Korean J Biol Sci 7: 317-325, 2003

Corticostriatal Connections of the Superior Temporal Regions in the Macaque Monkey

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Key Words:

Corticostriatal projection
Superior temporal gyrus
Ventral striatum
Ventromedial caudate nucleus
Auditory association area
Monkey
Retrograde tracing

Corticostriatal connections of auditory areas within the rostral and caudal portions of the superior temporal gyrus (STG) and in the supratemporal plane (STP) of pigtail macaque (*Macacca nemestrina*) were studied with particular emphasis on specific projections to the ventral striatum. Retrograde tracers were injected into five different regions of the ventral striatum such as the ventromedial caudate nucleus, ventral shell, central shell, dorsal core of the nucleus accumbens (NA), and ventrolateral putamen to identify the cells of origin. There were only few projections from the auditory areas in the STP to the ventral striatum. However, the association (or belt) areas of the STG collectively had widespread corticostriatal projections characterized by differential topographic distributions. The rostral parts of the STG strongly projected to the ventromedial caudate nucleus. The mid-portion of the STG also projected to the same ventral striatal regions, but the connections were relatively less extensive. Interestingly, the caudal portion of the STG had no connection to all subregions of the ventral striatum. These differential patterns of corticostriatal connectivity suggest that the ventromedial caudate nucleus would be a major auditory convergence area and mainly involved in sound recognition rather than spatial localization of sound sources.

The temporal lobe of the primate neocortex has been known to be closely associated with sensory perceptions, such as vision and audition (Baylis et al., 1987). In particular, the cortical auditory system has long been known to be within the superior temporal region in both human and nonhuman primates (Von Economo and Horn, 1930; Walker, 1938). In the superior temporal region, the caudal portion of the supratemporal plane (STP) is regarded as an auditory area whereas the superior temporal gyrus (STG) is regarded as an auditory association (or belt) area. However, relatively little information is available regarding the auditory-related superior temporal cortices, even though the corticostriatal projections of frontal, parietal, and occipital areas to the ventral striatum have been examined in detail.

Previous studies using degeneration pathway tracing methods demonstrated that there were restricted projections from certain portions of the STG to caudal sectors of the putamen and to the tail of the caudate nucleus (Whitlock and Nauta, 1956; Kemp and Powell, 1970). However, in recent years, there has been increasing interest about the functional roles of specific portions of the superior temporal cortex (STC) (Colombo et al., 1990; Morel et al., 1993; Rauschecker et al., 1995) due to the possibility that there may be two functional streams of auditory information processing analogous to those of the cortical visual system (Mishkin et al., 1983; Colombo et al., 1996). The rostral portion of the STG, the rostral stream, is involved in sound recognition, whereas the caudal portion, the caudal stream, subserves spatial localization of sound sources (Mishkin et al., 1983; Van Essen and Maunsell, 1983; Colombo et al., 1996).

The ventral striatum has long been considered as an interface between the limbic cortex and motor response to stimuli (Heimer et al., 1982; Kalivas et al., 1993). 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 subdivided into the shell and core subterritories which have different connectional, histochemical, and pharmacological properties (Berendse et al., 1992; Deutch and Cameron, 1992; Zahm and Heimer, 1993). Behavioral studies indicated that subterritories of the ventral striatum are differentially involved in specific goal-directed behaviors (Nishino et al., 1984; Schultz, 1992). Thus, differential connections between the sensory association areas and the ventral

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striatum would provide different contributions to the generation of motor behavior through the sensory-limbic integration.

To understand more fully the neural underpinnings of the differential roles of the STC, we injected retrograde tracers into the ventral striatum and determined the topographical organizations of corticostriatal projections from different levels of the STC to various functional domains of the ventral striatum. We demonstrated strong cortico-ventral striatal connectivity of the rostral auditory association areas with the ventromedial caudate nucleus, which might be specifically involved in auditory perception rather than in spatial localization of sounds. The present detailed information regarding connectional relationships of these regions supports the hypothesis that the rostrocaudal organization of corticostriatal projections is in general related to functional differentiation of the ventral striatum (Robbins and Everitt, 1996).

Materials and Methods

Retrograde tracing study

Seven adult pigtail macaques (*Macacca nemestrina*) 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. After monkeys were placed in a Kopf stereotaxic apparatus, a midline scalp incision was made and then muscle and fascia were displaced laterally to expose the skull. A craniotomy (2-3 cm^2) was made over the region of interest, and small dural incisions were made only at recording or injection. 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 μl Hamilton syringe. After the injection, the syringe remained in place for 20 min to prevent leakage up into the needle track. After finishing tracer injections, the wound was closed in layers. Monkeys were again deeply anesthetized 10-12 d after the surgery with phenobarbital and perfused with saline followed by 4% paraformaldehyde solution containing 1.5% sucrose in 0.1 M phosphate buffer, pH 7.4. The brains were cryoprotected in increasing gradients of sucrose (10, 20, and finally 30%). Serial sections (50 μm) were cut on a sliding microtome and put into 0.1 M phosphate buffer or stored in a cryoprotectant solution.

