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Projections from the visual areas to the neostriatum in rats. A re-examination

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Abstract. Neostriatal afferents from the primary visual cortex in rats were studied using dextran-biotin, biocytin, and Fluoro-Gold. The area V1 was found to project only to a dorsomedial, longitudinal region of neostriatum (NS), bordering on the lateral ventricle and subcortical white matter. The preterminal fibres in the NS form fluffs which increase in number and density in the cases with larger injections. This target region is poorly stained for calbindin and yet belongs to the matrix compartment. The secondary visual areas also project to the dorsomedial NS region but they also innervate the deeper tissue in the same general region. Iontophoresis of Fluoro-Gold into the dorsomedial NS labelled some pyramidal neurones in the fifth layer of the primary visual cortex. The cortical areas that surround the visual cortical complex project to other regions of the NS: the somatosensory cortex to a dorsolateral longitudinal region and the auditory area to the medial half of the caudalmost portion of NS. Thus, major sensory cortical divisions project to non-overlapping NS regions. Since NS in monkeys and cats does not receive afferents from the primary visual cortex and in a number of other species does, we conclude that visual systems in different mammals differ with respect to their projections to NS.

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INTRODUCTION

Silver impregnation of degenerating axons indicated presence of projections from all cortical areas to different parts of the neostriatum (NS). Such findings were reported in rats (Webster 1961) rabbits (Carman et al. 1963), cats (Webster 1965) and monkeys (Kemp and Powell 1970). The NS projection target of the primary visual area in the monkey appeared very small (Kemp and Powell 1970).

The techniques based on axonal transport, that are more sensitive as well as precise than the silver--impregnation techniques, have shown that the primary visual area in rhesus monkeys (Saint-Cyr et al. 1990) as well as in Galago and Saimiri (Johannes Tigges, personal communication) does not project to the NS. The same results in cats were reported by Battaglini et al. (1982) and Updyke (1993). On the other hand, axonal transport techniques in rabbits (Holländer et al. 1979), hamsters (Rhoades et al. 1982), mice (Rhoades et al. 1985) and tree shrew (Vivian Casagrande, personal communication) did demonstrate NS afferents from the primary visual cortex. In the rat, such projections were reported by Faull et al. (1986) and by McGeorge and Faull (1989). Donoghue and Herkenham (1986) reported data similar to those by Faull et al. (1986) and added the observation that the primary visual cortex projects to the matrix compartment. Veening et al. (1980) failed to detect labelled cell bodies in the primary visual area after injections of horseradish peroxidase in different loci of NS. Unlike McGeorge and Faull (1989), however, Veening et al. (1980) missed the dorsomedial part of NS. Collins and Caston (1979) combined penicillin-induction of local epilepsy and 2-deoxyglucose technique and reported coactivation of the penicillin-injected primary visual cortex and the caudalmost portion of the NS. This region was different from the region demonstrated by axonal transport techniques. Thus, both the within-species and across-species comparisons suggested a re-investigation of cortico-NS relations within the visual system of rats. We relied on recent tracers of axonal transport which can be considered more sensitive (Fluoro-Gold vs. horseradish peroxidase) or more precise (dextran-biotin vs. radioactive amino-acids) than the tracers available to Faull and his collaborators. Some sections were stained to reveal both the dextran-biotin-containing fibres and calbindin. The data have been presented at the IBAGS IV conference (López-Figueroa et al. 1992).

METHODS

Seventy-seven Wistar albino rats, seventy-five of them males, weighing 200-300 g, were used. Fifty-six rats (including two females) received injections of biocytin (Sigma). In retrospect, the problems we had with biocytin were caused by inadequate fixative (Izzo 1991). Only 13 of the latter rats were used for analysis of the projections and only two are illustrated (cases: AXR and AZB). Eight additional rats received injections of dextran-biotin (Molecular Probes) in the same cortical areas. Four of them were selected for analysis and illustrations (BDR, BDS, BDT and BEP). In three of the latter animals some series of sections were double--stained for dextran-biotin and, immunohistochemically, for calbindin (see below). Finally, in 13 rats a retrograde fluorescent tracer, Fluoro-Gold (FG, Fluorochrome Inc.) or True blue (Dr. Illing) was delivered to the NS iontophoretically. Eleven of these cases gave useful staining and one was used for illustration.

