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Striatal input from the ventrobasal complex of the rat thalamus

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Abstract We have analyzed whether caudal regions of the caudate putamen receive direct projections from thalamic sensory relay nuclei such as the ventrobasal complex. To this aim, the delivery of the retrograde neuroanatomical tracer Fluoro-Gold into the caudal caudate putamen resulted in the appearance of retrogradely labeled neurons in the ventral posteromedial and ventral posterolateral thalamic nuclei. These projections were further confirmed with injections of the anterograde tracers biotinylated dextran amine or *Phaseolus vulgaris* leucoagglutinin into these thalamic nuclei, by showing the existence of axonal terminal fields located in the caudal striatum. These results support the existence of direct projections linking the thalamic ventrobasal complex and the caudal striatum in the rat, probably via collateralization of thalamocortical axons when passing through the caudate putamen, and therefore supporting the putative involvement of the caudal striatum in sensory-related functions.

Keywords Basal ganglia · Striatum · Caudate putamen · Thalamostriatal projections · Neuroanatomical tracers

Introduction

Thalamostriatal projections originating from the intralaminar and midline thalamic nuclei have been widely studied in the rat as well as in other animal species (Royce 1978; Sato et al. 1979; Veening et al. 1980; Beckstead 1984; Jarayaman 1985; Berendse and Groenewegen 1990; Nakano et al. 1990; Giménez-Amaya et al. 1995; Steriade et al. 1997; de las Heras et al. 1998). However, little attention has been paid to striatal input coming from the sensory relay thalamic nuclei in mammals (Lin et al. 1984). Veening et al. (1980) in the rat demonstrated the existence of a projection to the neostriatum from a variety of posterior thalamic structures by injecting HRP in different sites of the caudate putamen (CPu). They found that rostral nuclei of the ventral group project mainly to rostral striatal areas, while the posterior thalamic regions reach the caudal CPu (Veening et al. 1980).

This caudal region of the striatum in the rat includes the CPu located caudally to the decussation of the anterior commissure. This part of the striatum is characterized by different immunohistochemical properties and projection patterns when compared to the main body of CPu. The striatal immunoreactivity for calcium-binding proteins such as calretinin and calbindin in the rat shows a marked rostrocaudal gradient with a much greater density of immunoreactive cells located in the rostral rather than in the caudal parts of CPu (Gerfen et al. 1985; Bennet and Bolam 1993). In addition, differing gradients in the ontogeny of preproenkephalin expression in the rostral versus the caudal CPu suggest some anatomical and developmental differences between these two regions (Song and Harlan 1993).

Taking into account the possible topographical organization of the thalamostriatal projections arising from the specific thalamic nuclei and the rostrocaudal heterogeneity of the striatum, the present study in the rat was designed to verify the origin of the thalamostriatal projection to the caudal striatum from the ventrobasal complex by using retrograde and anterograde tracing methods.

Materials and methods

Sixteen female Wistar rats (body weight ranging from 210 to 250 g) were used in this study. Animals were deeply anesthetized (0.1 ml/100 g) with an intramuscular injected mixture of ketamine and xylazine, and placed in a stereotaxic frame. A 2% solution of Fluoro-Gold (FG; Fluorochrome, Englewood, Colo., USA) in 0.1 M cacodylate buffer, pH 7.3, was iontophoretically injected through a glass micropipette (inner tip diameter of 20–30 µm)