Immunocytochemical stain

We used immunocytochemical techniques to visualize the tracer. Before incubation with primary antiserum, tissue was incubated in a solution containing 10% methanol and 3% H_2O_2 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 to be immunoreacted with anti-LY (Molecular Probes) or anti-WGA (Sigma) serum were then preincubated for 30 min in 10% normal goat serum (NGS) diluted with PB-T (NGS-PB-T). The tissue was placed in the primary antiserum, anti-LY diluted 1:1000 or anti-WGA-HRP diluted 1:2000 in NGS-PB-T for four nights at 4°C. Avidin-biotin reaction (rabbit Vectastain ABC kit; Vector Laboratories, Burlingama, CA) was used to visualize the LY and WGA. The tissue was rinsed in PB-T before incubating in biotinylated goat anti-rabbit 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. Antisera 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% H_2O_2 in 0.5 M Tris buffer. For intensified staining, the tissues were rinsed several times and then 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 superior temporal region 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 nomenclature and abbreviations used are 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 cytoarchitetonic subdivisions of the superior temporal region as described by Galaburda and Pandya (1983). On the basis of frontal association connections, the belt areas of the STG were further subdivided into three major sectors in rostrocaudal direction; the rostral, middle, and caudal association areas, respectively (Chavis and Pandya, 1976). The caudal auditory association area consists of the TPt, PaAL, and the caudal portion of the area ST3. The middle auditory association area is composed of the rostral portion of the area ST3, while the rostral auditory association area includes the areas ST1 and ST2.

Abbrebiations

lf, lateral fissure; NA, nucleus accumbens; PaAL, paraauditory cortex, lateral part; PaAR, paraauditory cortex, rostral part; PaIL, parainsular cortex, lateral part; PaIM, parainsular cortex, medial part; ProKM, prokoniocortex, medial part; Pu, putamen; ST1, superior temporal sulc area 1; ST2G, superior temporal sulc area 2, gyral; ST2S, superior temporal sulc area 2, sulcal; ST3, superior temporal sulc area 3; STC, superior temporal cortex; STG, superior temporal gyrus; STP, supratemporal plane; sts, superior temporal sulcus; TPt, temporoparietal area

Results

Location of retrograde tracer injection sites in the ventral striatum

Total six injections were placed in five different parts of the ventral striatum (Fig. 1), as previously described by Jung and Hong (2003). One injection was placed in the ventromedial caudate nucleus (Case MN13). Three injection sites were located in the shell of NA, two in the ventral shell of the NA (Cases MN94 and MN96) and one in the central shell of the NA (Case MN26). Another site was centered in the dorsal core of the NA (Case MN38) and the final site laterally into the ventrolateral putamen (Cases MN40).

Projections from the superior temporal regions to the ventral striatum

After injection of retrograde tracers (HRP or LY) into various regions of the ventral striatum, labeled cells seen in the superior temporal regions were summarized in Table 1.

Projections to the ventromedial caudate nucleus (Case MN13)

In the STP, there were no HRP-labeled cells seen in the primary and secondary auditory areas. A few HRP-labeled cells were observed in the rostral (PaAR) and lateral (PaAL) parakoniocortical areas (Fig. 2B, C), which surround the primary auditory koniocortical area (Pandya and Sanides, 1973; Jones and Burton, 1976). Small numbers of HRP-labeled cells were also seen in the medial (PaIM) and lateral (PaIL) parainsular belt areas (Fig. 2B).

However, the ventromedial caudate nucleus received the densest projections from the STG. Most of the labeled cells, distributed in layers V and VI (Fig. 2A1), were limited to the rostral and middle parts of the STG. Rostral auditory association areas (areas ST1 and ST2) contained the largest number of HRP-labeled cells, while the middle auditory area (area ST3) contained moderate numbers of HRP-labeled cells (Fig. 2A-C). Interestingly,

