The Intrinsic Architectonic and Connectional Organization of the Superior Temporal Region of the Rhesus Monkey

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ABSTRACT

The superior temporal region (STR) in the rhesus monkey includes the circular sulcus (Cis), the supratemporal plane (STP), and the superior temporal gyrus (STG). Rostrally the STR is continuous with the periallocortices of the prepyriform and anterior insular regions; caudally it borders the isocortices of the inferior parietal lobule and the superior temporal sulcus. The STR contains 12 cytoarchitectonic areas: four fields on the Cis, four on the STP, and four on the STG. The sulcal fields (root fields) are adjacent to the insula and resemble it in the possession of a relatively strong layer V; the STP fields (core fields) are characterized by well-developed layer IV; and the STG fields (belt fields) exhibit strong differentiation of layer III. In each line of fields the more rostral ones show relative prominence of the deeper layers, with increasing prominence of the superficial layers occurring caudally in a stepwise fashion.

Analysis of the connectional organization of the fields within the STR suggests an assembly of four rostrocaudal stages, each composed of one field from each line—a root, a core, and a belt field. There is a specific arrangement of connections among the fields of a given stage and between fields in adjacent stages. Projections directed caudally from one field to another field in the adjacent stage arise in layers V and VI and terminate in the superficial layers (mainly layer I). Projections directed to a field in a rostrally adjacent stage arise from layer III neurons and terminate in layers III and IV, usually in columns. There is also a laminar specificity between fields lying within a given stage.

Key words: superior temporal region, architectonics, connections, auditory

It has been long known that the superior portions of the temporal lobe of the primate brain (superior temporal region, STR) contain the cortical representations of the auditory system. Early architectonic parcellations of this region in the monkey identified a granular field on the superior temporal plane (STP) surrounded by several less granular architectonic areas (Brodmann, '05; Walker, '37; von Bonin and Bailey, '47). These fields were subsequently shown to coincide to a large extent with the physiologically derived primary and association auditory cortices (Ades and Felder, '42; Merzenich and Brugge, '73; Imig et al., '77). In addition the auditory relationship of these fields has been supported by studies of cortical and subcortical connections (Walker, '37; Pandya et al., '69; Jones and Powell, '70; Mesulam and Pandya, '73; Pandya and Sanides, '73; Fitzpatrick and Imig, '80).

More recently connectional and physiological studies

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dealing primarily with the cortical representation of the visual system (Zeki, '78; Van Essen, '79) have disclosed multiple representations arranged in complex fashion and including architectonic areas previously unsuspected of having visual functions. Although the auditory system has not been studied in similar detail, a variety of data suggest that its complexity and extent are greater than hitherto known. For instance the connectional relationship to the auditory system of the more anterior portions of the STR is beginning to emerge. On the basis of architectonic analysis and corticocortical connections it has been shown that the auditory region may include additional architectonic areas, some of which reach all the way to the temporal pole (Pandya and Sanides, '73; Jones and Burton, '76). In addition projections from the caudal part of the medial geniculate nucleus have been shown to reach rostral temporal fields (Wegener, '83; Mesulam and Pandya, '73). Similarly the connections, architecture, and physiology of fields lying in the posterior portions of the superior temporal gyrus (STG) near the temporoparietal junction suggest that they are also part of the auditory system (Merzenich and Brugge, '73; Mesulam and Pandya, '73; Pandya and Sanides, '73; Jones and Burton, '76; Fitzpatrick and Imig, '80; Leionen et al., '80). These findings suggest that the classical view of auditory representation in the cortex may be excessively conservative. The purpose of this study was to explore the architecture and connectional interrelations among areas on the STR in order to better specify the organization of the cortical auditory representation.

In previous studies emphasis had been placed on the long corticocortical connections of the superior temporal areas (Jones and Powell, '70; Chavis and Pandya, '76), while the connections between neighboring auditory architectonic areas in the STR (intrinsmic connections) have been only partially defined (Fitzpatrick and Imig, '80). In the visual system it has been shown that adjacent rostrocaudal architectonic fields in the occipitotemporal cortex maintain a specific laminar connectional arrangement in terms of cells of origin and termination (Rocland and Pandya, '73; Tigges et al., '81). The present study is concerned primarily with the intrinsic connections of the STR and their laminar organization. The findings reported here suggest that the rostral and caudal fields of the STR are architectonically and connectionally linked to the classical auditory areas. Moreover there exists a sharp correspondence between architectonic and connectional patterns, an orderly arrangement of architectonic areas with a uniform scheme of interconnections, and a predictable laminar pattern of cells of origin and termination.