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using a 5-μA positive-pulsed direct current (7 s on/off for 10 min) into the caudal region of CPu of ten animals. A 10% solution of biotinylated dextran amine (BDA; Molecular Probes Europe, Leiden, The Netherlands) in 0.01 M phosphate buffer, pH 7.25, was iontophoretically delivered into the ventrobasal complex in four animals, according to the same iontophoretic parameters described above for the FG injections. Finally, a 2.5% solution of *Phaseolus vulgaris* leucoagglutinin (PHA-L; Vector Laboratories, Burlingame, Calif., USA) in 0.05 M TRIS-buffered saline, pH 7.4, was delivered by iontophoresis into the ventrobasal complex of two more animals. Stereotaxic coordinates were taken from the atlas of Paxinos and Watson (1998). Animals were handled at all times according to the European Communities Council Directive 86/609/EEC. After a survival time of 7 days, the animals were anesthetized with an intraperitoneal overdose of 10% chloral hydrate in distilled water and perfused transcardially. Perfusion was conducted with a Ringer rinsing solution at body temperature, immediately followed by 500 ml fixative containing 4% paraformaldehyde, 0.1% glutaraldehyde, and 0.2% saturated picric acid in 0.125 M phosphate buffer, pH 7.4. After perfusion, the skull was opened and the brain removed and stored in a cryoprotective solution prepared according to Rosene et al. (1986). Ten series of coronal frozen sections (40 μm thick) were obtained in a sliding microtome and collected in 0.125 M phosphate buffer, pH 7.4. The FG protocol was carried out according to a PAP procedure (Van Bockstaele et al. 1994) by using a primary antiserum against FG raised in rabbit (1:2000; Chemicon, Temecula, Calif., USA) and finally stained with DAB as a chromogen. Transported BDA was histochemically detected with an ABC solution (avidin biotin complex; Vector) and finally reacted with DAB. The PHA-L protocol was conducted by using a primary antibody raised in rabbit (1:2000; Vector), followed by a biotinylated goat anti-rabbit antiserum (1:100; Vector), then reacted with an ABC solution, and finally stained with DAB. Once the staining was completed, the sections were mounted on glass slides using a 2% solution of gelatin in 0.05 M TRIS/HCl, pH 7.6, dried, dehydrated in ethanol, cleared with xylene, and coverslipped with DePex.

The location of the injection sites both in CPu and in the thalamus, the retrogradely labeled neurons in the thalamus, and the anterogradely labeled fibers in CPu were directly plotted using a camera lucida. Adjacent sections were processed for acetylcholinesterase and Nissl stains for chemoarchitectural and cytoarchitectural references.

In one extra series of each individual case and once the tracer was first visualized with DAB, an additional counterstain with thionin was performed. This procedure allowed us an unequivocal localization of the injection sites as well as the structures displaying labeling.