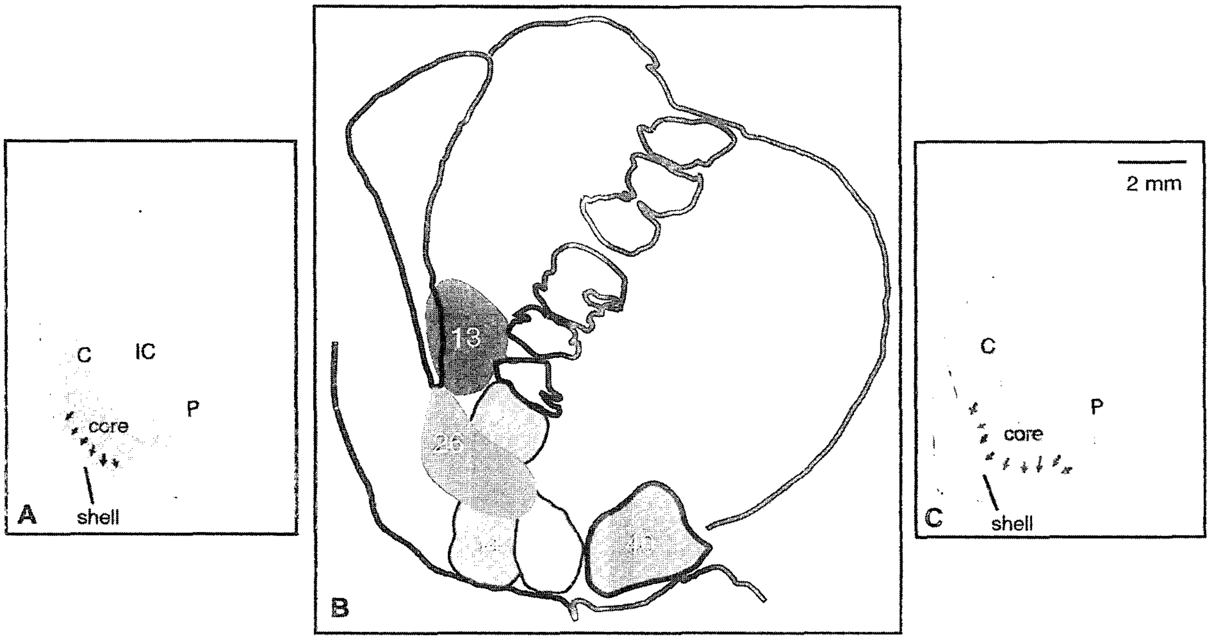


Fig. 1. Locations of retrograde tracer Injection sites. Retrograde tracers, HRP or LY, were used in this study to evaluate the superior temporo-striatal projections to the ventral striatum in the adult pigtail macaque (*Macacca nemestrina*). A, A photomicrograph of the rostral striatum showing CaBP-immunoreactivity, which was relatively lower in the shell of NA compared to the core regions outside of the shell. Arrows indicate the border line separating the shell area from the core region of NA. B, Schematic drawing at a given level of the ventral striatum illustrating the six injection sites (Cases MN13, 26, 38, 40, 94, 96). C, A photomicrograph of a retrograde tracer injection site from Case MN96. Photomicrographs of other injection sites were previously illustrated in Jung and Hong (2003). C, caudate nucleus; P, putamen; IC, internal capsule.

Table 1. Summary of retrogradely labeled cells in superior temporal regions

Superior temporal region	Ventral striatal injection site				
	Ventromedial caudate nu	Ventral shell of NA	Central shell of NA	Dorsal core of NA	Ventrolateral Pu
Auditory area in STP					
Primary auditory area	–	–	–	–	–
Secondary auditory area	–	–	–	+	+
Parakoniocortical belt areas	+	–	+	–	–
Parainsular belt areas	++	+	–	+	+
Auditory association area in STG					
ST1	++++	++	–	+	+
ST2	++++	+	+++	+	+
ST3	+++	+	+	+	–
TPt	–	–	–	–	–

This summary is based on relative densities of retrogradely labeled neurons in each of the subregions of the superior temporal regions (STG) as seen in the representative drawings, where - represents no retrogradely labeled cells observed and + to ++++ represent increasing relative densities from occasional cells to very dense labeling. Each of the cases had a different number of representative drawings. Thus, the relative densities of retrogradely labeled neurons in each case were weighted accordingly for more accurate comparison with the other cases. Nu, nucleus.

there were no labeled cells in the caudal STG (TPt). Therefore, the ventral striatum is mainly connected with the rostral auditory association areas in STG, which might be involved in sound recognition rather than sound localization.

