

Ventral Striatal Connections of Unimodal and Multimodal Cortex of the Superior Temporal Sulcus in Macaque Monkeys (*Macacca nemestrina*)

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Extrinsic connections between the cortex of the superior temporal sulcus (STS) and the ventral striatum in pigtail macaque monkeys (*Macacca nemestrina*) were studied by injection of retrograde tracers into the ventromedial caudate nucleus, the ventral and central shells of the nucleus accumbens (NA), the dorsal core of the NA, and the ventrolateral putamen. In the present study, we demonstrate that the projections from the unimodal (area TAa, IPa, TEa, and TEm) and the multimodal (area TPO and PGa) sensory association areas in the STS mainly terminate in the ventromedial caudate nucleus as well as in the ventral and central shells of the NA. However, there are only few projections to the dorsal core of the NA and the ventrolateral putamen from the sensory association cortex in the STS. Based on these differential neural connections between the subterritories of the ventral striatum and the sensory association areas, the ventromedial caudate nucleus and the shells of NA appear to be major integration sites for sensory input from the STS and functionally different from the dorsal core of NA and the ventrolateral putamen.

In the superior temporal sulcus (STS), two multimodal sensory regions (areas PGa and TPO) are found along the upper bank and in the fundus of the STS (Jones and Powell, 1970). Physiological studies have shown that multimodal neurons within the area PGa and TPO respond to visual, auditory, and somatosensory stimuli (Baylis et al., 1987; Mistlin and Perrett, 1990). Anatomically, these multimodal regions are surrounded by the unimodal areas including the area TAa at the rim of the upper bank, the area IPa at the fundus, and the areas TEa and TEm in the lower bank (Seltzer and Pandya, 1989). The area TAa receives its cortical input from the adjoining auditory association areas of the superior temporal gyrus (STG) as well as from the lateral and medial zones of the frontal cortex (Galaburda and Pandya, 1983; Cipolloni and Pandya, 1989; Seltzer and Pandya, 1989). The area IPa was originally classified as a unimodal somatic sensation-related area because it receives input from the parietal cortex along the lower rim of the intraparietal sulcus (Desimone and Ungerleider, 1986; Seltzer and Pandya, 1989). However, it has been shown that the area IPa also receives input from the visual parts of the STS (Boussaoud et al., 1990). The

areas TEa and TEm have vision-related cortical input coming exclusively from the inferotemporal cortex (Rockland and Pandya, 1981; Ungerleider et al., 1989).

The ventral striatum has long been considered as an interface between the limbic cortex and motor responses to stimuli (Heimer et al., 1982; Kalivas et al., 1993). Behavioral studies indicate that subterritories of the ventral striatum are differentially involved in specific goal-directed behaviors (Robbins and Everitt, 1996; Schultz, 1992). Thus, differential connections between the sensory association areas and the ventral striatum would provide different contributions to the generation of motor behaviors through sensory-limbic integration. In primates, the ventral striatum includes the nucleus accumbens (NA) as well as the adjacent ventral caudate nucleus and putamen (Alheid et al., 1990; Haber et al., 1990). The NA has been divided into the shell and the core subterritories which have different connectional, histochemical, and pharmacological properties (Berendse et al., 1992; Deutch and Cameron, 1992; Zahm and Heimer, 1993).

To understand more fully the neural connections between the ventral striatum and the cortex in the STS, we determined the corticostriatal projections using retrograde tracers from different levels (rostral, middle, and caudal) of the cortex in the STS to the five subterritories of the ventral striatum (the ventromedial caudate nucleus; the ventral and central shells of the NA;

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the dorsal core of the NA; and the ventrolateral putamen). This would support the hypothesis that the rostrocaudal organization of corticostriatal projections is in general related to the functional differentiation of the ventral striatum (Ferry et al., 2000).

Materials and Methods

Retrograde tracing study

Six adult macaque monkeys (*Macacca nemestrina*; age, 3-4 years; weight, 3-5 kg) were used in these experiments. Initial anesthesia was administered by an intramuscular injection of ketamine (10 mg/kg). A deep surgical level of anesthesia was maintained by intravenous injection of phenobarbital (initial dose, 20 mg/kg, i.v. and maintained as needed). Temperature, heart rate, and respiration were monitored throughout the surgery. Using a Kopf stereotaxic apparatus, a craniotomy (~2-3 cm²) was made over the region of interest, and small dural incisions were made only at recording or injection sites. Electrophysiological mapping was performed to locate appropriate injection sites as described earlier (Haber et al., 1990). Retrograde tracers, wheat germ agglutinin conjugated to horseradish peroxidase (WGA-HRP) (40-50 nl, 4%; Sigma, St. Louis, MO), or Lucifer yellow (LY) conjugated to dextran amine (20-40 nl, 10%; Molecular Probes, Eugene, OR), were pressure-injected over 10 min into discrete regions of the ventral striatum using a 0.5 µm Hamilton syringe. After the injection, the syringe remained in place for 20 min to prevent leakage up the needle track. After finishing tracer injections, the wound was closed in layers. Monkeys were again deeply anesthetized with phenobarbital 10-12 days after the surgery and perfused with 0.1 M phosphate buffer solution (pH 7.4) containing 4% paraformaldehyde and 1.5% sucrose. The brains were cryoprotected by increasing sucrose gradients (10, 20, and finally 30%). Serial sections (50 µm) of the brain were kept in 0.1 M phosphate buffer or stored in a cryoprotectant solution.