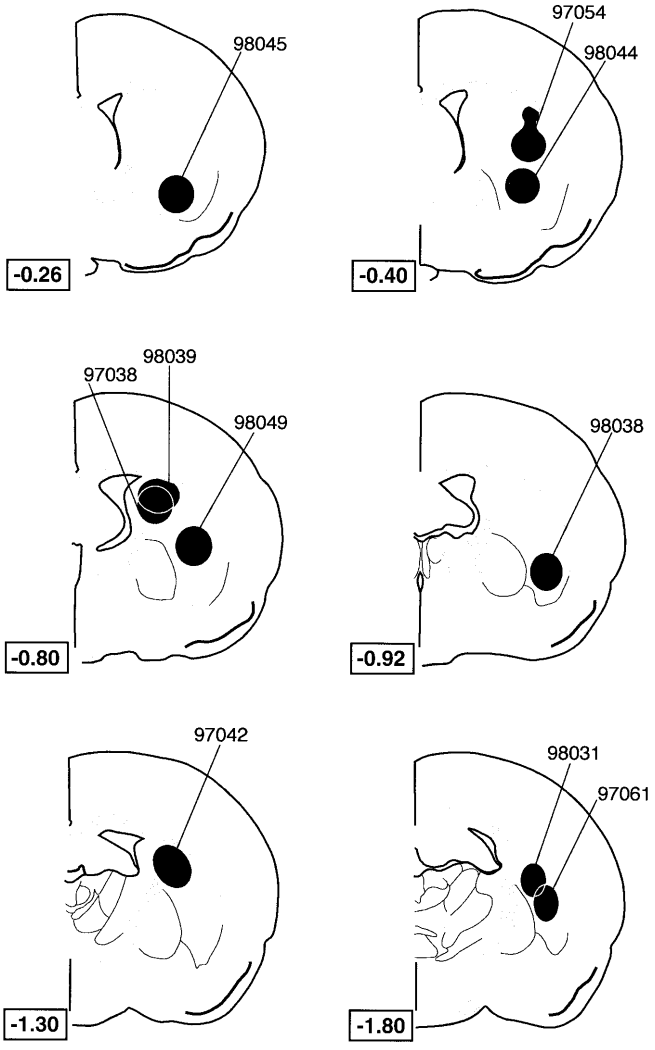


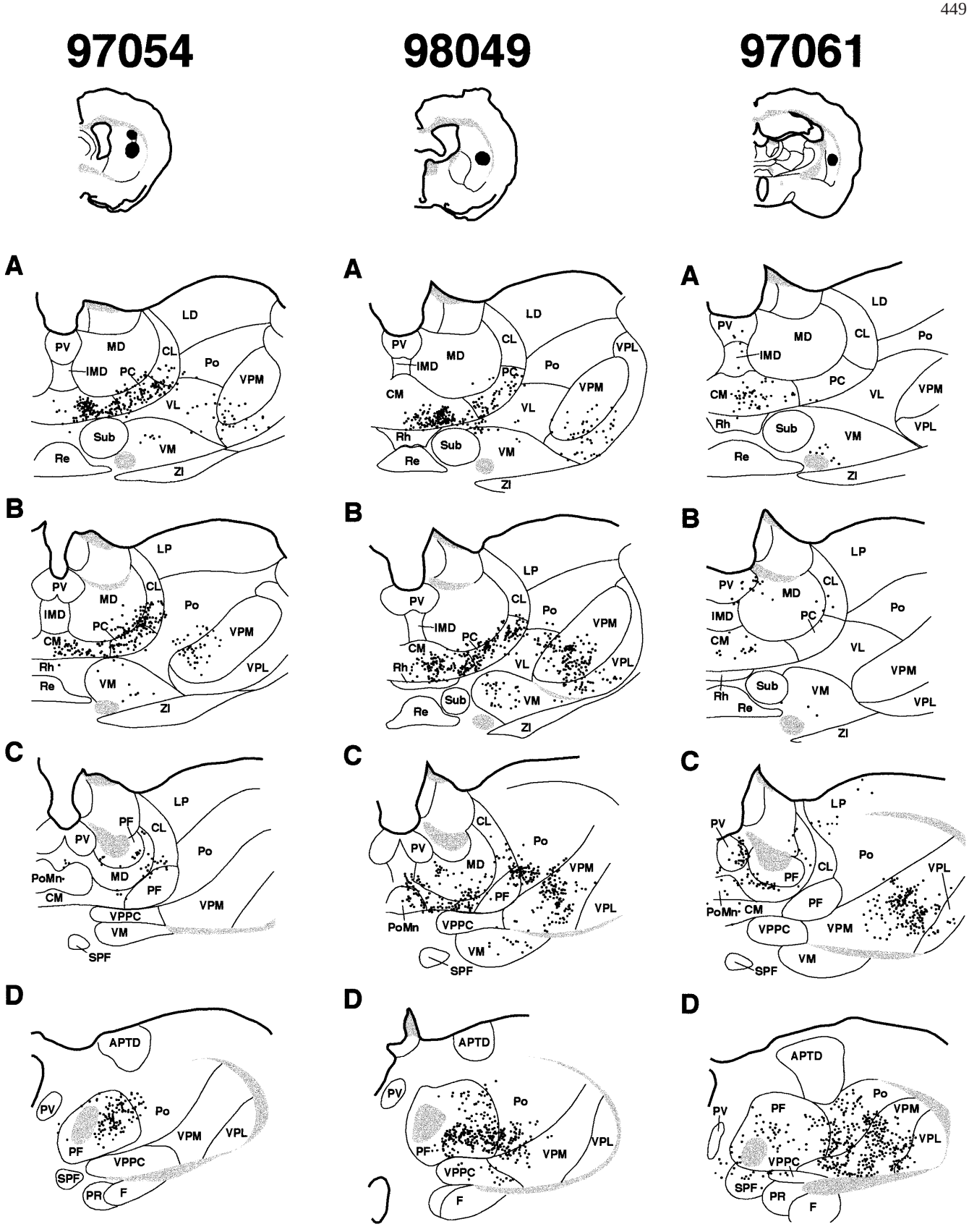
Fig. 1 Schematic drawings showing the localization of the Fluoro-Gold (FG) injection sites within the caudal caudate putamen (CPu) as well as the distance from bregma of each injection

Results

Retrogradely labeled neurons in the thalamus

The retrograde tracer FG was delivered into ten different locations of the caudal striatum (Fig. 1). The caudal striatum was considered to be the region located caudally to the decussation of the anterior commissure. A high number of retrogradely labeled neurons were always found in the rostral intralaminar thalamic nuclei (the central medial, paracentral, and centrolateral) and in the parafascicular thalamic nucleus irrespective of the location of the FG injections within CPu. When FG injections sites were placed ventrally within CPu (cases 98044 and 98038), a moderate number of cells were also noticed in the midline thalamic nuclei (paraventricular, intermediodorsal, rhomboid, and reuniens). All FG deposits result-

