). The primary sensory area of each modality projects first to an adjacent area in parietal, occipital, or temporal cortex. This is the beginning of a sequential order of cortical areas that make up a pathway for that modality. Each area in the sequence projects not only to the next in line but also to a discrete area of the frontal cortex, which in turn reciprocates by sending fibers back to the projecting area. The fields that constitute the third link in each of the three pathways, namely, parietal area 7 (somatic), temporal area 22 (auditory), and inferotemporal area 21 (visual), project to the prefrontal cortex and, in addition, to the cortex in the dephts of the superior temporal sulcus, which constitutes another multimodal area. Although the termination fields show considerable overlap, especially around the principal sulcus of primates, a strong topography of these afferents exists, resulting in a distinct pattern of connections for each of the subdivisions of PFC (primates: Jones and Powell, 1970; Pandya and Yeterian, 1990; rodents: Condé et al., 1995; Reep et al., 1996).

Taken together, the organization of sensory input to the NCL strongly resembles the pattern described above for mammalian PFC (Leutgeb et al., 1996; present study). In addition, it is reciprocally connected with the avian homologue of the amygdala (present study), a connection which is also characteristic for mammalian PFC (Sesack, et al., 1989; Barbas and DeOlmos, 1990; Condé et al., 1995; Reep et al., 1996), and projects to most parts of the somatic and limbic striatum, as well as the sensorimotor archistriatum (cf. Fig. 19; Veenman et al., 1995b; Leutgeb et al., 1996). Furthermore, the NCL and PFC share a dense dopaminergic input (Divac and Mogensen, 1985; Waldmann and Güntürkün, 1993; Divac et al., 1985, 1994; Wynne and Güntürkün, 1995), and a functional importance for processes which serves executive functions (working memory: Mogensen and Divac, 1982, 1993; Gagliardo et al., 1996, 1997; Güntürkün, 1997; behavioral flexibility: Hartmann and Güntürkün, 1998; behavioral inhibition: Güntürkün, 1997). With regard to memory functions, it has been proposed that the PFC performs a unitary function, that of holding information gathered by the other association cortices "on-line" in short-term memory (Goldman-Rakic, 1987; Kimberg and Farah, 1993). Judging from the anatomical data and the behavioral studies cited above, the NCL seems well capable of occupying the position of such a central excecutive in the avian brain.