The biocytin-injected rats were operated in anaesthesia induced by Ketamine (87.5 mg/Kg, Parke-Davis) and Xylazin (Rompun) (15 mg/Kg, Bayer). Biocytin (Sigma) was dissolved in artificial CSF in the concentration of 5% and stereotaxically injected into different areas of the cortex with a gas-tight Hamilton syringe that had a gauge 31 needle. In some rats an attempt was made to hit specific areas at the following coordinates obtained from Zilles (1985) atlas: For the primary visual area, A: -7.5 mm (to bregma); for the monocular field, L: 2.5-2.7 mm and for the binocular field, L: 4.0-4.2 mm lateral to the midline. For the posterolateral injections, A: between -6.5 and -7.0 mm from bregma; L: 6.5 mm. Each site received 0.1-0.4 µl

through a hypodermic needle whose tip was obliquely bevelled and reached 2 mm from the dural surface. In this way the opening of the needle was right in the visual cortex. These rats survived 20-48 h and were perfused in deep anaesthesia with saline followed by 4% paraformaldehyde in buffered neutral saline.

The rat brains were left in the same fixative for about 8 h and then overnight in 15% sucrose in phosphate buffer. The brains were cut in a vibroslice at 50 µm. Two series of sections were processed for detection of biocytin with Vector ABC kit (details of the technique in King et al. 1989), one of them was counterstained with neutral red. The third series was stained with cresyl violet. The sections were screened under a microscope for the fibres in the NS, and photographed.

The rats that received dextran-biotin and/or FG or True blue were operated in Equithesin anaesthesia (composition in Divac et al. 1987) with addition of 1 mg/kg of atropine. All these rats survived for 21 days. The animals which received dextran-biotin injections were treated like the biocytin-injected ones, even when they had additional deposit of a fluorescent tracer. The fluorescent tracer was dissolved in cacodylate buffer in concentration of 2%. The filled pipette with the tip about 20 µm was stereotaxically lowered through a hole in the skull (coordinates: A: -0.3 from bregma, L: 2.2 and H: 3.3 from dura). Positive DC of 5 µA was delivered in 7 seconds on-off pulses by means of a Midgard Electronics power supply for 15-20 min. The pipette was left in situ for further 10 min and then slowly pulled out. The rats which had received only fluorescent tracers were perfused in anaesthesia using the protocol by De Olmos and Heimer (1980). The brains were left overnight in the same fixative with 20% sucrose at 4°C. When a brain sank, it was rapidly frozen by dipping in isopenthane cooled to -70°C by dry ice. The brains were cut in a cryostat at 20 µm. Every 11th section was mounted on slides which were exposed to vacuum at 4°C for 48 h, left in xylene 2 x 10 min and coverslipped with Entellan (Merck). Every 12th section was mounted on separate slides and stained with cresyl violet. The fluorescence series were kept at -20°C when not screened. The sections were photographed in a scanner similar to that described by Mårtensson and Björklund (1984) in order to obtain fluorescence pictures under low magnifications. Some series of sections from the brains injected with dextran-biotin were first processed to show biotin in fibres by the technique described above. The same sections were stained next immunohistochemically (Gerfen et al. 1985) for calbindin, without addition of ammonium nickel sulphate. We could discriminate thus black fibres from brown calbindin stain.

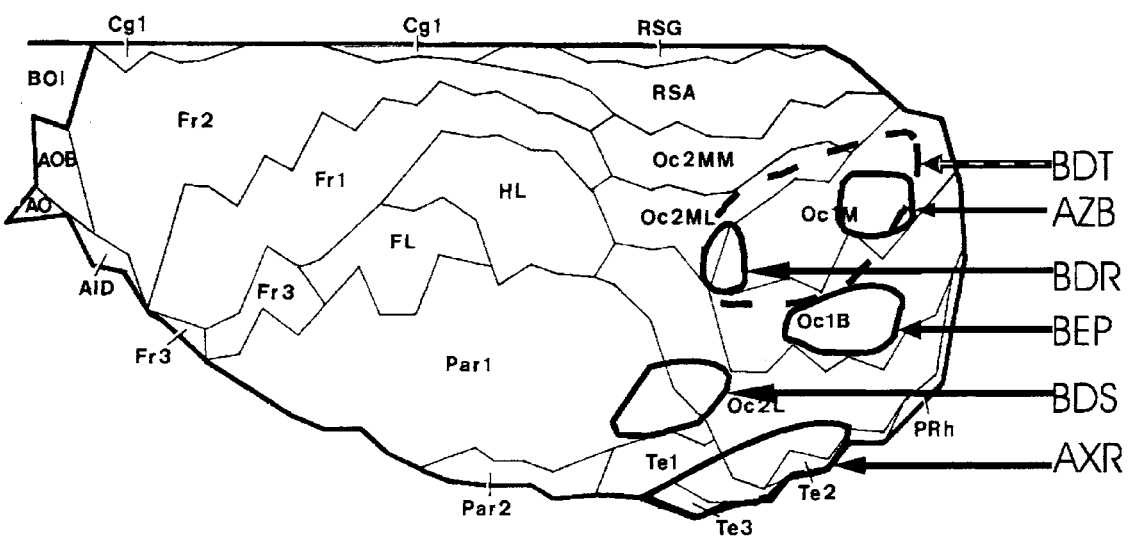

Fig. 1. Ilustration of the injection sites in the six representative cases on a diagram modified after Zilles (1985).