Fig. 2 Schematic drawings of four coronal sections through the thalamus, arranged rostrocaudally (**A–D**), showing retrogradely labeled neurons found after three different injections within the caudal CPu, illustrated at the top. Each *black dot* represents a retrogradely labeled neuron. Note the difference in number and distribution of the neurons placed in the ventrobasal complex as a function of the FG placement throughout the rostrocaudal axis of the caudal CPu. *APTD* Anterior pretectal nucleus, dorsal part, *CL* centrolateral thalamic nucleus, *CM* central medial thalamic nucleus, *F* nucleus of the fields of Forel, *IMD* intermediodorsal thalamic nucleus, *LD* laterodorsal thalamic nucleus, *LP* lateral posterior thalamic nucleus, *MD* mediodorsal thalamic nucleus, *PC* paracentral thalamic nucleus, *PF* parafascicular thalamic nucleus, *Po* posterior thalamic group, *PoMn* posteromedian thalamic nucleus, *PR* prerrubral field, *PV* paraventricular thalamic nucleus, *Re* reuniens thalamic nucleus, *Rh* rhomboid thalamic nucleus, *SPF* subparafascicular thalamic nucleus, *Sub* submedius thalamic nucleus, *VL* ventrolateral thalamic nucleus, *VM* ventral medial thalamic nucleus, *VPL* ventral posterolateral thalamic nucleus, *VPM* ventral posteromedial thalamic nucleus, *VPPC* ventral posterior thalamic nucleus, parvicellular part, *ZI* zona incerta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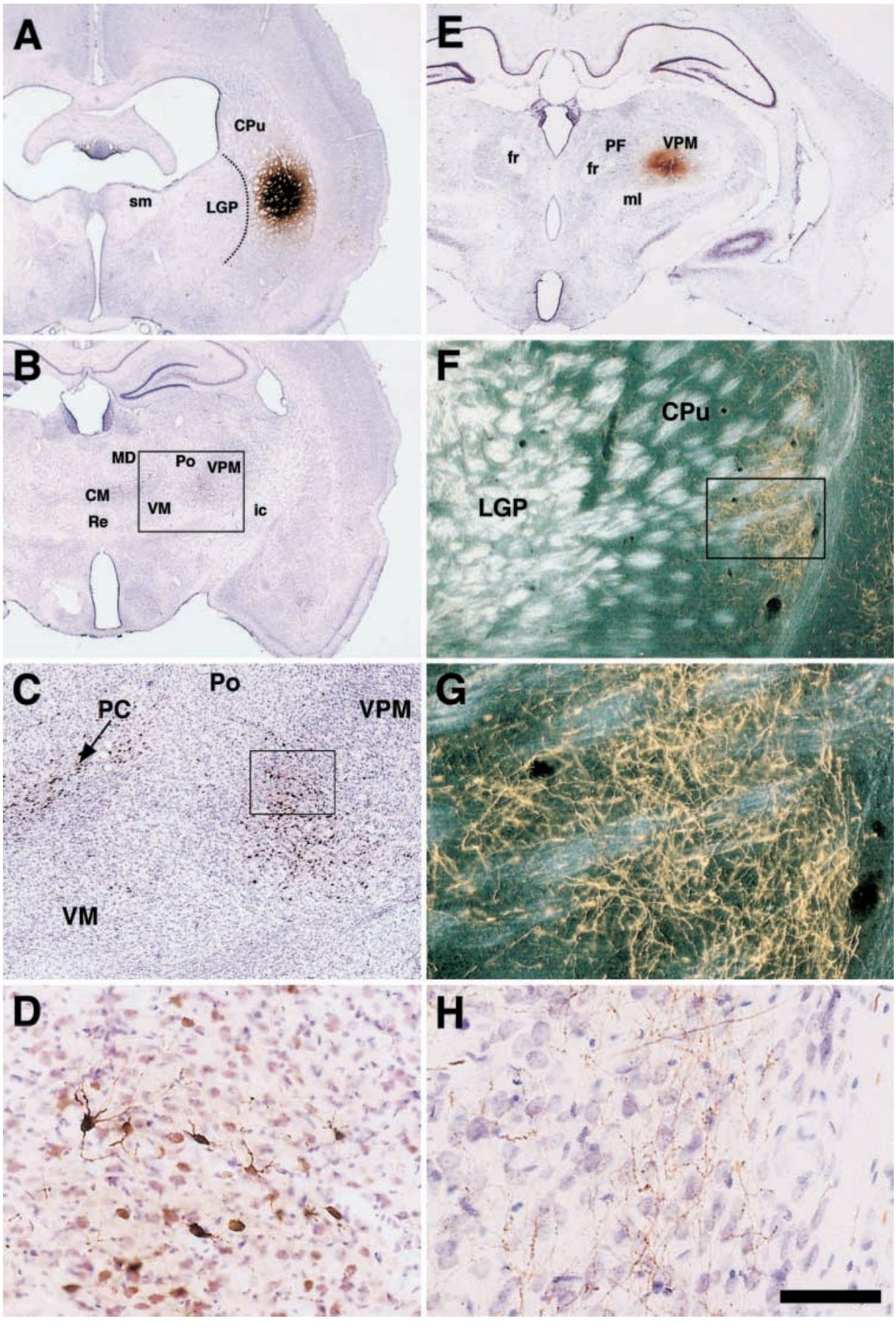
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ed in the appearance of labeled neurons within the ventrobasal complex, although some differences may be appreciated as a function of the FG placement throughout the rostrocaudal axis of the caudal CPu. After FG injections located rostrally within the caudal CPu (cases 98045, 98044, and 97054), a moderate number of labeled neurons were noticed in the ventral posteromedial (VPM) and ventral posterolateral (VPL) thalamic nuclei, particularly in their rostral regions (Fig. 2). The ventromedial and ventrolateral thalamic nuclei showed scattered cells retrogradely labeled in these cases. When considering FG injections located in more caudal regions of CPu (cases 97038, 98039, 98049, and 98038), the retrograde labeling found in the ventrobasal complex was more abundant and was situated in more caudal territories (Figs. 2, 3B–D). A moderate number of labeled cells could also be observed in the posterior thalamic group and in the ethmoid thalamic nucleus. The highest number of labeled neurons located caudally within the ventrobasal complex and in the posterior thalamic group was found after those injections placed in the most caudal regions of CPu (cases 97042, 97061, and 98031; Fig. 2). Overall, retrogradely labeled neurons were always found more abundantly in VPM than in VPL thalamic nuclei.