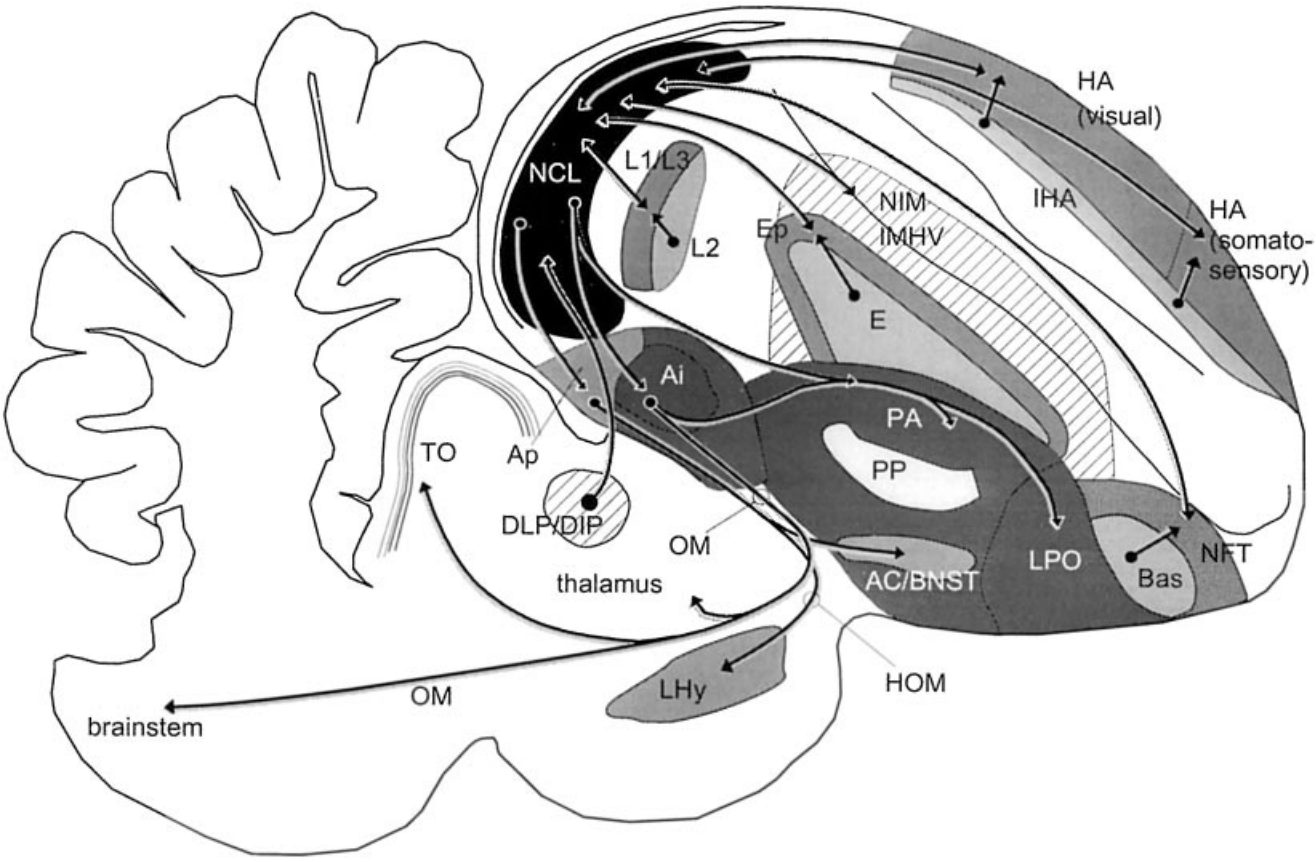

Fig. 19. Diagrammatic summary of the circuitry in which the NCL participates as it emerges from this study. The neostriatum caudolaterale (NCL) is reciprocally connected with the secondary sensory of all modalities as well as at least two parasensory areas. It projects to the avian equivalents of the amygdala (Ap, Av) and premotor cortex (Ai), as well as limbic and somatic parts of the avian striatum, which taken together by means of their long descending projections, exert control over limbic and motoric centers in the diencephalon, midbrain, and brainstem. For abbreviations, see list.

However, at least one important difference hampers comparisons between NCL and PFC: the afferents from the mediodorsal (MD) nucleus of the thalamus serve as a common hallmark for the delination of the PFC across mammalian species (Rose and Woolsey, 1948; Akert, 1964; Preuss, 1995). Thalamic afferents to the NCL arise mainly from DLP and surrounding structures. DLP, however, is very likely not the avian version of mammalian MD. Based on its afferents and electrophysiological properties, DLP was suggested to be equivalent to the posterior complex of nuclei and especially its suprageniculate component (Korzeniewska, 1987; Korzeniewska and Güntürkün, 1990). Like the posterior nuclei, DLP is dominated by afferents from the vestibular nuclei (mammals: Mickle and Ades, 1954; birds: Wild, 1988; Korzeniewska and Güntürkün, 1990), dorsal column nuclei (mammals: Feldman and Kruger, 1980; Berkley et al., 1986; birds: Funke, 1989; Wild, 1989; Korzeniewska and Güntürkün, 1990), superior colliculus (mammals: Hicks et al., 1986; Katoh and Benedek, 1995; birds: Gamlin and Cohen, 1986; Korzeniewska and Güntürkün, 1990), and reticular formation (mammals: Hicks et al., 1986; birds: Korzeniewska and Güntürkün, 1990). Amygdalar or hypothalamic afferents to mammalian posterior thalamic nuclei (Jones, 1985) or avian DLP (Korzeniewska and Güntürkün, 1990) have not been reported. Contrary to this pattern, mammalian MD is reported to receive, among others, afferents from the amygdaloid complex, diagonal band of Broca, and different hypothalamic and preoptic structures (Siegel et al., 1977; Sapawi and Divac, 1978; Velayos and Reinoso-Suarez, 1982; Irle et al., 1984; Russchen et al., 1987; Cornwall and Phillipson, 1988; Groenewegen, 1988). Based on this evidence, any general connectional similarity between MD and DLP could be denied. This view results from a comparison between DLP and the whole MD. If, however, DLP is compared with only lateral MD (rats: paralamellar MD portion, Cornwall and Phillipson, 1988; Groenewegen, 1988; cats: intermediate and lateral MD component, Velayos and Reinoso-Suarez, 1982; monkeys: parvocellular and multiform lateral MD portion, Russchen et al., 1987), the picture changes. The lateral MD portion does not receive afferents from the amygdala but is reached by inputs from vestibular nuclei, superior colliculus, and reticular formation. It thus resembles the pigeon's DLP in many aspects. It is the lateral portion of MD in cats and monkeys which heavily projects onto the dorsolateral component of prefrontal cortex (Markowitsch and Pritzel, 1979; Giguere and Goldman-Rakic, 1988; Ray and Price, 1993), which is known to be of prime importance in delay tasks. The paralamellar MD in rats is innervated by deep layers of superior colliculus and projects to medial precentral cortex (Groenewegen, 1988), an area which has been