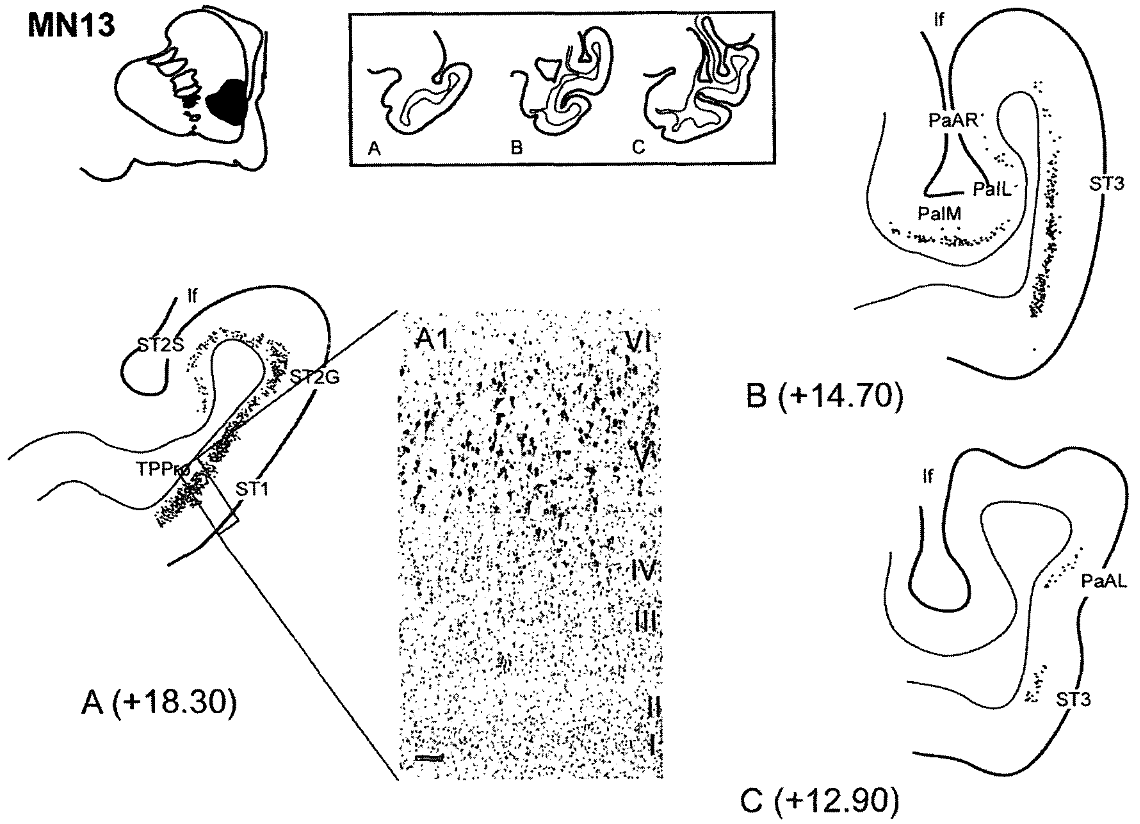
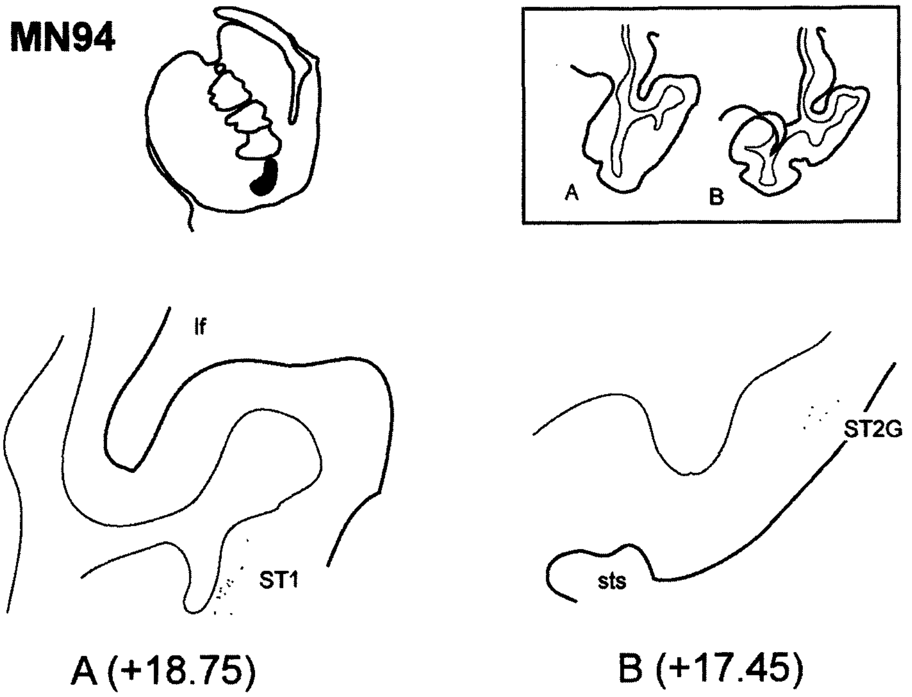