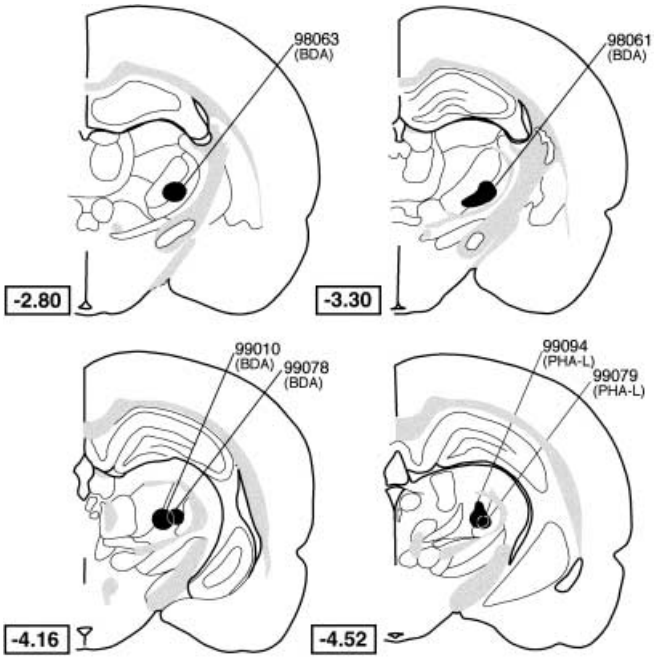

Fig. 4 Schematic drawings showing the BDA and *Phaseolus vulgaris* leucoagglutinin (PHA-L) injection sites within the ventrobasal complex as well as the distance from bregma of each injection

Anterogradely labeled fibers in CPu

Restricted BDA injections within VPM and VPL thalamic nuclei (Figs. 3E, 4) resulted in the appearance of anterogradely labeled bundles of fibers traversing the caudal CPu. These BDA-labeled fibers were thick and they were located within the axonal bundles that belong to the internal capsule as part of the thalamocortical projection system. Furthermore, a moderate density of BDA-labeled terminal fields were always found in the striatal parenchyma located among the bundles of thick thalamocortical axons (Fig. 3F–H). These terminal fields consisted of a moderate density of thin and ramifying fibers, most of them showing many varicosities (Fig. 3H). The density of terminal fields within the striatum was always higher after caudal injections into VPM and VPL thalamic nuclei than after injections into the rostral parts of these thalamic nuclei. No BDA terminal fields were seen in CPu located rostrally to the decussation of the anterior commissure. As expected, the primary somatosensory cortex showed a high density of BDA terminal fields.