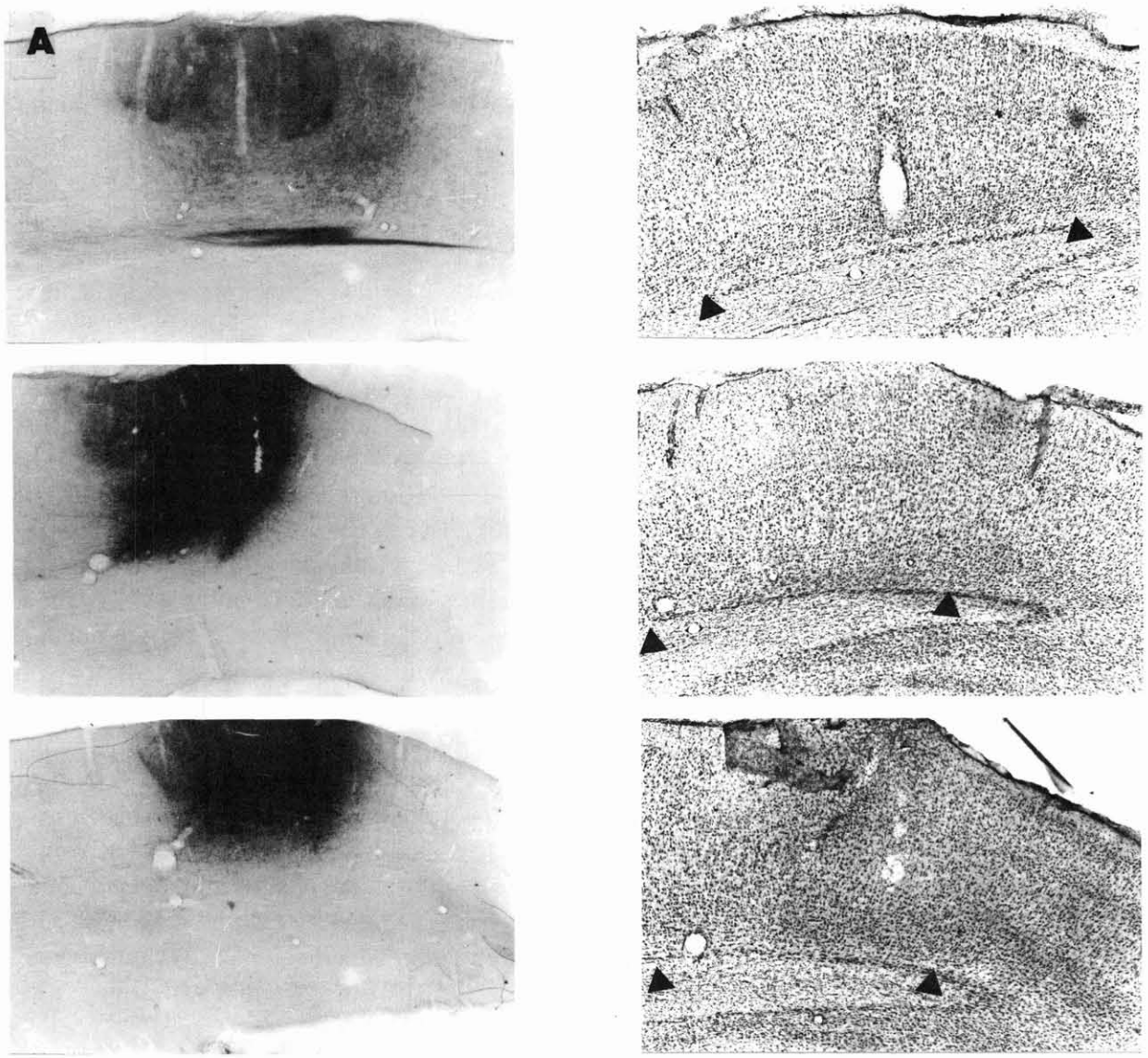

Fig. 2. A, adjacent sections from brains AZB (A) and BEP (B) stained for the presently used tracers or Nissl. The photographs aimed at the same site in the adjacent sections and were made under the same magnification. Each brain is illustrated with three levels: at the rostral end (top row), centre (middle row), and caudal end (bottom row) of the injection site. Reference to the Nissl stained photographs shows that the injetions are within the primary visual cortex. Approximate borders of the Oc1M (in A) and Oc1B (in B) are indicated by black triangles. Bar: 0.3 mm.

Both the fluorescent and biocytin-reacted sections were scanned and processed in the MCID image analyser (Imaging Res. , St. Catherines, Canada).