Fig. 2. Schematic drawings illustrating the distribution of the retrogradely labeled cells in the different levels of the STG, after HRP injections placed in the ventromedial caudate nucleus (Case MN13). Schematic drawings in a square box illustrate the whole view of the temporal lobes at given levels.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



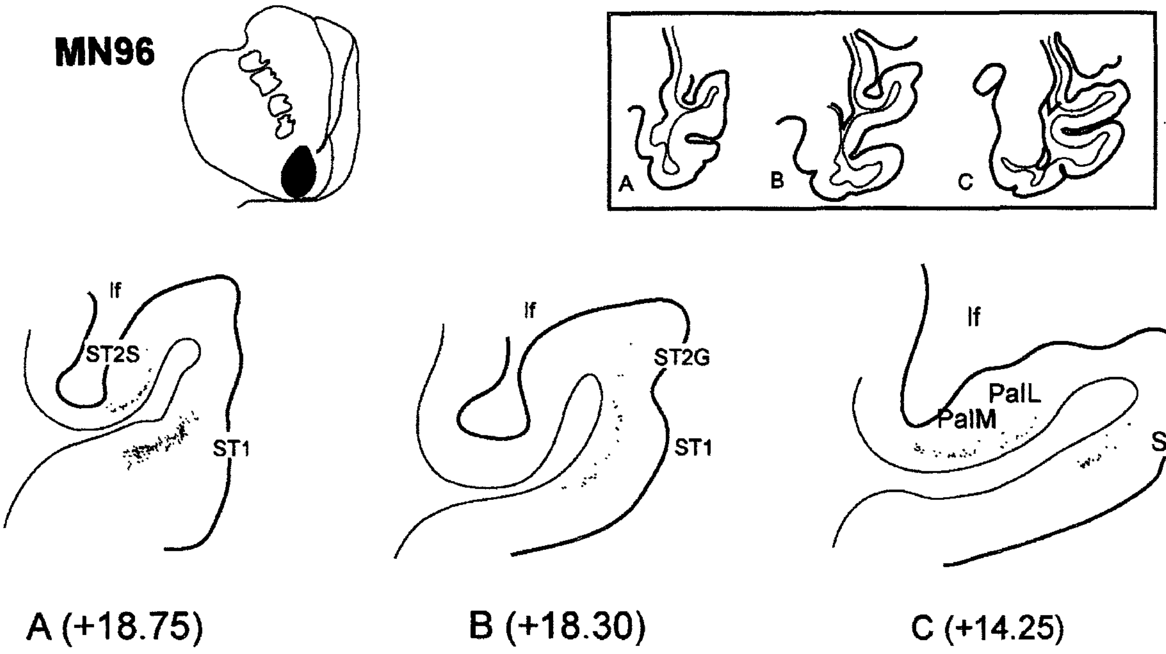
A (+18.75)

B (+17.45)

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

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

Case MN94. In the STP, there were no HRP-labeled cells in the primary and secondary auditory areas or in



A (+18.75)

B (+18.30)

C (+14.25)