Similar results were also obtained in two more animals in which the anterograde tracer PHA-L was injected into the caudal VPM and VPL thalamic nuclei (Fig. 4). In these two cases, the anterogradely labeled terminal fields within the caudal CPu (Fig. 5) were seen to extend over the same territories covered by the BDA terminal fields as shown in the former experiments, that is, a lateral band situated in the ventrolateral region of the caudal CPu, adjacent to the white matter.

◀ **Fig. 3** **A** Low power magnification photomicrograph of one FG injection site into the caudal CPu (case number 98049), stained with DAB and counterstained with thionin. **B** Low power magnification photomicrograph of a coronal section through the caudal thalamus showing the distribution of the FG-labeled neurons within VPM. These neurons were labeled after the tracer deposit illustrated in Fig. 1A. **C** *Inset* taken from **B** showing the distribution of labeled neurons within PC and VPM. **D** *Inset* taken from **C** showing the morphological features of the retrogradely labeled neurons within VPM. Please note that only a subpopulation of neurons within VPM seems to give rise to thalamostriatal projections. **E** Low power magnification photomicrograph illustrating one biotinylated dextran amine (BDA) injection site within VPM (case number 99010), stained with DAB and counterstained with thionin. **F** Dark field photomicrograph taken from a coronal section through the caudal CPu showing a terminal field of BDA-labeled fibers. **G** *Inset* taken from **F** showing the former BDA terminal field at higher magnification. **H** High power magnification photomicrograph showing a BDA terminal field located in the caudal CPu. This axonal plexus was composed by ramifying fibers with many varicosities. *CM* Central medial thalamic nucleus, *CPu* caudate putamen, *fr* fasciculus retroflexus, *ic* internal capsule, *LGP* lateral globus pallidus, *LP* lateral posterior thalamic nucleus, *MD* mediodorsal thalamic nucleus, *ml* medial lemniscus, *PC* paracentral thalamic nucleus, *PF* parafascicular thalamic nucleus, *Po* posterior thalamic group, *Re* reuniens thalamic nucleus, *sm* stria medullaris of the thalamus, *VM* ventral medial thalamic nucleus, *VPM* ventral posteromedial thalamic nucleus. *Scale bar* 2000 μm in **A**, **B**, **E**; 500 μm in **C**; 400 μm in **F**; 100 μm in **D**, **G**; 50 μm in **H**