MATERIALS AND METHODS

In ten rhesus monkeys, intracortical injections of labelled amino acids (H-leucine and/or proline) were made at different sites in the STR, guided by the architectonic parcellation described by Pandya and Sanides (73). The isotope injections varied between 0.4 and 0.6 μl at a concentration of 25-50 μCi/μl. After a survival period of 5-8 days, three of the animals were deeply anesthetized and perfused transcardially with physiologic saline followed by 10% formalin solution. Two days prior to sacrificing the remaining animals they received an additional intracortical injection of a 20% solution of horseradish peroxidase (HRP; 0.05-0.08 μl/site) in STR areas of the hemisphere opposite the isotope injection. These animals were perfused according to the protocol described by Rosene and Mesulam (78). The brains were then removed, and the hemispheres to be processed for autoradiography were stored in 50% ethanol. The HRP-injected hemispheres were stored in a sucrose-buffer solution for 24 hours at 4°C, cut into 40-μm sections on a freezing microtome, and the sections prepared for the tetramethyl benzidine incubation procedure of Mesulam (76). The isotope-injected hemispheres were embedded in paraffin, cut at a thickness of 10 μm, and processed according to the technique described by Cowan et al. (72). Exposure time varied between 3 and 7 months. The distribution of labelled fibers and HRP-positive neurons was recorded on tracings made of each section. This information was then reconstructed on diagrams made from photographs of each hemisphere semistylized to show the banks of the lateral fissure and superior temporal sulcus. Architectonic areas and borders were checked in the experimental material which was counterstained with thionine (autoradiography) and neutral red (HRP). These areas were additionally compared with cell reveal-embedded material stained by the Nissl and Loyez methods for cell bodies and myelinated fibers, respectively.

Architectonic parcellations of the STR were made in three normal brains. These brains had been embedded in celloidin and cut serially in three planes and at 35 μm thickness. Every tenth section was prepared for cell stain with cresylechtviolet, and the adjacent section for myelin stain with the Loyez method. The architectonic borders found in the Nissl-stained material were compared with those obtained in the myelin sections, and reconstruction of architectonic subdivisions was carried out on the photographs of superior temporal regions of each brain.

RESULTS

Description of cytoarchitectonic areas

The architectonic findings in the present study are in essential agreement with the previous observations of Pandya and Sanides (73), although minor differences are apparent (Figs. 1B,C, 2). Thus we found that the temporopolar proisocortex extends medially around the temporal pole and occupies a portion of the rostral end of the circular sulcus. In addition, in our observations area Ts, abuts Ts, in the dorsal bank of the superior temporal sulcus. The temporal isocortex is topographically separated from allocortical formations by two structurally intermediate regions, the periallocortex (pAll), adjacent to the allocortex, and the proisocortex (Pro), adjacent to the six-layered isocortex proper. In the rhesus monkey the temporal pAll lying rostrally in the circular sulcus and pole of the temporal lobe can be shown to abut the prepyriform region of the orbital surface of the frontal lobe rostral to the insula (Fig. 3). This pAll, like other cortices which are adjacent to primitive allocortical formations, is essentially a two-strata cortex. The outer stratum is composed of sparsely populated cell layers II and III, and the inner stratum is made up of layers V and VI; a virtually cell-free lamina dissecans separates the two strata. In pAll there is a distinct emphasis in cell size and packing density of the inner stratum and complete fusion of layers V and VI. In the outer stratum layer II shows condensations of coarse neurons. The step from pAll to the proisocortex (Pro) is characterized by an increase in granularization of the cortex and the beginning of a distinct (albeit narrow) layer IV. Layers V and VI are virtually fused, although there is the incipient separation of these two layers. Layer II is somewhat accentuated, but it
The superior temporal region can be subdivided into three subregions according to topography and architectonic characteristics: a medial one along the circular sulcus, a lateral one along the superior temporal gyrus, and (interposed between these two) a central one on the supratemporal plane (Fig. 1A).

The fields of the medial line are characterized by relative strong development of layer V. In it the rostralmost field, area Pro, extends in a caudal direction along the medial half of the circular sulcus (Fig. 1B). Parinsular area paI, still on the sulcus, then lies lateral and caudal to Pro. paI is characterized by the further increase in granularity of a now well-defined layer IV and an increase in emphasis of layer III, although the deeper stratum is still stronger than the outer one (Fig. 4B). Caudal to area paI, along the circular sulcus, lies prokoniocortical area proA (Fig. 4C). Again there is a stepwise increase in granularity and thickness of layer IV and the third layer is still better developed, exhibiting moderate size pyramids in IIIc. In proA the inner stratum is only mildly more emphatic than the outer stratum in cell size and packing density. The caudalmost stage in the circular sulcus line is represented by retroinsular-temporal area reIt (Fig. 4D). This area has a well-developed layer IV and a slightly greater emphasis on the outer, as opposed to the inner stratum. The increasingly stratified appearance of this cortex reflects its proximity to the parietal lobe.