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

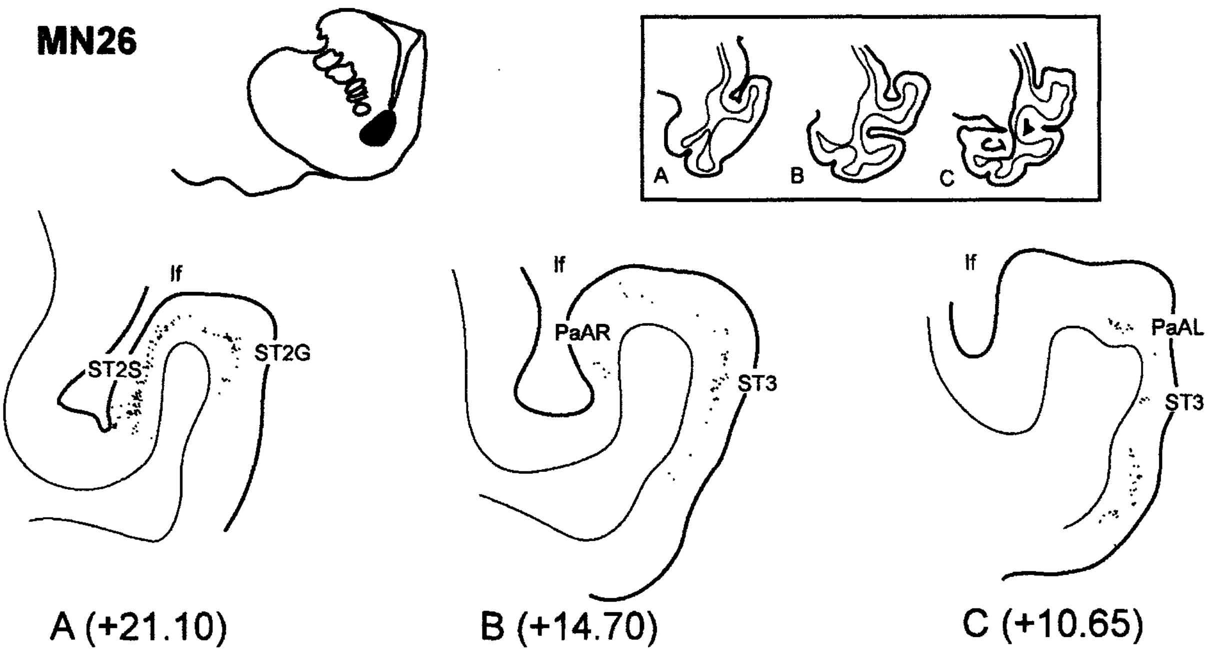


Fig. 5. Schematic drawings illustrating the distribution of the retrogradely labeled cells in the different levels of the STG, after HRP injections placed in the central shell of the NA (case MN26). Schematic drawings in a square box illustrate the whole view of the temporal lobes at given levels. Numbers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

the parakoniocortical and parainsular belt areas. In the STG, a small number of HRP-labeled cells were found in the ST1 and ST2G (Fig. 3A, B) but there were no labeled cells seen in the caudal STG.

Case MN96. A few HRP-labeled cells were found in the parainsular belt areas of the STP (Fig. 4C). But no labeled cells were seen in the primary and secondary auditory areas, and parakoniocortical belt areas. In the STG, the majority of labeled cells were seen in the areas ST1 and ST2 (Fig. 4A, B) and a few labeled cells were