Immunocytochemical stain

We used immunocytochemical techniques to visualize tracer. Before incubation with primary antiserum, tissue was incubated in a solution with 10% methanol and 3% H₂O₂ in 0.1 M phosphate buffer to inhibit endogenous peroxidase, followed by extensive rinsing with 0.3% Triton X-100 in 0.1 M phosphate buffer (PB-T), pH 7.4. Sections were preincubated for 30 min in 10% normal goat serum (NGS) diluted with PB-T (NGS-PB-T) before immunoreaction with anti-LY (Molecular Probes) or anti-WGA (Sigma) serum. The tissue was placed in the rabbit primary antiserum (anti-LY diluted 1:1000 or anti-WGA-HRP diluted 1:2000 in NGS-PB-T) for 4 nights at 4°C. The avidin-biotin reaction (rabbit Vectastain ABC kit:

Vector Laboratories, Burlingame, CA) was used to visualize the LY and WGA. The tissue was rinsed in PB-T before incubation in biotinylated goat anti-rabbit IgG (1:400 NGS-PB-T) at room temperature for 45 min. After rinsing, the tissue was incubated in the rabbit avidin-biotin complex (1:200) at room temperature for 1 h. Antiserum binding was visualized by incubating the tissue for 10-12 min in a solution of 0.05% 3,3'-diaminobenzidine tetrahydrochloride (DAB) and 0.01% H₂O₂ in a 0.5 M Tris buffer. For intensified staining, the tissue was treated with 0.025% cobalt chloride and 0.02% nickel ammonium sulfate to yield a black reaction product. After thorough rinsing, sections were mounted onto gel-coated slides and counterstained with cresyl violet using a standard Nissl procedure.

Charting

Retrogradely labeled cells in the cortex of the STS were charted using a light microscope fitted with a drawing tube. With the aid of a drawing tablet, charts were traced into a Power Macintosh computer to create composite images. The same nomenclature and abbreviations were used as those that have been employed in the rhesus monkey brain in stereotaxic coordinates (Paxinos et al., 2000). Using Nissl-stained coronal section, we determined the boundaries of cytoarchitectonic subdivisions in the cortex of the STS as described by Bonin and Bailey (1947). The rostral (above the interaural 10.00 mm) and caudal (below the interaural 10.00 mm) terms used for the unimodal and polymodal areas of the STS were based on the AP level in the rhesus monkey brain atlas.

Abbreviations

If, lateral fissure; FST, fundus in the sts; IPa, IP associated area of the sts; NA, nucleus accumbens; TPO, temporoparietooccipital association area in the sts; PGa, PG associated area of the sts; Pu, putamen; STS (sts), superior temporal sulcus; TAa, TA associated area of the sts; TE1, temporal area TE1; TEa, temporal area TEa; TEa; TEa, temporal area TEa, medial part.

Results

Injection of retrograde tracer into the ventral striatum

Total of six injections of retrograde tracers were placed in the ventral striatum (Fig. 1). One injection site was in the ventromedial caudate nucleus (Case MN13). Two injection sites were located in the ventral shell of the NA (Case MN94 and MN96) and one injection site was confined to the central shell of the NA (Case MN26). Another injection was centered in the dorsal core of the NA (Case MN38) and the final one was made in the ventrolateral putamen (Case MN40).