RESULTS

Six representative cases illustrate our findings (Fig. 1). In one of them (BDT) dextran-biotin was injected in an area involving a large part of the primary visual cortex and spreading into the medial extrastriate cortex (Fig. 3a, b and c). In three other animals the injections were restricted to the visual cortex: the monocular part of the primary visual cortex (AZB), the binocular part of the same cortex (BEP), (Fig 2, Zilles et al. 1984) and a rostral border between the primary and secondary visual cortex (BDR). In further two rats the injection was largely outside the visual cortex: involving the somatosensory area (in BDS) and auditory areas (in AXR) (Fig. 1).

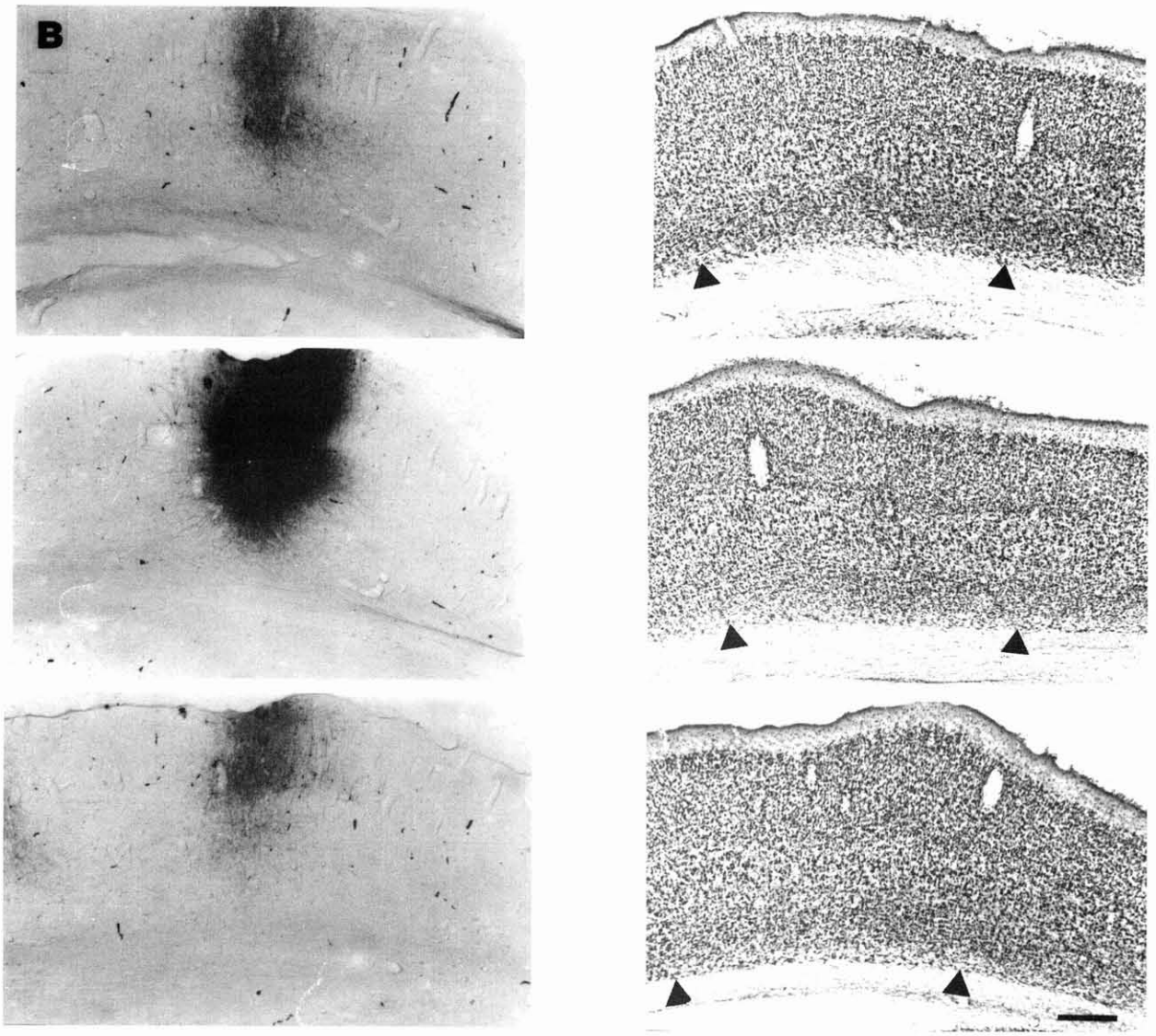

Fig. 2. B.

In the thalamus, the lateral geniculate and the latero-posterior nuclei contained labelled fibres and an occasional cell body in all rats with injections in the visual areas. In rats BDS and AXR the lateral geniculate was not labelled; labelled axons were seen in the medial geniculate in AXR, and in the ventro--posterior nucleus in BDS (not illustrated).