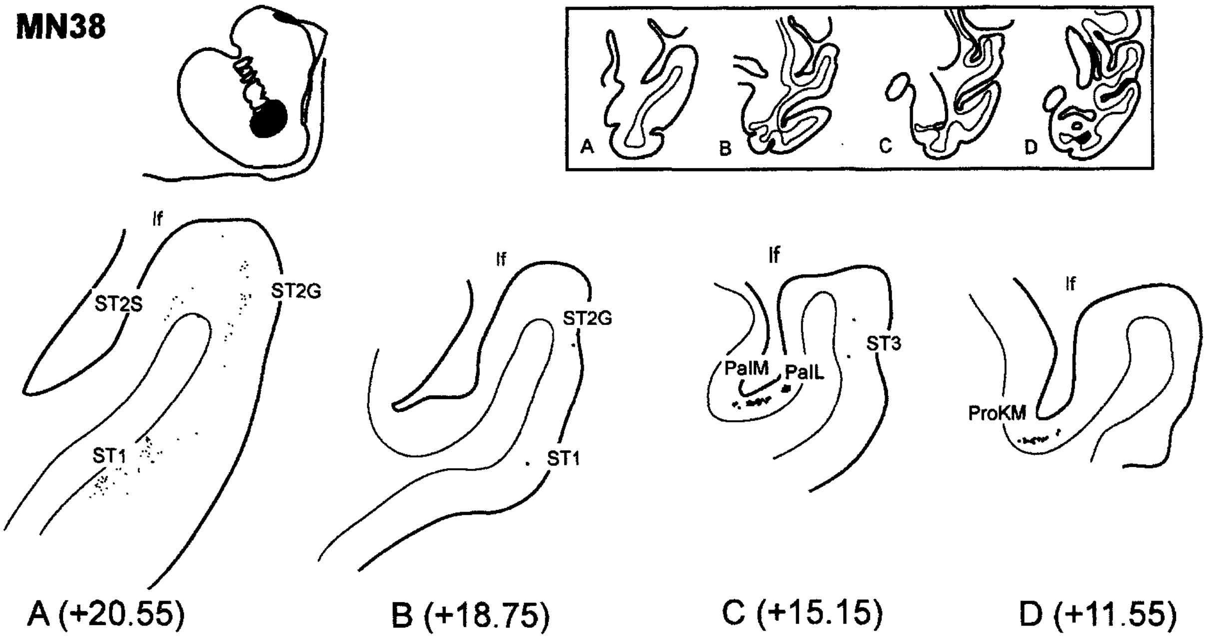
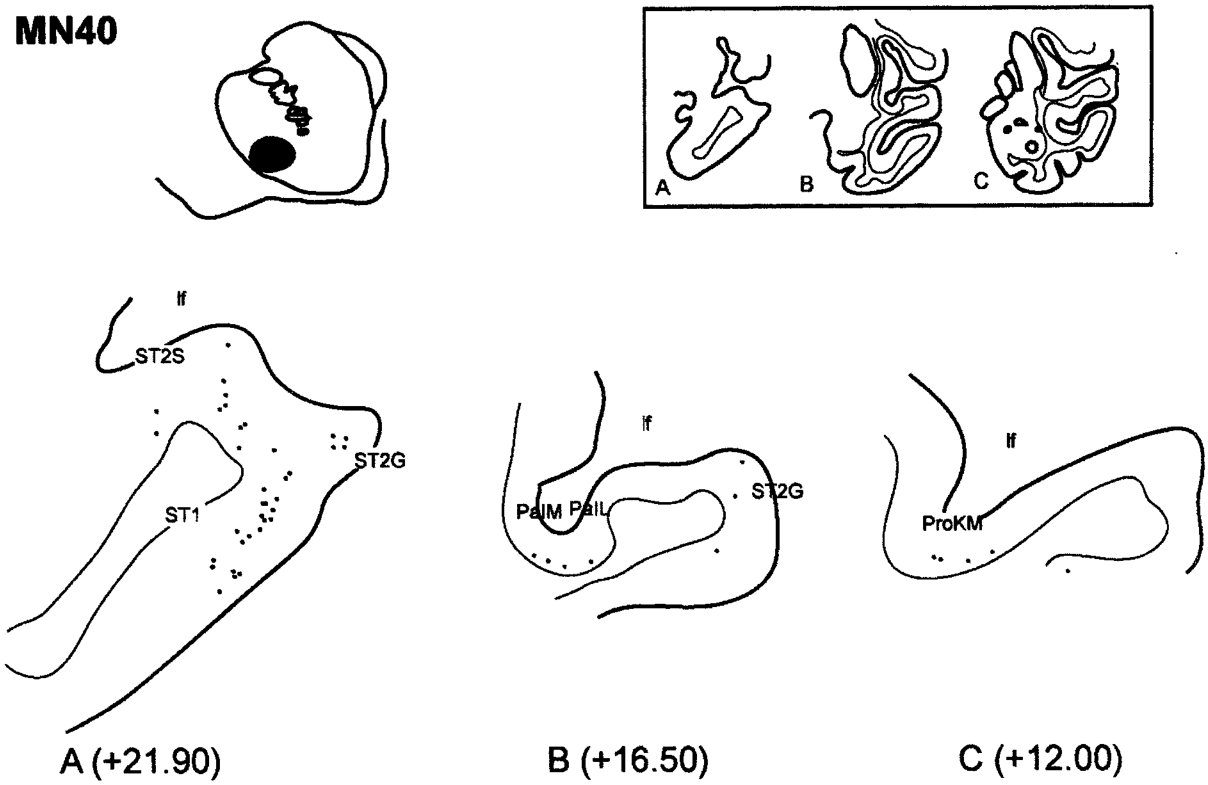


Fig. 6. Schematic drawings illustrating the distribution of the retrogradely labeled cells in the different levels of the STG, after LY injections placed in the dorsal core of the NA (Case MN38). Schematic drawings in square boxes illustrate the whole view of the temporal lobes at given levels. Numbers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



A (+21.90) B (+16.50) C (+12.00)

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

also seen in the ST3 (Fig. 4C). There were no labeled cells in the caudal STG.

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

In the STP, a few HRP-labeled cells were observed in the rostral and lateral parakoniocortical belt areas, but labeled cells were not observed in the primary and secondary auditory areas (Fig. 5B, C). HRP-labeled cells were seen in the areas ST2 and ST3 of the STG, but the concentration of labeled cells was much denser in the area ST2 (Fig. 5A) than in the area ST3 (Fig. 5B, C). No cells were labeled in the caudal STG.

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

There were no labeled cells in primary auditory areas in the STP. In contrast to the previous cases MN13, MN94, MN96, and MN26 (the injections into the ventromedial nucleus, the ventral and central regions of the shell), a few LY-labeled cells were observed in the secondary auditory area (ProKM) (Fig. 6D). In addition, a few LY-labeled cells were also seen in the parainsular belt areas (Fig. 6C). In the STG, small numbers of labeled cells were found in areas ST1 and ST2G (Fig. 6A, B). A few cells were also seen in the area ST2S (Fig. 6A). Only sparsely scattered labeled cells were located in the ST3 (Fig. 6C). There were no labeled cells in the caudal STG.