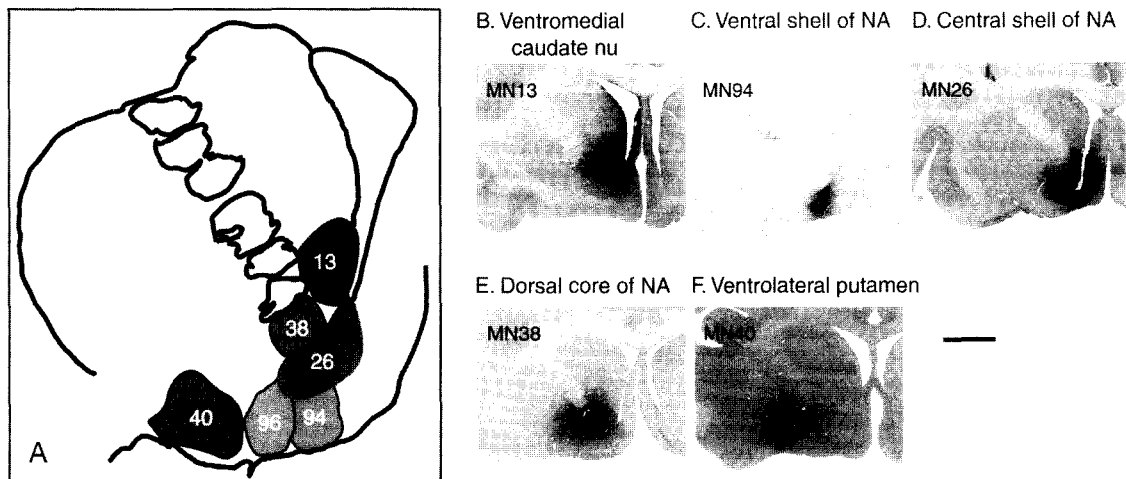


Fig. 1. Locations of retrograde tracer injection sites. Retrograde tracers, HRP or LY, were used in this study to evaluate projections from the cortex in the superior temporal sulcus (STS) to the ventral striatum in the primate adult macaque monkeys (*Macacca nemestrina*). A, Schematic drawing at a given level of the ventral striatum illustrating the six injection sites (Cases MN13, 26, 38, 40, 94, 96) as previously shown in Jung and Hong (2003a and b). B-F, Photomicrographs of representative injection sites in the ventral striatum showing the extent of ventral striatal tissues occupied by the retrograde tracers. Scale bar=2 mm.

Topography of retrogradely labeled cells

After injection of retrograde tracers (HRP or LY) into the ventral striatum, distribution and relative densities of labeled cells in the sensory association areas of the STS were summarized in Table 1. The extent and distribution of labeling were different depending on the location and extent of injection sites. However, a major difference in labeling patterns was found in the rostrocaudal position of labeled cells. The laminar organization of labeled cells was similar for all these injection sites to the extent that the majority of labeled cells were seen in the deep layers V and VI throughout the cortex of the STS, although some were also located in layer III.

Projections to the ventromedial caudate nucleus (Cases MN13)

In the unimodal sensory association areas, the highest concentration of HRP-labeled cells was found in the

rostral TAa (Fig. 2A-B), whereas small numbers were seen at the rostral levels of the areas IPa, TEa, and TEm (Fig. 2A-C). In the multimodal sensory association areas, the largest number of HRP-labeled cells was detected in the area TPO (Fig. 2A) and these were restricted to the rostral level of the area TPO. In the rostral TPO, labeled cells were mainly distributed in the intragranular layers V/VI and the supragranular layer III with intragranular dominance (Fig. 2A1). There were a few labeled cells in the rostral PGa (Fig. 2A). These results indicate that the ventromedial caudate nucleus could be a major site for receiving projections from the sensory association areas in the rostral STS.

Projections to the ventral shell of the NA (Cases MN94 and MN96)

Case MN94

The areas IPa, TEa, and TEm at the rostral level

Table 1. Summary of retrogradely labeled cells in the cortex of the STS

Cortex in STS	Ventral Striatal Injection Sites				
	Ventromedial Caudate Nu	Ventral shell of NA	Central shell of NA	Dorsal core of NA	Ventrolateral Pu
Unimodal association areas in STS					
TAa (auditory)	++++	++	++	+	+
TEm (visual)	+++	+++	++	+	-
TEa (visual)	+++	+++	+	+	-
IPa (somatosensory)	+++	++	++	+	+
Multimodal association areas in STS					
TPO	++++	+++	++	+	+
PGa	+++	+++	++	-	+