The lateral line of differentiation can be traced mainly along the superior temporal gyrus (Fig. 1A). It begins rostrally with area Ts1 (Fig. 1B). When compared to adjacent area Pro, Ts1 has a well-defined layer IV, and layer III is richer in cell numbers. The infragranular layers V and VI, however, retain the feature of near-fusion (Fig. 4J). In its caudal border Ts1 is met in the dorsal bank of the superior temporal sulcus by area Ts3. Area Ts3, is more granular; the pyramids in layer III are numerous, well developed, and typically arranged in columns four to eight cells in depth; and layers V and VI are clearly segregated (Fig. 4J). Caudal to Ts3 lies area paAlt. This field is externodense, i.e., the outer stratum is more pronounced than the inner; layer IV is one step more developed than in Ts3; layer III is...
richer in small pyramids, and its deeper portion (IIIc) contains the largest pyramids in the superior temporal region; and layer V is impoverished of cells, resulting in a striking separation between V and VI (Fig. 4K). Caudal to paAlt lies the caudalmost field in this lateral line—area Tpt. This temporoparietal area Tpt, as the name denotes, shows some features of the adjacent parietal cortex. Thus, the cortex acquires a more stratified appearance, layer IV begins to regress, and pyramids in layer V increase in size and number. A striking feature of this area is the bandlike appearance of the central layers, as the pyramids in IIIc and Va encroach upon layer IV and intermingle with each other (Fig. 4L).

The central line is found interposed between the medial and lateral lines, and the areas which compose it lie mainly on the supratemporal plane (Fig. 1A). The rostralmost cortex in this line is area Ts2, which extends into the STG (Fig. 1B). In this area the inner stratum is still somewhat prominent; compared with Pro and Ts1, however, area Ts2 has a much better developed layer IV; layers V and VI are clearly separable; and the pyramids in layer III are small and tend to assume a teardrop configuration (Fig. 4E). Caudal to Ts2 lies area paAr. This area is clearly extrudense, and layer IV is better developed than in the medially lying area paI and in the laterally adjacent Ts1. Area paAr is easily identifiable by its striking parvocellularity (Fig. 4F). Caudal to paAr lies koniocortical area KA.1 The

\[1\] In the present study the subdivisions of the koniocortex, KAm and KAAl (Pandya and Sanides, '73), have been combined into a single area KA.
striking externodense appearance of KA reflects the high cell packing density of the outer stratum in contrast with the marked paucity of cells in layer V. This area achieves the highest degree of granularity and width of layer IV in the entire superior temporal region (Fig. 4G). Caudal to KA lies a cortex which represents the final step in the central line - area paAc. When compared with KA, paAc shows a decrement in strength of the outer stratum. Still, layers III and IV are better developed than in adjacent areas relt and Tpt, and layer V pyramids are smaller and fewer in number than in these areas (Fig. 4H). A peculiar characteristic of area paAc is the presence of occasional large cells in layer 11IC, often occurring in clusters.

In summary, the areas lying on the circular sulcus, supratemporal plane and superior temporal gyrus lose prominence of the deeper layers and acquire greater laminar and cellular differentiation in a stepwise fashion as one proceeds caudally from the temporal pole. Four steps can be identified in each line, beginning with the rostral fields and ending caudally with fields which exhibit features of transition to the parietal lobe.

Autoradiography

Isotope injections were made in ten animals (Fig. 5A). For this study descriptions of terminations will be restricted to those found in areas confined to the STR. In case I the injection was aimed at the medial portion of the temporal pole, and the isotope was found primarily in area pAll, with a small amount of spread into adjacent area Pro (Fig. 6A). As shown in the figure, terminal label was observed in discrete clusters in medial Pro and its extension along the circular sulcus, as well as in the lateral portions of Ts1 and Ts2. In area Pro label was observed in all layers (open and closed circles in the figure); in Ts1, the grains were mainly seen in the first layer (open circles in figure); and in Ts2, although label was heaviest in layer I, occasional grains could be found in the other layers as well, intermixed with labelled fibers.