compared with the frontal eye field in the monkey (Reep, 1984), a caudal portion of prefrontal cortex (Fuster, 1989; Pandya and Yeterian, 1990). But despite these similarities between lateral MD of mammals and avian DLP, important differences also exist. For example, the pigeon's DLP receives a prominent innervation by the cuneatus-gracilis complex and consequently the majority of neurons in this structure respond to somatosensory stimuli either as uni-, bi-, or multimodal units (Korzeniewska and Güntürkün, 1990; Wild, 1994), which is clearly different from the anatomical and physiological pattern found in lateral MD. Thus, at the present state of knowledge, the initial suggestion of Korzeniewska and Güntürkün (1990) that the DLP is equivalent to the mammalian posterior complex of nuclei and not to MD still seems to be the most valid concept. Nevertheless, the pigeon's DLP might serve functions similar to MD, because DLP lesions were shown to disrupt working memory tasks (Güntürkün, 1997). Veenman et al. (1997) have suggested that DLP might be homologous to the intralaminar nuclei in mammals. In our view, this seems not very likely because the mammalian intralaminar nuclei receive extensive afferents from medial hypothalamus, preoptic area, lateral septum, bed nucleus of the stria terminalis, ventral subiculum, perirhinal cortex, and amygdala (Price, 1995). Additionally, they are characterized by a dense cholinergic input (Tohyama and Takatsuji, 1998), and their lesion effects are well characterized (Orem et al., 1973). A comparable pattern does not exist for DLP (Korzeniewska and Güntürkün, 1990; Güntürkün, 1997; Veenman et al., 1997). The suggestion of Miceli and Repérant (1985) that the avian SRt, which also projects onto NCL, is an intralaminar structure thus seems to be more likely, given the hodological data provided by these authors.

Recently, Metzger et al. (1996, 1998) suggested that the MNH of chicks might constitute the avian PFC. This hypothesis is based on the observation that MNH is characterized by a medium density of dopaminergic afferents (Metzger et al., 1996), a high density of dopaminoceptive neurons (Schnabel et al., 1997), and afferents from the DMA (Metzger et al., 1996). If avian DMA should prove homologous to mammalian MD (Veenman et al., 1997), the hypothesis of Metzger et al. (1996, 1998) would obviously gain weight. Yet, as discussed above, data on the connections of DMA and MNH are limited. However, the DMA is known to project not only onto MNH, but also to the accumbens (Veenman et al., 1997), medial LPO (Székely et al., 1994), and piriform cortex (Bingman et al., 1994), projections which have not been shown for mammalian MD (Groenewegen, 1988; Price, 1995). Given these contradictions in the DMA-MD comparison and the complete lack of functional data on DMA, clearly more information is needed to clarify the comparison between avian MNH and mammalian PFC. These discussions on the organization of avian associative structures and mammalian PFC demonstrate that simple equivalencies between avian and mammalian prefrontal systems will not hold, even if two entities resemble each other with regard to their anatomical organization and function. However, difficulties in establishing homologous areas are not specific to comparisons between vertebrate classes, but also apply to intraclass comparisons, as reflected in the recent discussion about the criteria that delineate prefrontal cortex in rats (Condé et al., 1995; Preuss, 1995).

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