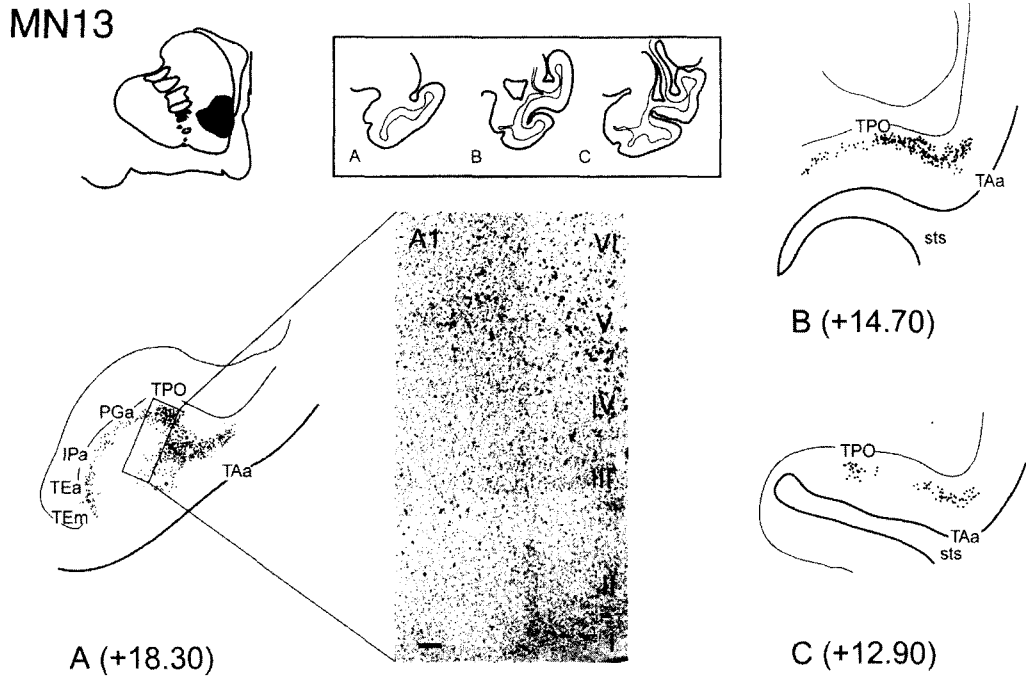


Fig. 2. Schematic drawings illustrating the distribution of the retrogradely labeled cells in the different levels of the cortex in the STS, after HRP injections placed in the ventromedial caudate nucleus (Case MN13). Schematic drawings in a square box are illustrating the whole view of the temporal lobes at a given levels. Inset A1, Labeled cells at the rostral TPO are found in layers III and V/VI of the six-layered cortex. Numbers next to labels indicate approximate AP (anteroposterior) level, relative to interaural zero. Scale bar = 100 μ m.

contained small numbers of HRP-labeled cells, whereas the area TAa contained no labeled cells (Fig. 3A-C). The

rostral TPO contained a moderate number of HRP-labeled cells (Fig. 3A-B). The area PGa also contained a

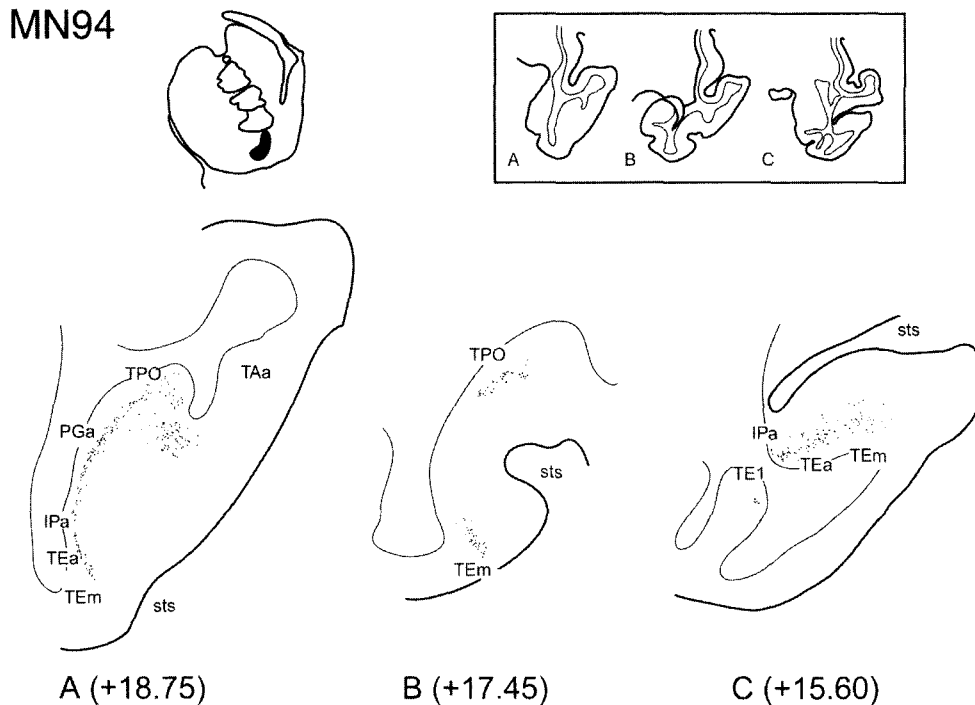


Fig. 3. Schematic drawings illustrating the distribution of the retrogradely labeled cells in the different levels of the cortex in the STS, after HRP injections placed in the ventral shell of the nucleus accumbens (NA) (Case MN94). Schematic drawings in a square box are illustrating the whole view of the temporal lobes at a given levels. Numbers next to labels indicate approximate AP level, relative to interaural zero.