In all rats with injections into the visual cortex, including the cases AZB and BEP, we found fluff--like fibre formations in the dorsomedial part of the ipsilateral NS, right under the white matter. The dorsomedial NS region, in which the fibres were found, extended rostro-caudally from the level of Fig. 14 to Fig. 29 in Paxinos and Watson (1986). In the caudalmost region, however, the label was found in passing fibres (Fig. 3c) rather than in preterminal fluffs (Fig. 3b). Only in the cases with large injections and a strong labelling (BDT and similar) did we find sparse labelled fibres in the symmetrical region of NS in the contralateral hemisphere (not illustrated). Large injections were characterized by a larger number and a higher density of the fluffs than the cases with smaller injections. (Compare Figs. 3b and 4f). In some brains one could see a section with several fluffs close to it a section with only one fluff (Fig. 3e and f).

When a somatopetal tracer invaded secondary visual areas the labelled fibres were also seen in the dor-

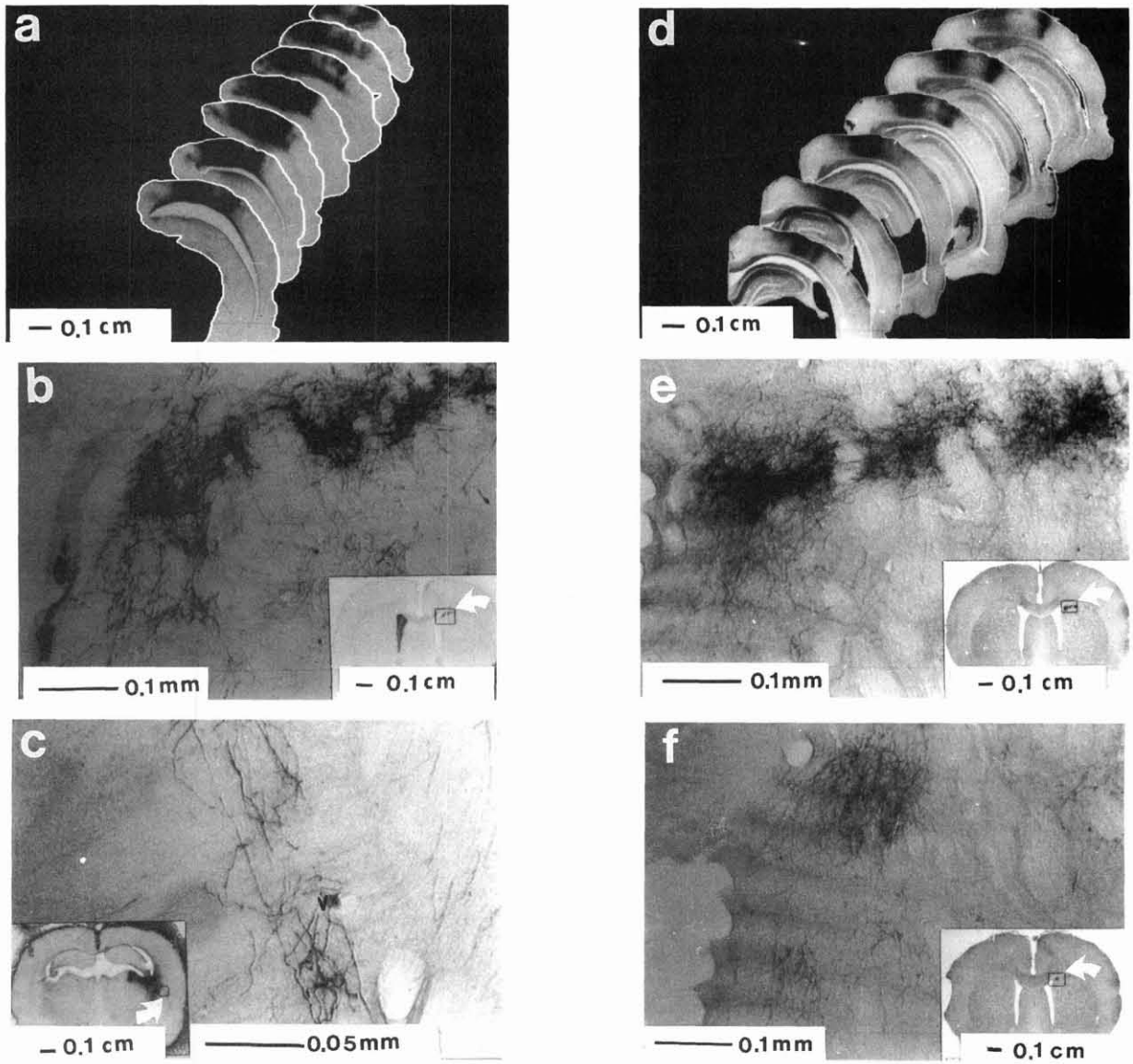

Fig. 3. Illustrations of the injection sites and labelled fibres in the neostriatum. The label in the cortex shows not only the injection site but also the resulting cortico-cortical projections. This accounts for the apparent discrepancy with Fig. 1 which shows the injection sites alone. The rectangles in the inserts emphasized by arrows indicate the position of the microscopic picture. For further description, see the text. In the rat BDT with a large injection only fibres of passage are seen in the caudal part of the NS and dense preterminal fluffs rostrally. In the rat BDR, with the rostralmost injection in the visual cortex, the labelled preterminals are also found dorsomedially. The bars at each figure indicate the magnification, respectively.