In cases II and III, the injections were directed at the lateral portions of Ts1 and Ts2, respectively, but in both cases the isotope was confined primarily to Ts1. Whereas in case II it extended slightly into area Pro (Fig. 6B), in case III there was a small amount of spread to adjacent Ts2 (case not illustrated). As in case I discrete clusters of label were also noted in case II, this time in areas pAll, Pro, pa1, Ts1 and Ts2 (Fig. 6B). In pAll and Pro the grains were found diffusely in all layers. In pa1 there was label in all layers, but the heaviest concentration was seen in layer I. In Ts1, grains were seen in all layers diffusely, while in Ts2 and Ts3, label was primarily in layer I. The basic pattern of grain distribution in case III was the same as that in case II, except that in the former grains in Ts2 were seen in all layers.

In case IV the injection involved the lateral and supratemporal portion of Ts3 and a small amount of Ts2 and adjacent paAlt (Fig. 6C, 8B). Labelled terminals were seen in areas Pro, Ts1, Ts2, paAlt, Tpt, paAr, KA, pa1, and proA. Rostral to the injection, in areas Pro, Ts1, and Ts2, label was present in the form of discrete columns and in layer IV between the columns (see Fig. 8A). Caudal to the injection, there were grains in area paAlt and a few in area Tpt. In both of these areas, in contrast to the rostral projections, the label was present predominantly in layer I (Fig. 8C). Likewise, on the supratemporal plane, areas paAr and KA exhibited label in the first layer only. The medial areas Pro, pa1, and proA showed grains diffusely in all layers (Fig. 8B).

In case V the injection was confined to the lateral portion of Ts3 and extended caudally into area paAlt (Fig. 6D). The basic pattern of terminations was similar to that of case IV except that no grain was seen in areas paAr and KA in this case. However, areas Tpt and paAc exhibited
Fig. 4. Photomicrograph to show root fields (A–D), core fields (E–H), and belt fields (I–L). For description of nomenclature, topography, and architectonic features refer to text.
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Fig. 5. Composite diagram showing the injection sites on the STR for isotope (A) and HRP (B).

more grains. The laminar distribution of grain was identical to that of case IV, such that rostrally directed projections terminated predominantly in a columnar fashion whereas caudal projections were chiefly found in layer I.

Cases VI and VII received an injection in the supratemporal plane. Isotope in case VI occupied predominantly the medial and caudal portion of KA, extending slightly to adjacent proA (Figs. 6E, 8E) whereas in case VII it involved the entire area KA, extending into adjacent proA, paAr, and paAlt (case not illustrated). Although the basic pattern of projections was similar in both cases, we describe here case VI because it had a smaller injection. Terminal labelling was found in areas Ts, paAlt, Tpt, paAr, KA, paAc, paI, proA, and reIt. Laterally most of the grain was seen in paAlt, but some label was also present in Ts, and Tpt. In these three lateral areas the grain was distributed predominantly in the deeper cell layers. In the supratemporal plane, rostrally lying paAr contained label in and around layer IV and with a tendency to form columns (Fig. 8D). The rostral part of KA not involved in the injection was diffusely labelled. Area paAc, caudal to the injection, exhibited label in layer I mainly (Fig. 8F). The medial zone areas paI, proA, and reIt had label distributed throughout all cell layers (Fig. 8F).

Cases VIII, IX, and X received isotope predominantly in area Tpt with some spread onto adjacent areas paAlt and Ts, (case IX is shown in Figs. 6F, 8G–I). Terminal labelling was seen in areas Ts, paAlt, Tpt, KA, paAc, proA, and reIt. Rostrally in Ts, and in paAlt the label was present in columns and in layer IV between columns (Fig. 8G). Caudal and medial to the injection still within Tpt, grain was seen diffusely in all layers. On the supratemporal plane both areas KA and paAc had grains in layer 1 (Fig. 8I). In the medial zone both areas proA and reIt showed a diffuse pattern of label accumulation.

Horseradish peroxidase

Horseradish peroxidase injections were made in seven animals (Fig. 5B). For the purposes of this study, descriptions of identified labelled neurons will be limited to areas in the superior temporal region. In case I the injection was placed in the medial portion of the temporal pole and remained restricted to the proisocortex (area Pro; Fig. 7A). HRP-positive neurons in this case were observed in areas Pro, Ts, and Tp, and some in TS, paAr, and paI. In Pro and paI labelled neurons were seen in both third and fifth layers (open and closed triangles), while in areas Ts, Ts, and paAr they were observed mainly in the third layer.