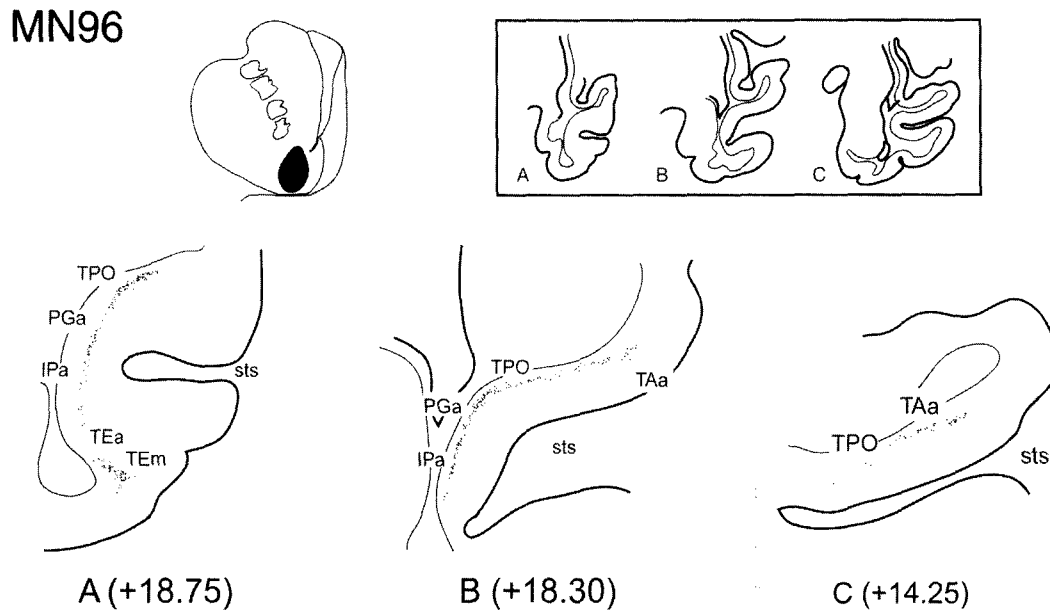


Fig. 4. Schematic drawings illustrating the distribution of the retrogradely labeled cells in the different levels of the cortex in the STS, after HRP injections placed in the ventral shell of the NA (Case MN96). Schematic drawings in a square box are illustrating the whole view of the temporal lobes at a given levels. Numbers next to labels indicate approximate AP level, relative to interaural zero.

few HRP-labeled cells at the rostral level (Fig. 3A).

Case MN96

The rostral portions of the areas IPa, TEa, and TEm contained small numbers of HRP-labeled cells (Fig. 4A-B). Some HRP-labeled cells were also detected in the rostral TAa (Fig. 4B-C). The areas TPO and PGa at the rostral level contained a small number of labeled cells (Fig. 4A-C).

Projections to the central shell of the NA (Case MN26)

Few HRP-labeled cells were seen at the rostral (Fig. 5A) and caudal (Fig. 5D) levels of the area IPa. The areas TEa and TEm also contained few labeled cells at the rostral and middle levels (Fig. 5C-D). In general, there were few HRP-labeled cells throughout rostrocaudal extent of the area TAa (Fig. 5A-E). Both the unimodal and the multimodal association cortices were found to have relatively less labeled cells throughout the rostrocaudal extent in comparison to the injections into the ventromedial caudate nucleus and the ventral shell (see Table 1). Thus, the central shell of the NA appeared to be less extensively connected to the sensory association cortex than the ventromedial caudate nucleus and the ventral shell.

Projections to the dorsal core of the NA (Case MN38)

There were none or very few LY-labeled cells in both the unimodal and multimodal association areas. Specifically,

occasional scattered labeled cells were observed in the unimodal area (IPa, TEa, TEm, and TAa) and the multimodal area (TPO) at the rostral level (Fig. 6A-C). These results indicate that the dorsal core of the NA receives very few sensory information.

Projections to the ventrolateral putamen (Case MN40)

Occasional scattered labeled cells were observed in the STS. There were a few LY-labeled cells in the rostral and caudal levels of the area IPa (Fig. 7A-C). The rostral TAa also contained a few labeled cells. However, there were no labeled cells found in the area TEa and TEm. Thus, the ventrolateral putamen receives a little somatosensory and auditory information but almost no visual information. Only sparsely labeled cells were observed throughout the rostrocaudal extent of the area TPO. A few labeled cells were also seen in the rostral PGa as well as the caudal PGa.