somedial quadrant of NS but mainly further away from its circumference in comparison with the projections from the primary visual cortex (not illustrated).

In the cases with injections into the areas surrounding the visual cortex, the fibres were not found in the dorsomedial NS region. In the animal BDS, with injection into the somatosensory cortex (Par1), the projections were seen also in the rim just under the white matter, but lateral to the area innervated by the visual cortex (Fig. 4c and d). In the rat AXR, the injection into the auditory cortex (Te1-3) was found to send very dense projections to the medial part of the NS tail. (Fig. 4g and h). The lateral border of the innervated area is surprisingly sharp.

Several series of sections were stained to show both the projections from the visual cortex and dis-

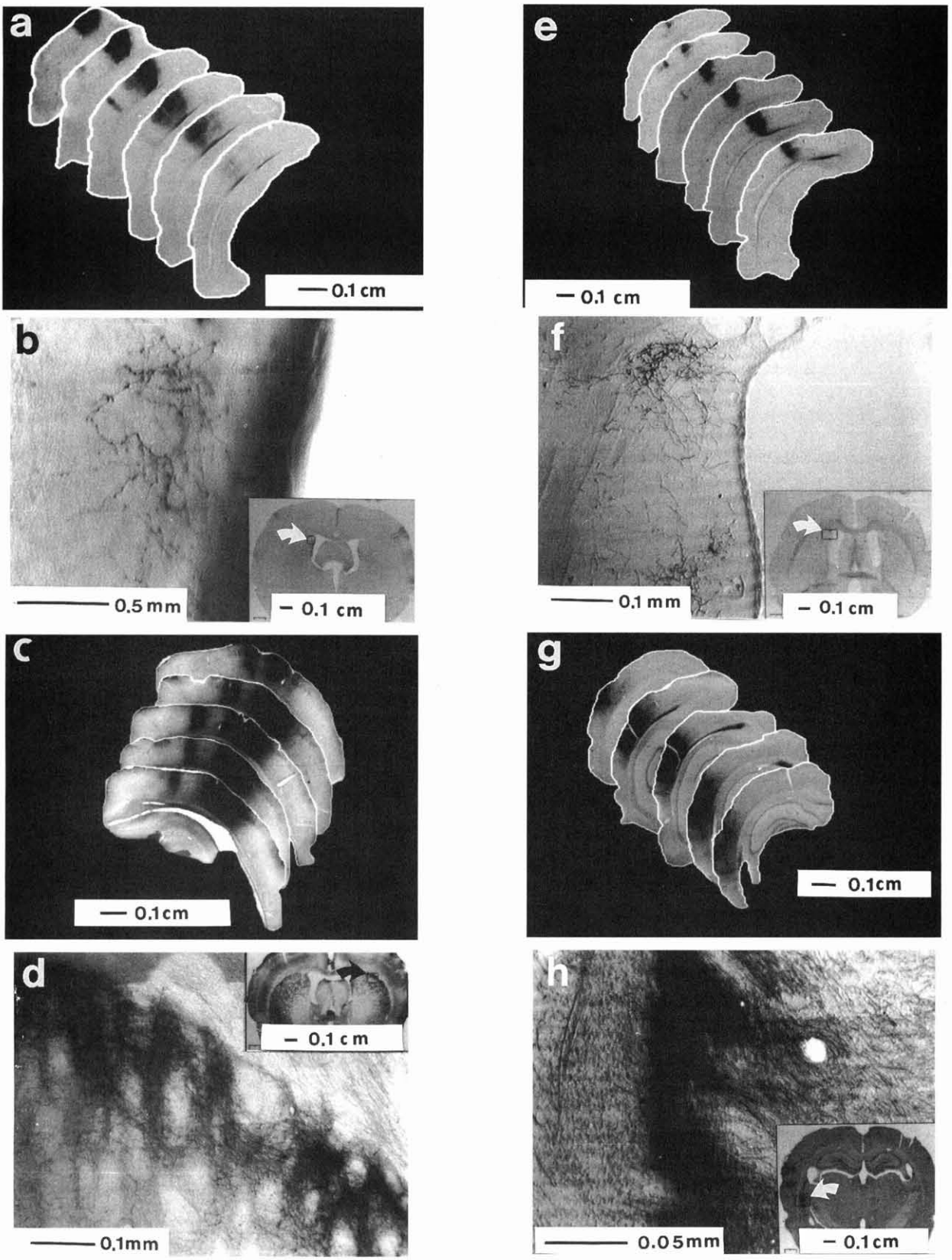

Fig. 4. Injection sites and the respective innervation of the NS are shown for four cases: a and b: rat AZB; e and f: rat BEP; c and d: rat BDS; g and h: rat AXR. Compare with Figs. 1 and 3.