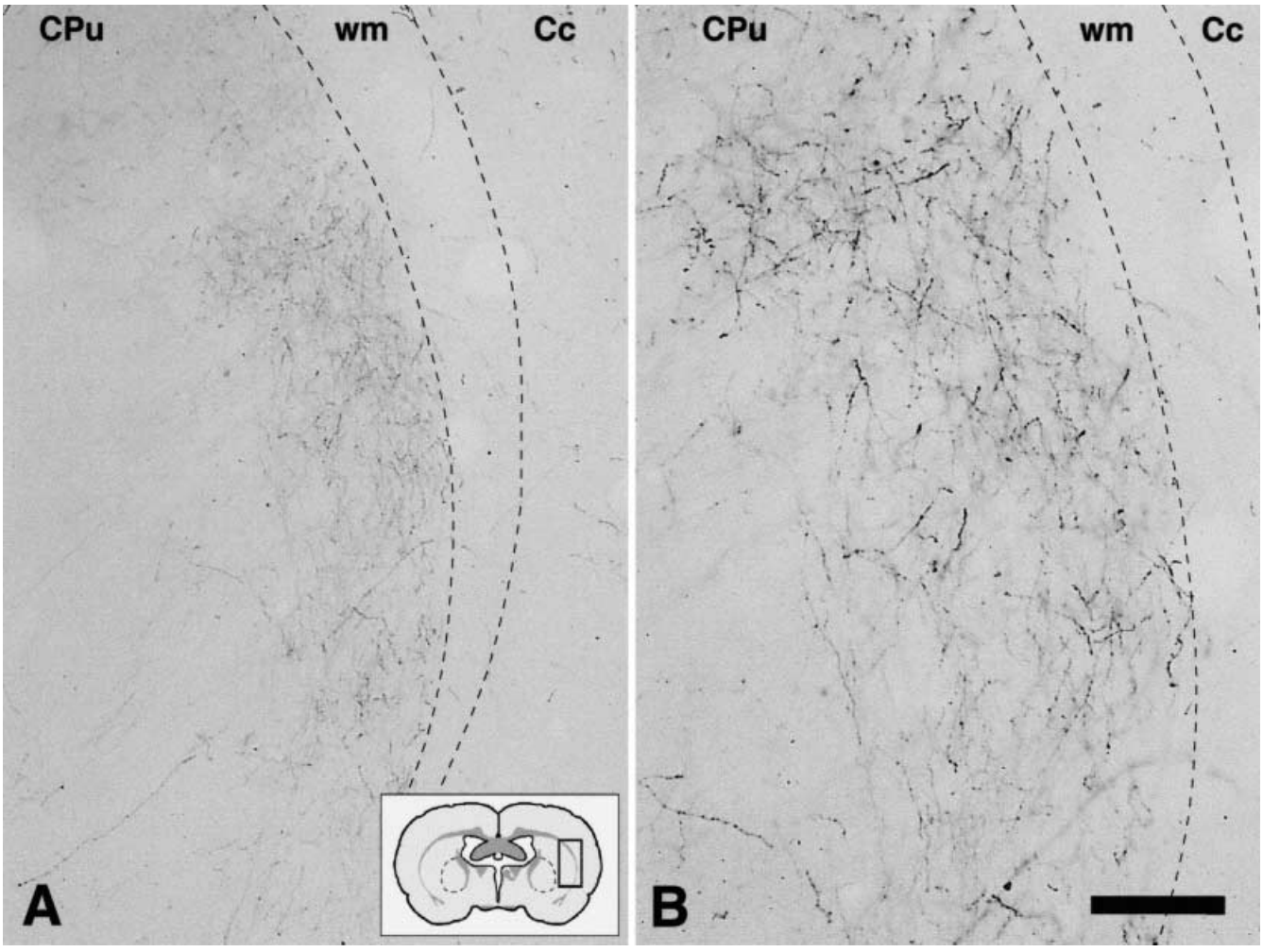

Fig. 5 **A** Low power magnification photomicrograph illustrating a PHA-L terminal field located in the caudal CPu (case number 99094). **B** *Inset* taken from **A** showing the former terminal field at higher magnification. This axonal plexus contains a moderate density of thin fibers with many varicosities. *Cc* Cerebral cortex, *CPu* caudate putamen, *wm* white matter. *Scale bar* 440 μm in **A**; 220 μm in B

Discussion

Technical considerations

The neurons found in VPM-VPL thalamic nuclei after the retrograde tracer injections into the postcommissural CPu could be considered to be thalamocortical cells filled by the retrograde transport of FG from cortical terminals or from fibers of passage, instead of truly thalamostriatal labeled cells. There is currently some controversy dealing with the FG uptake by fibers of passage (Schmued and Fallon 1986; Pieribone and Aston-Jones 1988; Dado et al. 1990). We have considered that most of the retrogradely labeled thalamic neurons observed in this study originate from terminals located in CPu, rather than either from fibers of passage or from cortical terminals, because the uptake of FG by damaged fibers traversing the injection site is kept to a minimum by means of the iontophoretic delivery of the dye (Schmued and Heimer 1990). Cortical contamination from leakage of the tracer along the injection track was never noticed in any of the cases included in this study. Furthermore, in order to verify the former results, we have injected two different anterograde tracers into the ventrobasal complex of the thalamus. The anterogradely labeled fibers and terminals found within the caudal striatum could be considered to be corticostriatal axons filled by the retrograde transport of the anterograde tracer by corticothalamic fibers giving rise to collateral branching fibers to the striatum (Chen and Aston-Jones 1998). This possibility could take place following BDA injections (Veenman et al. 1992) but it seems to be very unlikely with our procedure. We have used a maximum of 7 days of survival time which reduces the retrograde transport of BDA, and this retrograde transport has only been observed in the peri-injection halo. In addition, the density of terminal fields found in the striatum after BDA injections into the ventrobasal complex has been higher after small injections located into the caudal ventrobasal complex rather than after larger deposits located into the intermediate or rostral ventrobasal complex, where fewer retrogradely labeled neurons have been previously found. Therefore,