Discussion

In the present study, we demonstrated that, in primates, the main projections from the unimodal and multimodal sensory association areas in the STS were terminated in the ventromedial caudate nucleus and the shells of the NA. In contrast, there were few projections to the dorsal core of the NA and the ventrolateral putamen from the sensory association areas in the STS. These results indicate that, in the ventral striatum, the ventromedial caudate nucleus and the shell of the NA are the major integration sites for sensory input and are functionally

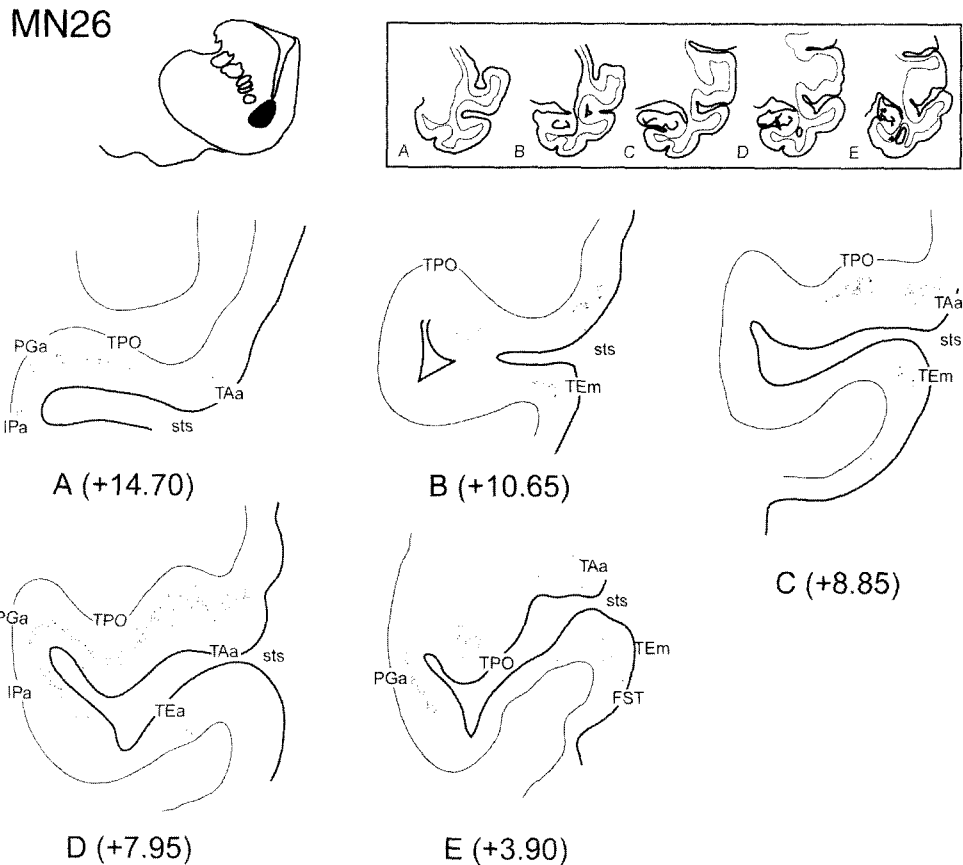


Fig. 5. Schematic drawings illustrating the distribution of the retrogradely labeled cells in the different levels of the cortex in the STS, after HRP injections placed in the central shell of the NA (Case MN26). Schematic drawings in a square box are illustrating the whole view of the temporal lobes at a given levels. Numbers next to labels indicate approximate AP level, relative to interaural zero.

different from the dorsal core of the NA and the ventrolateral putamen.

Connectivity between the ventral striatum and the sensory association cortex in the STS

Several studies have shown that afferents from other limbic-related structures were also terminated in the ventromedial caudate nucleus and the shell of the NA (Kunishio and Haber, 1994; Lynd-Balta and Haber, 1994; Giménez-Amaya et al., 1995). These results suggest that the ventromedial part of the ventral striatum in primates is the main site for converging projections from the limbic and sensory association cortices. The ventromedial caudate nucleus and the shell of the NA also shared some afferent input from the orbitomedial prefrontal cortex (OMPFC) (Giménez-Amaya et al., 1995; Haber et al., 1995). Although the ventromedial caudate nucleus and the shell of the NA were both innervated by the unimodal and multimodal sensory association areas in the STS, the ventromedial caudate nucleus and the ventral shell received a larger portion of these projections than the central shell of the NA. This suggests that a

strong connectivity between the sensory association cortex in the STS and the ventromedial caudate nucleus as well as the ventral shell of the NA.

Ventral striatal projections from the unimodal sensory association cortex in the STS

The unimodal association cortex within the STS receives post-Rolandic input derived either from a single primary sensory cortex or an association cortex related to a single modality of sensation. There are some different ventral striatal projections between the rostral and caudal parts of the unimodal sensory association cortex of the STS. The rostral stream, which preferentially targets the orbitofrontal cortex, appears to be primarily engaged in phonetic processing (area TAa), visual recognition of face (area TEa and TEM), and somatosensory information for head, neck, and face (IPa) (Baylis et al., 1987; Seltzer and Pandya, 1989; Barnes and Pandya, 1992). We showed that most of the ventral striatal projections from the area TAa, IPa, TEa, and TEM were originated from the rostral parts of these areas. These findings suggest the possibility that the ventromedial caudate