Projections to the ventrolateral putamen (Case MN40)

In comparison with the previous cases, the fewest number of LY-labeled cells were observed both in the STP and STG. A few LY-labeled cells were found in the ProKM of the STP (Fig. 7C). This finding was similar to the Case MN38, where a few labeled cells were seen in the secondary auditory area. There were also a few scattered labeled cells in the parainsular belt areas (Fig. 7B). But, no labeled cells were found in the primary auditory areas. In the STG, a few labeled cells were observed in the areas ST1, ST2G, and ST2S (Fig. 7A, B), while no labeled cells were seen in the area ST3 and in the caudal STG.

Discussion

Connectivity between auditory areas in STP and the ventral striatum

The primary auditory area in monkey has been shown to be in the caudal portion of the STP (Walzl and Woolsey, 1943; Merzenich and Brugge, 1973). In the present study, retrograde tracing technique demonstrated that the primary auditory area in the STP had no projections to the ventral striatum. A similar pattern of corticostriatal connectivity has been reported for the primary visual area (Kemp and Powell, 1970). However, the secondary auditory area had very limited projections to the dorsal core of the NA and the ventrolateral putamen. Thus, these results indicate that the most limited ventral striatal connections of the auditory cortical system are present between the secondary auditory area and the dorsolateral part of the ventral striatum.

Strong connectivity between the lateral auditory association areas and the ventral striatum

Architectonic analyses of the STC have revealed a belt-like organization for the auditory areas, with a primary auditory area surrounded by association (or belt) areas (Jones and Burton, 1976; Galaburda and Pandya, 1983; Morel et al., 1993). The belts are composed of parakoniocortical and parainsular belt areas in the STP and lateral belt areas in the STG (Jones and Burton, 1976). The present study demonstrated that parakoniocortical and parainsular belt areas in the STP had a few projections to all subregions of the ventral striatum, whereas lateral belt areas in the STG had prominent projections to the ventromedial part of the ventral striatum. Although the ventromedial part of the ventral striatum had overlapping innervations from the lateral belt areas in the STG, the strongest projections from lateral belt areas were directed to the ventromedial caudate nucleus. Several studies described that the auditory cortices tend to project most strongly to the ventral portions of the head of the caudate nucleus and to the medial portion of the tail (Saint-Cyr et al., 1990; Yeterian and Pandya, 1995). These results indicate that the ventromedial caudate nucleus is the main projection site from the lateral auditory association areas in the STG.

Within the lateral association areas of the STG, there was a shift in the topographic distribution of corticostriatal projections from rostral to caudal regions. The rostral portion of the STG, in comparison with the middle region, had more marked connections to the ventromedial caudate nucleus. A similar overall pattern of corticostriatal connectivity from the rostral STG has been shown by other investigators (Van Hoesen et al., 1981; Selemon and Goldman-Rakic, 1985; Goldman-Rakic and Selemon, 1986). The relatively moderate projections from the middle STG were also directed to the ventromedial caudate nucleus. However, there were no projections from the caudal STG to the ventral striatum. Taken together, these results strongly indicate that the ventromedial caudate nucleus would be a major auditory convergence area for projections from the rostral and middle auditory belt areas, with relative rostral dominance.

Functional roles of the cortico-ventral striatal connections in audition

Previous studies proposed the existence of two streams of auditory information processing analogous to the ventral and dorsal streams in the cortical visual system. The rostral portion of the STG, the rostral stream, is involved in sound recognition, whereas the caudal portion, the caudal stream, subserves spatial localization of sound sources (Mishkin et al., 1983; Van Essen and Maunsell, 1983; Colombo et al., 1996). Similarly, other studies also proposed that the cortical auditory system of monkeys could be divided into at least two processing streams. A 'spatial' stream originating in the caudal part of the STG projects to the posterior parietal and dorsolateral prefrontal cortex, whereas a 'pattern analyzing' stream originating in the more rostral portions of the STG projects to the ventral and orbitofrontal prefrontal cortex (Hackett et al., 1999; Romanski et al., 1999; Rauschecker and Tian, 2000). Thus, according to the strong cortico-ventral striatal connectivity of the rostral auditory belt areas, the ventromedial caudate nucleus may be involved specifically in auditory perception rather than in spatial localization of sounds. On the other hand, the middle portion of the STG has been known to have a role in the encoding of species-specific communication sounds (Rauschecker et al., 1995).

Acknowledgements

This work was supported by a grant from Dongguk University Research Fund.

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[Received August 16, 2003; accepted September 8, 2003]