

Research Reports

LAMINAR ORIGINS AND TERMINATIONS OF CORTICAL CONNECTIONS OF THE OCCIPITAL LOBE IN THE RHESUS MONKEY*

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SUMMARY

Cortical connections within the occipital lobe (areas 17, 18 and 19) of the rhesus monkey are investigated with the autoradiographic and horseradish peroxidase procedures. Two efferent systems, each with a specific laminar organization, are observed. (1) Rostrally directed connections, from area 17 to 18, area 18 to 19, and area 19 to the inferotemporal region (area TE), originate from neurons in layer IIIc (and, in area 19, from a small complement of neurons in layer Va), and terminate in and around layer IV. (2) In contrast, connections in the reverse direction ('caudally directed' connections), from area TE to 19, area 19 to 18, and area 18 to 17, originate from neurons in layers Vb, VI and, to a lesser extent, IIIa, and terminate mainly in layer I. In addition, the laminar organization of several intrinsic and callosal connections are observed. Intrinsic connections within areas 18 and 19 originate from neurons in layers IIIc and, to a lesser extent, Va, and terminate in vertical bands in layers I to IV. Callosal connections from areas 18, 19, and the caudal inferotemporal region originate from neurons mainly in layer IIIc. From areas 18 and 19, these callosal connections terminate in vertical bands in layers I through IV. Thus, different cortical projection systems are characterized by specific laminar distributions of efferent terminations as well as of their neurons of origin.

INTRODUCTION

Neuroanatomical studies of the primate occipital lobe have indicated that there

* A preliminary report of these findings has been presented elsewhere²⁹.

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is a progressive outflow of cortical connections from area 17, to the circumstriate region and thence to the inferotemporal area^{17,50,52}. In addition to these well known 'rostrally directed' connections, evidence has been presented for a reciprocal projection system ('caudally directed' connections) from area 18 to area 17^{17,38,39}. These two systems appear to originate from and terminate in different cortical laminae. Thus, the rostrally directed efferents from area 17 to area 18 originate from neurons in the supragranular layers (II and III)^{20,21,25,36,48}, and terminate mainly in layer IV of area 18^{5,21,36,42}. In contrast, the caudally directed efferents from area 18 to area 17 are reported to originate from neurons in both the supragranular (II and III) and the infragranular (V and VI) layers^{25,38}. These caudally directed efferents terminate mainly in layer I of area 17 in the rhesus monkey¹⁷; in New World primates they terminate more widely in layers I, III, V, and VI, but not in layer IV^{12,39,48}. Besides these interconnections between areas 17 and 18, reciprocal connections have additionally been demonstrated between area 17 and the caudal part of the superior temporal sulcus (i.e. area MT in New World primates)^{35,45}. These connections also have distinctly different laminae of origin and termination. Thus, the projections from area 17 to MT originate from neurons in layers IIIc and VI and terminate mainly in layer IV^{20,31,33,34,35,45}, while the reverse connections from area MT to 17 originate from layers II, III, V, and VI and terminate in layers I, IIIc and VI^{35,45}.

These results, therefore, indicate that different visual cortical pathways have different patterns of laminar origin and terminations.

The present study was designed to investigate whether such laminar specificity exists for all interrelated cortical visual areas in the rhesus monkey. Our results in fact clearly establish that both rostrally directed and caudally directed connections interlink the parasensory visual areas, as well as the primary sensory and parasensory visual areas. These two projection systems have a distinct laminar distribution, both of terminations and their cells of origin.

MATERIALS AND METHODS

In 7 experimental animals, under Nembutal anesthesia and following a craniotomy, equal amounts of [³H]leucine and [³H]proline were injected in a given area in one hemisphere. Two to four injections of isotope, at final concentrations of 25–80 µCi/µl, were made (0.6 µl per injection). As a second procedure in these animals, a 20% aqueous solution of Sigma VI horseradish peroxidase (HRP) was injected in the opposite hemisphere 2 days prior to sacrificing the animal. Two injections of HRP (0.2–0.6 µl per site) were carried out. In 15 other animals, either tritiated amino acids or HRP alone was injected into one hemisphere only. The HRP injections involved all cortical layers. Occasionally some diffusion of HRP into underlying white matter was noted. An analysis of retrograde transport of HRP in these cases showed no significant difference. With regard to isotope cases, injections involved all cortical layers except for 3 cases (cases 6–8; Fig. 1) in which the injections were restricted to the supragranular layers.

After a survival period of 6–10 days (in two animals, 2 days) following the isotope injection, the animals were deeply anesthetized and perfused transcardially,

according to the protocol described by Rosene and Mesulam³⁰. The brains were then removed, and the hemispheres to be processed for autoradiography were stored in 50% EtOH solution, while the HRP-injected hemispheres were stored in sucrose-buffer solution for 24 h at 4 °C, and then cut into 40 µm sections on a freezing microtome. In order to identify the retrograde transport of HRP, either the benzidine dihydrochloride or the tetramethyl benzidine (TMB) incubation procedures described by Mesulam^{22,23} were used. The isotope-injected hemisphere was embedded in paraffin 2–3 weeks after the perfusion, cut in the coronal plane at 10 µm, and processed according to the technique described by Cowan et al.⁴. Exposure times ranged from 3 to 7 months.

The distribution of termination fields and HRP-positive neurons was charted with the aid of X-Y plotter. This information was then reconstructed on a tracing of the photograph of each hemisphere.