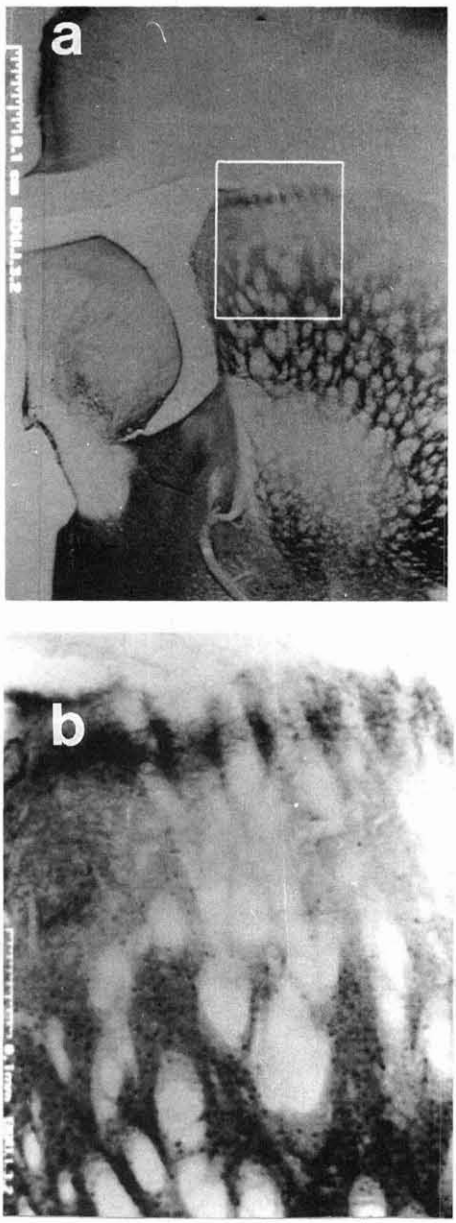

Fig. 5. Two magnifications of a section stained for biotin and calbindin. The fluffs of labelled fibres are seen in a calbindin--free zone just under the white matter.

tribution of calbindin. In these sections the fibres were seen only in the medial part of the calbindin--free rim under the subcortical white matter (Fig. 5).

The dorsomedial NS region was successfully infiltrated with somatopetal tracers in seven of thirteen brains. In all seven cases, some pyramidal neurones in the fifth layer of the primary visual cortex were fluorescent (Fig. 6). In these brains there was no labelling of neurones in the central gray, except the cell bodies in raphe nuclei. In no brain in which the dorsomedial rim of NS was missed in iontophoresis did we see labelling in the primary visual cortex. Accidental spread of FG into the somatosensory-motor cortex was unrelated to the labelling of neurons in the primary visual cortex.

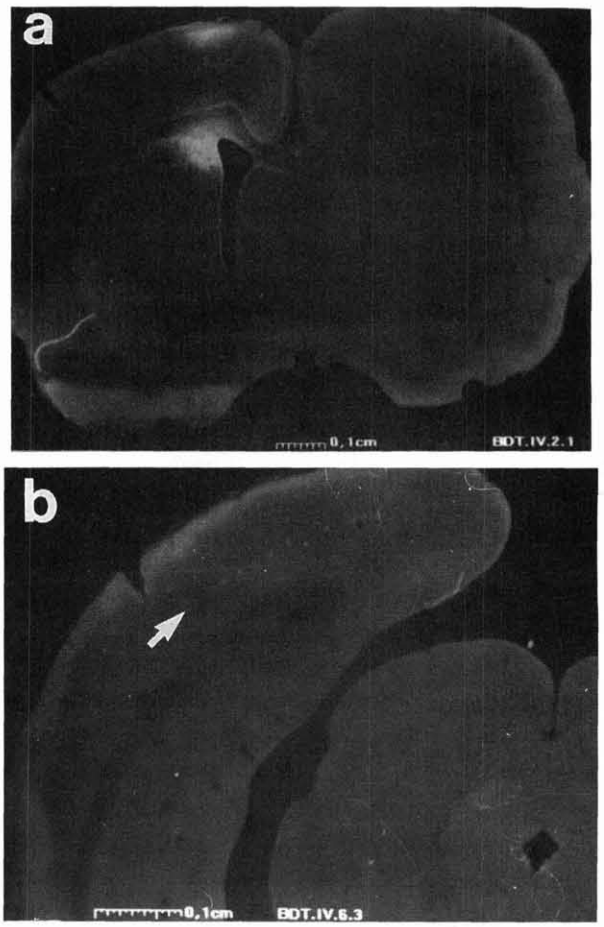

Fig. 6. Photographs of two sections from a rat with iontophoretic application of FG to the dorsomedial part of the NS. The injection site is shown in a and labelled pyramidal neurones in the fifth layer of the primary visual cortex in b (arrow).