our findings obtained after BDA injections into the thalamus showed a clear correspondence with the neuronal distribution obtained after FG injections into the caudal CPu. To confirm these data we have used anterograde tract-tracing with PHA-L in two cases. This tracer is not taken up by fibers of passage, and it is considered to be almost exclusively anterograde and, therefore, not transported along axon collaterals of retrogradely labeled cells (Gerfen and Sawchenko 1984; Groenewegen and Wouterlood 1990). Accordingly, the PHA-L anterogradely labeled fibers found in the striatum after the injections of this tracer into the ventrobasal complex have to be considered specific of this thalamostriatal projection.

Striatal projections from the ventrobasal complex

The present study supports the possible existence of a direct projection from the ventrobasal complex of the thalamus to the caudal CPu in the rat. The results from our BDA and PHA-L injections into VPM and VPL thalamic nuclei support the findings obtained with deposits of retrograde neuroanatomical tracers into the caudal part of CPu. These results confirm those reported by Veening et al. (1980) who described a projection from the posterior thalamic area to the caudoventral part of CPu after injecting the retrograde tracer HRP into the rat striatum. This posterior thalamic area of the rat was considered to comprise the medial part of the medial geniculate body and the contiguous part of the ventral nucleus receiving afferents of the spinothalamic tract. Our findings, however, are rather discrepant to those reported by Deschênes et al. (1995) who did not find striatal projections after biocytin injections in the ventrobasal complex of the rat. This discrepancy may be due to the different anterograde tracers employed (BDA and PHA-L versus biocytin) and also because Deschênes et al. (1995) injected biocytin only in two neurons of the ventrobasal complex, which could not be representative of such a wide nucleus. Furthermore, our results suggest that the reported thalamostriatal projections arise only from a subpopulation of neurons within VPM and VPL thalamic nuclei, while a large population of projection neurons from these nuclei seems to be only devoted to the thalamocortical pathway.

Thalamostriatal fibers arising from the midline and intralaminar thalamic nuclei provide sensory inputs of various modalities to the striatum (Berendse and Groenewegen 1990). Specific sensory information reaches CPu primarily via the thalamo-corticostriatal connections (Wright et al. 1999), although striatal afferents from certain specific thalamic relay nuclei such as the medial division of the medial geniculate body and the suprageniculate nucleus in the rat (LeDoux et al. 1985) and in the cat (Takada et al. 1985), and the pulvinar and medial geniculate body in the primate (Lin et al. 1984), have been described. However, it has not been generally recognized that other relay nuclei for ascending sensory pathways to the cortex, may also give rise to prominent projections to the striatum (Lin et al. 1984). In the cat, there is evidence supporting that the ventrobasal nucleus projects to the ipsilateral CPu (Adrianov 1977). In the primate, Smith and Parent (1986) have reported retrogradely labeled cells into VPL, lateral posterior, and pulvinar thalamic nuclei after injections of WGA-HRP into the putamen.

Ventrobasal complex projections to the striatum reach preferentially the caudal CPu. This pattern supports the suggestion about the functional heterogeneity of the striatum (Takada et al. 1985). Whereas the rostral nuclei of the ventral group, which are the recipients of motor-related input coming from the cerebellum and the globus pallidus, reach the rostral regions of CPu (Veening et al. 1980) or the rostral caudate nucleus in the cat (de las Heras 1998), the projections from thalamic nuclei involved in sensory functions reach the caudal striatum (Takada et al. 1985). Furthermore, rostral parts of the basolateral amygdaloid nucleus project to caudal portions of the striatum in the rat (Russchen and Price 1984; Kita and Kitai 1990), making evident the link between the caudal striatum and the limbic system represented by the amygdala.

The caudal division of CPu in the rat has been characterized by different cellular morphology, immunohistochemistry, and projection patterns as compared with the main body of the striatum (Gerfen et al. 1985; Bennet and Bolam 1993; Song and Harlan 1993). The existence of direct sensory inputs from the thalamus to the striatum seems to be a primitive feature of the basal ganglia in mammals (Marín et al. 1998). The exact role of this projection can not be answered with this study. However, the direct access of somatosensory information to the caudal part of CPu supports the hypothesis that this striatal territory is directly related with the sensory processing of information required to perform motor responses. Further experiments in other mammalian species are required in order to better understand its function.

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