In case 2 the injection involved the lateral portion of Pro and a small amount of adjacent Ts, (Fig. 7B). Labelled neurons were found in pAll, the medial portion of Pro, Ts, and Tp. In the periallocortex, the labelled neurons were located predominantly in the deeper layers (open triangles), whereas in the medial Pro (in the circular sulcus), a distinctive labelling was seen in superficial as well as deep neurons. In Ts, labelled neurons were found predominantly in layer III, a few also were found in the deep layers. In Ts, and Ts, most of the labelled neurons were seen in layer III.

In case 3 the injection was confined to Ts and a small portion of adjacent Ts and paAr (Fig. 7C). Labelled cells were seen in discrete patches rostrally in areas pAll, Ts, and Pro and the rostral parts of Ts, not involved by the injection. Caudally label was observed in areas paI, Ts, paAr, paAlt, and some in area KA. In pAll, Pro, and Ts labelled neurons were predominantly located in the fifth and sixth layers (see Fig. 9B). Areas Ts, and Ts, showed labelled neurons both in the third and fifth layers (see Fig. 9C). In paI labelled neurons were located predominantly in the deeper layers, whereas in paAr and KA they appeared mostly in the third layer (see Fig. 9A). Similarly paAlt exhibited neurons predominantly in layer III, although an occasional labelled neuron was also observed in the infragranular layers.

In cases 5 and 7 (latter not illustrated) the injection was
Fig. 6. Diagrammatic representation of the superior temporal region (see Fig. 1) to show the sites of isotope injection (shown in black) and resulting terminal label (shown by circles) in six experimental animals. Open circles denote first layer terminations; filled circles represent terminations around the fourth layer; and paired open and filled circles determine sites of terminations in all layers.
Fig. 7. Diagrammatic representation of the superior temporal region (see Fig. 1) to show the sites of HRP injection (shown in black) and resulting labeled neurons (shown by triangles) in six experiments. Open triangles denote neurons in infragranular layers; and filled triangles represent neurons in the third layer.
Fig. 8. Darkfield photomicrographs to show examples of isotope injection and resulting terminal label. The center panel (B,E,H) shows sites of injection in three cases. Left panel (A,D,G) shows more rostral fields exhibiting a columnar pattern of grain distribution. Right panel (C,F,I) shows more caudal fields with first layer terminations. Also note diffuse projections in core fields pal (B) and reIt (F) (A,B,D-I, X 7; C X12).

placed in the supratemporal plane. In case 5 it involved KA and portions of adjacent areas paAr and paAlt (Fig. 7E), while in case 7, the injection was restricted to paAr. Labelled neurons in case 5 were present rostrally in Ts2, Ts3, paAlt, pal, and paAr. Caudally and medially label was seen in proA, reIt, paAc, and Tpt. HRP-positive neurons in pal and Ts2 were located in the deeper layers, whereas those in Ts3, paAlt, and paAr occupied the third, fifth, and sixth layers. In proA most labelled neurons were found in layers V and VI, although some appeared in layer III. In contrast the caudal areas reIt, paAc, and Tpt contained labelled cells predominantly in layer III. In case 7 the distribution of labelled neurons was similar to that of case 6. Thus rostral to the injection site labelled neurons in Ts2 were located in layers V and VI, while in KA they were found in layer III. The distribution of labelled neurons in the portions of paAr not involved by the injection was in layer III as well as in layers V and VI.

Case 6 received HRP mainly in Tpt with some extension into rostrally adjacent areas Ts2 and paAlt (Fig. 7F). Labeling of neurons was seen rostral to the injection in areas Ts3, Ts2, and a few in Ts3. Label was also present in Pro, pal, proA, KA, paAc, and reIt. Some labelled cells were also seen in paAr. The laminar localization of labelled neurons was mainly to the infragranular layers in rostral areas Ts3, Ts2, and paAr, as well as in Pro and pal. Labelled cells were located in both supra- and infragranular layers in areas Ts3, paAlt, and proA. In Ka and paAc the HRP-positive neurons were seen predominantly in layer III, while area reIt showed such labelling in layers III, V, and VI.
DISCUSSION

Previous architectonic studies have suggested that the cortical auditory regions of the rhesus monkey extend to the temporopolar and insular proisocortex and differentiate in stages in a caudolateral direction in the superior temporal region (Pandya and Sanides, '73). The findings of the present study support this notion and provide additional details concerning the architectonic and connectional organization of this region. The correlation between architectonic and connectional findings has helped the formulation of some conclusions concerning the intrinsic organization of the superior temporal region.