DISCUSSION

Our results obtained with the most sensitive tracers of axonal flow support and expand observations of Webster (1961), Faull et al. (1986), McGeorge and Faull (1989) and Donoghue and Herkenham (1986). We are confirming that in rats some neurones in layer V of the primary visual area project predominantly ipsilaterally to the matrix

compartment of the NS, along the dorsomedial edge. This information has now been complemented by visualization of axons and their preterminal branching. The axonal bundles appear "combed", whereas the preterminal fibres form fluffs (see the case BDT in Fig. 3). The number and density of these fluffs is proportional to the size of the injection of the tracer, but they remain in the dorsomedial strip. In successive coronal sections the number of fluffs may increase or decrease (Fig. 3e and f). Even the smallest injections produced more than one fluff, which agrees with the observed divergence of cortico-neostriatal information (Brown et al. 1995). A hypothesis about functional significance of multilocular projections from a single cortical area to the NS is available (Brown et al. 1994). Injections of the somatofugal tracers into the auditory or somatosensory cortex labelled fibres in quite different NS regions. Thus, major divisions in the rat sensory cortex appear to have non-overlapping targets in the NS. The strong innervation of the medial part of the caudalmost NS region by the auditory cortical area suggests that epileptic discharges, thought to be localized in the visual area in the rats studied by Collins and Caston (1979), involved the auditory cortex. Double staining with anti-calbindin antibody showed localization of these preterminals in calbindin-free rim of NS tissue (Gerfen et al. 1985). This region does not bind opiate ligands (Donogue and Herkenham 1986, Desban et al. 1993) and by this definition should be the matrix, in spite of pale staining for calbindin.

The NS receives direct projections from V1 area in rats and other small mammals (tree shrews, Vivian Casagrande, personal communication; rabbits, Hollander et al. 1979; hamsters, Rhoades et al 1982; mice, Rhoades et al. 1985), but not in monkeys (Saint-Cyr et al. 1990, Johannes Tigges, personal communication) or cats (Battaglini et al. 1982, Updyke 1993). This difference is relevant for understanding the organization and evolution of both the visual system and the NS. The first issue is comparability among species of the cortical area named primary visual cortex (V1). The question is how to understand similarities and differences of properties of V1 in different species. The topic is too complicated to be discussed it this paper (Hughes 1977, Swaldlow 1983, Diamond et al. 1985, Sanderson et al. 1991). An illustration of these problems can be found in a comparison of V1 in monkeys and rats. Sanderson et al. (1991) have argued that area 17 in rats corresponds to area 17 in cats and monkeys. However, area V1 in monkeys appears to be different from the area V1 in rats not only in their connections to the NS: thus, in the V1 area of primates one finds a pronounced layer IV (Rockel et al. 1980) and stria Genari, which are reduced and absent in rats, respectively. Furthermore, columnar organization of V1 has been seen in monkey brains stained for cytochrome oxidase (Carroll and Wong-Riley 1984). In our rat material stained with the same technique no columns in the V1 could be identified (I. Divac and M.O. López-Figueroa, unpublished observations). A technical error could not account for this negative result since in the somato-sensory cortex of the same specimens we did find columnar organization (Divac et al. 1995).

In the monkey V1 area is unique in several ways in comparison with other cortical areas. Thus, V1 area binds more benzodiazepine ligand and less naloxone or quinuclidinyl benzylate as the ligands for opiate and muscarinic membrane receptors, respectively, than any other cortical area (Divac et al. 1981). On the other hand, V1 has the lowest amount of dopamine (Björklund et al. 1978). These data support the notion that V1 area in the monkey is indeed unique.

The differences in cortico-NS connectivity of V1 in primitive and advanced species may be taken to suport the notion that the latest stages of cortical evolution do not project directly to NS. This notion is based on the hypothesis of cortical evolution by Dart, Abbie and Sanides (review in Sanides 1972), according to which V1 area is the latest stage of evolution of the cortical visual system and therefore may be found in advanced but not in lower species. Another cortical area that evolved late is probably the cortex mediating language. That area also may be without direct connections to the NS. This possibility has interesting consequences for under-

standing symptomatology of basal ganglia diseases (discussed in Divac and Öberg 1992).

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