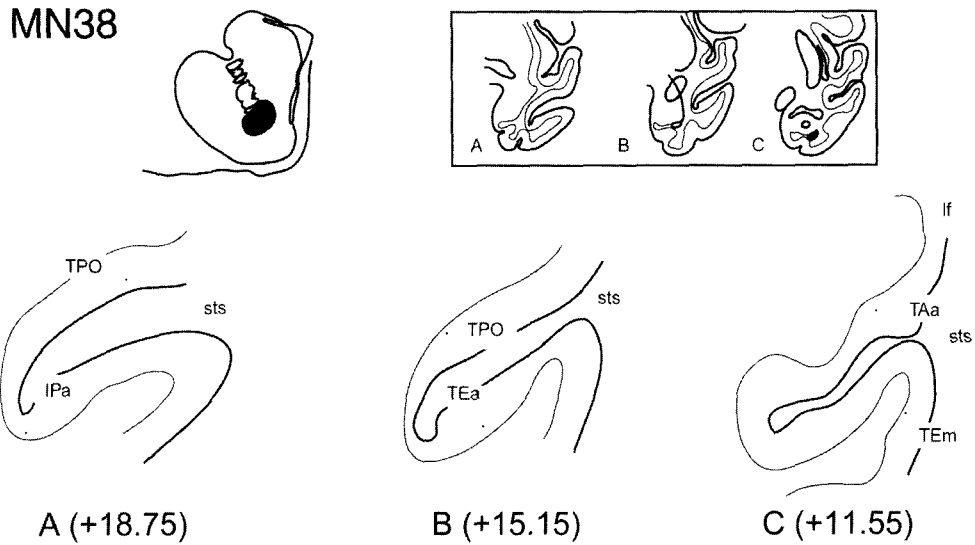


Fig. 6. Schematic drawings illustrating the distribution of the retrogradely labeled cells in the different levels of the cortex in the STS, after LY injections placed in the dorsal core of the NA (Case MN38). Schematic drawings in a square box are illustrating the whole view of the temporal lobes at a given levels. Numbers next to labels indicate approximate AP level, relative to interaural zero.

nucleus and the shell of the NA are closely associated with the face-related recognition memory.

Interestingly, however, the central shell of the NA had additional weak connections with the caudal TAa, IPa, TEa, and TEm. This caudal stream, associated preferentially with the lateral prefrontal cortex, is mostly involved in auditory-spatial processing, visuospatial, and

somatosensory information for the trunk and body (Jones and Powell, 1970; Barbas and Mesulam, 1981; Pandya, 1982; Schwartz and Goldman-Rakic, 1984; Baylis et al., 1987; Petrides and Pandya, 1988; Seltzer and Pandya, 1989). Thus, these observations indicate that the central shell of the NA seems to be weakly involved in processing of recognition and spatial sensory