Architectonics

Three distinct lines of cortical differentiation are discerned in the superior temporal region of the rhesus monkey (Figs. 1, 2, 10). The first of these lines lies along the circular sulcus in peri-insular location. It consists most rostrally of the proisocortex (Pro) equivalent to that which caps the ventral part of the temporal pole. Further caudally Pro is followed by area pAI, then by proA, and finally by area reft. According to the parcellation of Pandya and Sanides (73) area Pro is described on the temporal pole but not on the circular sulcus (Fig. 1C). However, the medial line clearly contains a portion of area Pro, as evidenced by
the architectonics of the rostral part of the circular sulcus (Figs. 2A, 3B). This is further corroborated by the pattern of its connections, whereby injections in areas projecting to area Pro disclose terminations in both its polar and medial extensions (cf. Fig. 6B).

The peri-insular line contains cortices which have more primitive architectonic features than the areas lying along the other two lines in the superior temporal region. Thus these areas tend to be relatively hypocellular and retain emphasis on the deeper layers. Progressive specialization in this line occurs in a caudal direction, and consists mainly of a stepwise decrease of the relative prominence of the deeper layers and an increase in cellularity in layers III and IV (Fig. 4A-D). Because the peri-insular fields exhibit these relatively more primitive features they have been termed root fields (Fig. 10).

Another line of differentiation is found along the superior temporal gyms and is termed the belt line because it represents the lateral border of the auditory region (Figs. 1, 2, 10). This line of differentiation is represented most rostrally by area Ts2, followed caudally by Ts3, paAlt, and finally area Tpt. In the belt line the most striking architectonic feature is the stepwise progressive differentiation of the third layer (Fig. 4I-L). Thus the pyramids in layer III are relatively better developed than in the adjacent two lines. For instance, these cells assume a teardrop appearance in Ts3, they form slender columns in Ts2, and they achieve a particularly large size in paAlt. In Tpt they remain strong but intermingle with layer IV granules. According to Pandya and Sanides ('73) Ts2 is thought to precede Ts3 in the sequence of differentiation which in turn precedes Ts1 in the same line. The present study, however, suggests that Ts2 belongs to the core line (see below) by virtue of its architectonic features and connections. In fact it is possible to demonstrate contiguity between Ts2 and Ts3 in the superior temporal sulcus (Fig. 2). Furthermore this notion is supported by Jones and Burton's observations ('76). According to these authors area T3, which corresponds in location to Ts2 and Ts3 together, also appears to be continuous along the superior temporal sulcus.

Interposed between the root and belt lines a core line of differentiation can be demonstrated to lie mainly on the supratemporal plane (Figs. 1, 2, 10). It is termed core line because its fields lie between the root and belt lines. In this core line the most rostralmost field is area Ts2, followed caudally by paAr, then KA, and finally paAc. Progressive rostrocaudal differentiation in this line is manifested primarily by the stepwise increase in the number of small neurons in all layers of the cortex and by the broadening of layer IV (Fig. 4E-H). Area Ts2, for example, is more parvocellular than adjacent Ts1, and exhibits a broader layer IV. These architectonic features suggested that Ts2 be included with the core line of differentiation despite its extension onto the STG. Area paAr is also more granular than adjacent
Ts, andPAL, and area KA achieves the highest degree of
granule cell proliferation of the entire superior temporal
region. Granularization begins to abate in paAc, but still
remains greater than in adjacent areas reIt and Tpt.

On further analysis the superior temporal region may be
divided into four stages on the basis of architectonic differ-
etiation (Fig. 10). Each stage contains a core field which is
flanked by a medial root field and a lateral belt field. Thus
the rostralmost stage (stage I) contains root areas Pro, area
Ts, from the core line, and Ts, from the belt line; stage II is
made up of areas Pal, PA Ar and Ts, respectively; stage III
has areas proA, KA, and PA Al; and stage IV is repre-
sented by roIt, paAc, and Tpt. Therefore each stage may be
thought of as a unit having a root field along the circular
sulcus, a belt (or association) field along the superior tem-
poral gyrus, separated by a granular core (or primary field)
on the supratemporal plane. Thus the classical auditory re-
gion composed of proA (second auditory area—AII of
Woolsey and Fairman, '46; and a of Merzenich and Bruggke,
'73), the primary cortex KA (AI), and the association area
PA Al (probably TB of v. Bonin and Bailey, '47) may repre-
sent but one of a series of stages organized in a similar
fashion rostrocaudally in the superior temporal region.

The architectonics of the rostral two stages (I and II) re-

deflects the temporopolar influence, while the last stage (IV)
exhibits the influence of the adjacent parietal lobe. The
classical auditory region represented in stage III appears
to be farthest from these two influences and shows the
greatest architectonic specialization in each of its divi-
sions, i.e., in proA, KA, and PA Al.

Connections

It should be pointed out that at the outset that, since there are
difficulties in restricting isotope and HRP entirely to a
given area, as well as in making injections that completely
fill an area, the substraction method has been employed to
help define the specific connections of a single area. Thus,
e.g., the connections of area PA Al may be surmised from the
analysis of two cases: one with an injection in PA Al
and TS,; the other with an injection in PA Al and Tpt. The
connections of PA Al are specified by the pattern common
to the two injections. A similar approach has been em-
ploved to outline the connectivity of small structures in
other neuroanatomical investigations (cf. Nauta and
Mehler, '66).

Intrinsic connections within each architectonic stage as well as between adjacent stages show specific and
consistent patterns (Fig. 10). It is this specificity and consis-
tency which reinforces the architectonic classification
presented above. Thus in the rostrocaudal direction two
adjacent fields lying along a given line of differentiation
are richly interconnected, whereas connections between
two nonadjacent fields are at best sparse. For instance,
few connections between nonadjacent areas Pro and proA
or PA Al and Ts, are found, whereas connections between
adjacent areas Pro and PAL or Tp, and TS, are abundant
(Fig. 10A). Similarly, oblique connections, e.g., between
Ts, and Ts, are less numerous.

The laminar distribution of connections between adja-
cent fields along a given line is also specific, albeit com-
plex. Caudally directed projections in all three lines origi-
nate in the deep layers (layers V and VI) and terminate in
the superficial layer (mainly layer I) in the adjacent region
(Fig. 11A). On the other hand rostrally directed projections
arise predominantly from layer III neurons in all three
lines, but the layers of the rostral terminations vary.
Whereas in the root line the rostral terminations are found
mainly in layer IV, in the belt and core lines (especially the
former) terminations exhibit a columnar arrangement with
label in all layers, as well as a continuous labelling of layer
IV (Fig. 11B). This pattern of termination is seen best in
the projections from Ts, to Ts, PA Al to Ts, Tpt to PA Al,
and KA to PaAc.

Connections between fields belonging to a given stage
e.g., Pro, Ts, and PA Al, or reIt, paAc, and Tpt, also manifest
stricting specificity and consistency. As shown in Figure
10B, all three architectonic regions are interconnected
each stage. Thus the root and belt fields exhibit con-
nexions with their respective core field. The cells of origin
in the belt areas are located mainly in the deeper layers,
and the terminations in the core fields are located in layer
I (Fig. 11D). The cells of origin in the root fields are found
throughout the cell layers, and the core field terminations
are again confined to layer I (Fig. 11E). Reciprocal connec-
tions from core to belt areas arise mainly in layer III and
terminate predominantly in the fourth layer (Fig. 11C). On
the other hand, reciprocal connections from core to root
fields arise in layer III but terminate throughout the corti-
cal thickness (Fig. 11F). The root and belt fields within
each stage are interconnected as well. Root-belt projec-
tions arise in all root layers and terminate mostly in belt
layer I (Fig. 11E), whereas belt-root connections arise pre-
dominantly in the third layer of the belt field and termi-
nate diffusely in all cell layers of the root field (Fig. 11F).

Projections arising and terminating within the same area
originate from cells placed in supra- and infragranular lay-
ers and end in all cell layers, without forming columns. The
study of Fitzpatrick and Imig ('80) in the owl monkey, and
in a more restricted portion of the superior temporal re-

gion, supports this pattern of laminar organization of con-
nexions. Thus rostrally directed projections (from A1 to
R) terminated mainly in layers III and IV and exhibited a
columnar pattern, while projections directed caudally
(from R to A1) terminated mainly in layer I.

Implicit in the above findings, but deserving explicit
mention, is the notion that these intrinsic connections re-
spect architectonic borders. In fact this was the situation
without exception. Sharp borders of projection fields cor-
responded exactly to sharp architectonic borders, whereas
tapering densities of terminations, or projection neurons,
mached transitional changes between adjacent architec-
tonic fields. In some instances the architectonic boundary
region was devoid of terminations. In some cases changes
in the pattern of termination could be seen at an architec-
tonic border. For instance, Ts, projections to Ts, are co-

dumnar, whereas its few projections to Ts, are mainly to
layer IV; the change occurs abruptly at the architectonic
border between Ts and Tp, in fact it is not inconceivable
that the differences in intrinsic connectivity of adjacent
areas contribute, at least in part, to their different architec-
tonic appearance.