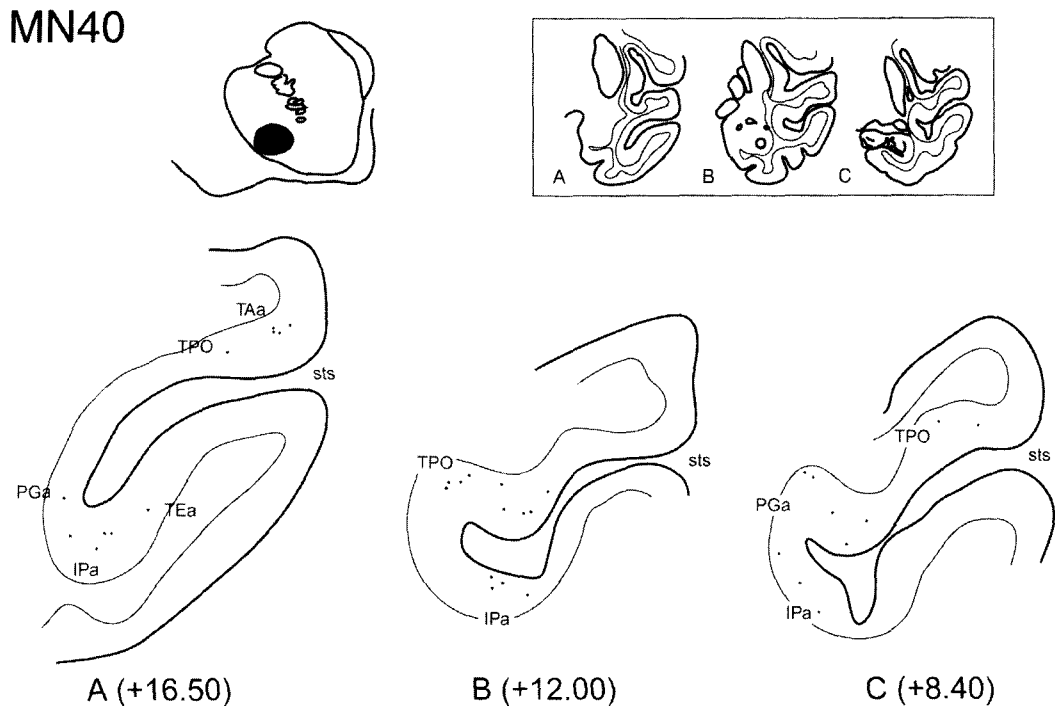


Fig. 7. Schematic drawings illustrating the distribution of the retrogradely labeled cells in the different levels of the cortex in the STS, after LY injections placed in the ventrolateral putamen (Case MN40). Schematic drawings in a square box are illustrating the whole view of the temporal lobes at a given levels. Numbers next to labels indicate approximate AP level, relative to interaural zero.

information and, therefore, functionally different from the ventromedial caudate nucleus and the ventral shell of the NA.

Ventral striatal projections from the multimodal sensory association cortex in the STS

In the multimodal sensory association areas, the rostral portion of the TPO was connected exclusively with the medial and orbital surfaces of the prefrontal cortex having extensive connections with the limbic system, while the caudal TPO predominantly projected to the dorsolateral prefrontal cortex around the principal sulcus, caudal prefrontal cortex, and premotor cortices (Seltzer and Pandya, 1989). The rostral TPO was also interconnected with the third (or rostral)-order sensory association areas and other sensory convergence areas, such as the inferior parietal lobule as well as the caudal parahippocampal gyrus (Pandya and Seltzer, 1982; Rosene and Pandya, 1983). The observation that most of the input to the ventromedial caudate nucleus and the ventral shell of the NA were derived from the rostral TPO suggests that the highest level of cortical integration of sensory and limbic information would be dealt with in the ventromedial caudate nucleus and ventral shell of the NA.

Interestingly, the area TPO has strong connections with the adjacent auditory association areas in the STG and the area TAa in the STS (Van Essen and Maunsell, 1983; Desimone and Ungerleider, 1986; Seltzer and Pandya, 1989). Thus, the strongest input to the ventromedial caudate nucleus from the areas TPO and TAa raises the possibility that the ventromedial caudate nucleus predominantly extends to the auditory modality and contributes to the processing of the higher auditory information.

The area PGa is related predominantly to the somatosensory association areas of the parietal lobe (Seltzer and Pandya, 1978). Projections from the PGa were evenly distributed in the ventromedial caudate nucleus and the ventral shell of the NA. The area PGa also received weak input from auditory-related cortices of the STG, and vision-related extrastriate cortices in a manner similar to the convergence of afferents noted in the area TPO. Thus, the ventromedial caudate nucleus and ventral shell of the NA seems to be a center for integrating sensory information.

No relevant experimental data exist at this time for the subparcellation of the STS polymodal cortex including the areas TPO and PGa. However, the nature of the different frontal lobe targets of the rostral and caudal polymodal cortex may provide some insight into possible differential functional specializations of these sectors and their frontal connections. Thus, the projections from the rostral polymodal cortex to the medial prefrontal cortex, which have extensive connections with limbic structures

(Nauta, 1972), may be a means by which complex sensory information are conveyed to the limbic system and invested with motivational and emotional significance. The projections from the caudal polymodal zones to the caudal prefrontal and premotor cortices may be conveying sensory information to a region where it can be further elaborated functionally for attention and orientation and can contribute to the production of motor sequences (Suzuki and Azuma, 1983; Vaadia et al., 1986). Thus, the ventromedial caudate nucleus and ventral shell of the NA could be involved in the integration of sensory and limbic information for motivating goal-directed behaviors.

Dual projections from the rostral TPO

The cortical layers V and VI of the rostral TPO have been known to be the main sites for reciprocal or "feedback" connections in the unimodal and multimodal association cortex of the STS (Vogt and Pandya, 1978; Tigges et al., 1981; Galaburda, 1983). In the present study, the retrograde tracer injections showed that most of the labeled cells in the rostral TPO were mainly localized in layers V and VI. These results indicate the presence of feedback corticostriatal projections from the layers V and VI to the ventral striatum for integration of higher order sensory and limbic information as previously suggested by Pandya et al. (1988) and Damasio (1989). However, labeled cells in the rostral TPO were also situated in layer III which gives rise to the feedforward projections within the temporal association cortex (Seltzer and Pandya, 1989). Taken together, these findings suggest that "feedforward" and "feedback" connections co-exist in the rostral TPO area. The dual connections of the rostral TPO with the ventral striatum may represent a kind of convergence node. Such a network has been postulated to be important for neural mechanisms underlying directed attention (Mesulam, 1983). Experimental lesions of the parieto-temporal cortex including the area TPO are known to cause states of inattention and neglect (Heilman et al., 1970).

Acknowledgements

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