Certain similarities may be noted between the intrinsic
organizations of the auditory and visual systems. Al-
though specific stages and lines of architectonic differen-
tiation, equivalent to those found in the superior temporal
region, have not been described for the visual areas, a hier-
archial caudorostral organization of architectonic areas
and projections appears to exist in the occipitotemporal
cortex of the visual system. Thus, for instance, area 17
(of Brodmann) projects to area 18; area 18 to 19; and 19
Fig. 11. Summary diagram to show patterns of laminar distribution of connections for fields of the superior temporal region (see Fig. 8). Arrows mark cells of origin and layers of termination. Laminar patterns are shown for fields of a given line (A, B) and for fields within a stage (C-F). Also see text.
The known pattern of long temporo-frontal connections is also concordant with the concept of a sequential rostrocaudal organization in the superior temporal region. Thus, it has been shown that temporopolar fields are connected preferentially with orbitofrontal and medial prefrontal cortex; midtemporal fields are mainly connected with the lateral prefrontal area; and the more caudal temporal fields project principally to the premotor region (Jones and Powell, ’70; Chavis and Pandya, ’76). The frontal fields receiving these temporal fibers are also disposed in a line of architectonic differentiation, the orbitofrontal and medial prefrontal fields showing the most primitive architectonic features, and the premotor region the most specialized of that line (Sanides, ’72; Barbas and Pandya, ’82).

The question as to whether the rostral parts of the superior temporal region in the rhesus monkey belong to the auditory system cannot be fully answered without further anatomical, physiological, and psychological data. The findings of this study, however, support the notion that these rostral areas are indeed part of the auditory system. Thus the observations that they are sequentially linked by a predictable architectonic progression to, and by connections with, the more classical posterior auditory areas, in addition to their similar style of intrinsic arrangement into root, core and belt fields, suggest that the rostral subdivisions of the STR belong to the same system as the posterior ones. The thalamic connections of these regions give additional support. Although the thalamic afferents to the rostralmost fields in the STR had not been specified in the past, recent studies have demonstrated connections from medial geniculate nucleus (MGN) to the rostral STR, including area Pro (Mesulam and Pandya, ’73; Wegener, ’76; Gower, ’81). The organization of thalamic afferents to this region permits speculation as regards the intrinsic organization of the STR. Thus, the bulk of the projections from the MGN (3Mpc portion) are directed to the supratemporal plane and involve the core regions. Some of the root fields, on the other hand, seem to receive fibers from the medial portion of MGN (2Mmc) and from the suprageniculate nucleus. The belt fields in the superior temporal gyrus, furthermore, receive the bulk of their thalamic projections from the pulvinar-LP complex (Mesulam and Pandya, ’73; Trojanovsky and Jacobson, ’76).

It is interesting to note that projections arising from architectonically more primitive types of cortex (as defined above) terminate in the first layer containing apical dendrites from all layers of adjacent more differentiated cortex. This laminar organization may provide the substrate for arousal of a given cortex by its more limbically related neighbor. The reciprocal connections from a more differentiated caudal area to a less differentiated rostral area, on the other hand, are much more sharply delineated, the terminations being mainly concentrated around layer IV. Since afferents from the periphery terminate mainly in this layer, the above-mentioned reciprocal connections may allow more caudal cortices to modify the response of more rostral cortices to peripheral auditory experience.

The significance of the existence of several stages of auditory representation is not clear. On the one hand, the sequential stages may represent evolutionary stages in the development of the auditory system (Sanides, ’72); on the other hand, they may reflect parallel developments for the purpose of auditory analysis at different levels; or a combination of both. It is striking, however, that each stage can be viewed to contain a root, a core, and a belt field, a situation which provides strength to the classical notion of primary fields, secondary fields and association areas, each set with its specific pattern of subcortical, neocortical, and limbic connections. It would be of great interest to see whether similar schemes of intrinsic organization into root, core, and belt fields disposed in stages are also present in other sensory representations.

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projects to 20 in a caudostral fashion (Rockland and Pandya, ’79; Tigges et al., ’81). Reciprocal rostrocaudal projections also exist in that system. Furthermore, the laminar arrangement appears to parallel the rostrocaudal pattern of the auditory system. Thus, caudally directed projections arise mainly in the deep layers and terminate predominantly in layer I of the immediately adjacent caudal field, whereas the reciprocal projections originate mostly from layer III neurons and end mainly in layer IV of the rostral field. A finding in the visual cortices not found in the superior temporal region, however, is the presence of a few caudally oriented fibers arising from cells in the upper part of layer III.

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