Nomenclature

The primate occipital lobe is composed of the primary visual area ('striate cortex'; area 17 of Brodmann³; or area OC of Bonin and Bailey^{1,2}), and surrounding circumstriate or prestriate cortex. Although circumstriate cortex in rhesus monkey was originally divided into two main subdivisions (areas 18 and 19³, or areas OB and OA¹), recent investigations of this region suggest more complex arrangement. Thus Zeki and coworkers^{42,50,52} have distinguished two separate striate recipient areas, V₂ and V₃, within the previously designated area 18. These investigators have also hypothesized similar intricate organization within area 19 (the 'V₄ complex'). In the present report, however, the classical view of circumstriate cortex as two subdivisions (areas 18 and 19 or areas OB and OA) is maintained. This present parcellation is based on a cytoarchitectonic and connectional analysis and its detailed account is presented elsewhere²⁸. Briefly, according to this scheme area 18 (OB) refers to that portion of circumstriate cortex which receives input from striate cortex, and area 19 (OA) refers to the cortical region that receives projection from area 18. These subdivisions correspond approximately with respectively areas V₂ and V₃ and the V₄ complex of Zeki^{42,50,52}. The cortical laminae and their subdivisions (or sublaminae) are numbered according to the scheme of Bonin and Bailey¹. Layer III is considered to consist of three sublaminae, IIIa, IIIb, and IIIc, with IIIc being the deepest portion of the layer. In describing striate cortex, however, the terminology of Hassler and Wagner⁸ and Spatz et al. is employed³⁶. Thus, the layer containing the stria of Gennari is termed layer IIIc instead of IVb.

RESULTS

The first group of experiments describes the laminar terminations of intrahemispheric efferents from areas 17, 18, and 19. The neuronal origins of these connections are subsequently described in a second set of experiments.

(I) Isotope injections

Distribution of efferents from area 17

In three animals (cases 1–3), isotope injections were made in different parts of

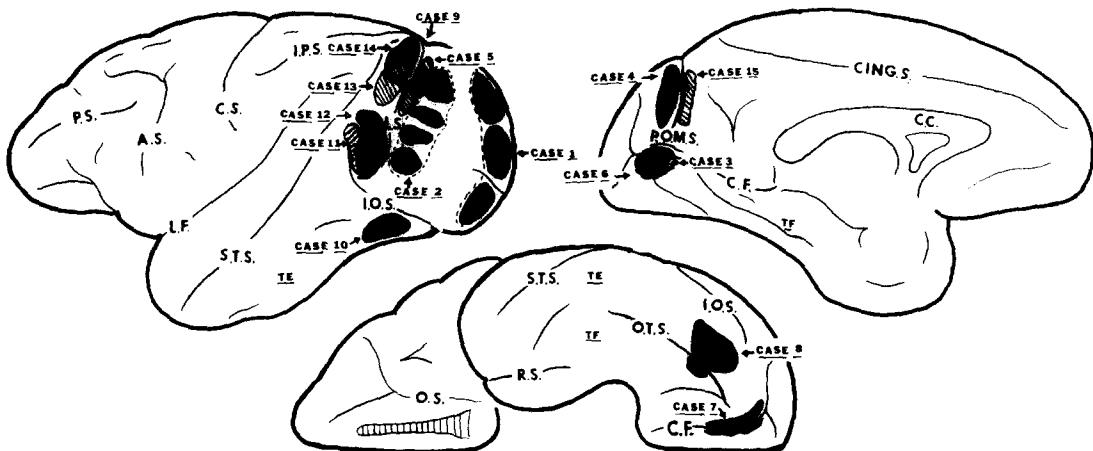


Fig. 1. Composite diagram showing the sites of isotope injections in area 17 (cases 1–3), area 18 (cases 4–9) and area 19 (cases 10–15). Injections in the inferotemporal region (cases 16 and 17) are not illustrated. Abbreviations: A.S., arcuate sulcus; C.C., corpus callosum; C.F., calcarine fissure; CING.S., cingulate sulcus; C.S., central sulcus; I.O.S., inferior occipital sulcus; I.P.S., intraparietal sulcus; L.F., lateral fissure; L.S., lunate sulcus; O.S., orbital sulcus; O.T.S., occipito-temporal sulcus; P.O.M.S., parieto-occipital medialis sulcus; P.S., principal sulcus; R.S., rhinal sulcus (fissure); S.T.S., superior temporal sulcus.

area 17, as shown in Fig. 1. In all cases, silver grains were seen in two regions of circumstriate cortex; namely, in area 18 and in the caudal part of the superior temporal sulcus. In both these regions, grains were heavily concentrated over layer IV, but also occurred in the contiguous layers IIIc and Va. Additionally, at regular intervals silver grains extended up to layer IIIb, forming intermittent 'sprays' about 300 µm in width at the base (Fig. 2A, B). Intrinsic connections, i.e. connections within area 17, were observed near the injection site. Here, short connections were organized in horizontal bands in layers I, IIIc, and V (Fig. 2D). Also, when the injection was restricted to the supragranular layers only, a distinct band of silver grains consistently appeared in layer V (Fig. 2C).

Distribution of efferents from area 18

Six animals (cases 4–9, Fig. 1) received injections in different parts of area 18. In one animal (case 9), an isotope injection was mainly restricted to area 18 in the caudal part of the annexent gyrus*. In four cases the injection also extended into adjoining area 17, and in one other case into adjoining area 19. In all these cases, silver grains occurred in area 19, in the caudal part of the superior temporal sulcus (STS) and in area 17, as well as within area 18. Like the efferents from area 17 to 18, those from area 18 to 19, and from area 18 to the STS terminated in layer IV and the adjacent layers IIIc and Va, with extensions of grains up to layer IIIb (fig. 3A). In contrast with these

* The annexent gyrus refers to buried cortex at the junction of the lunate, intraparietal and parieto-occipital sulci.

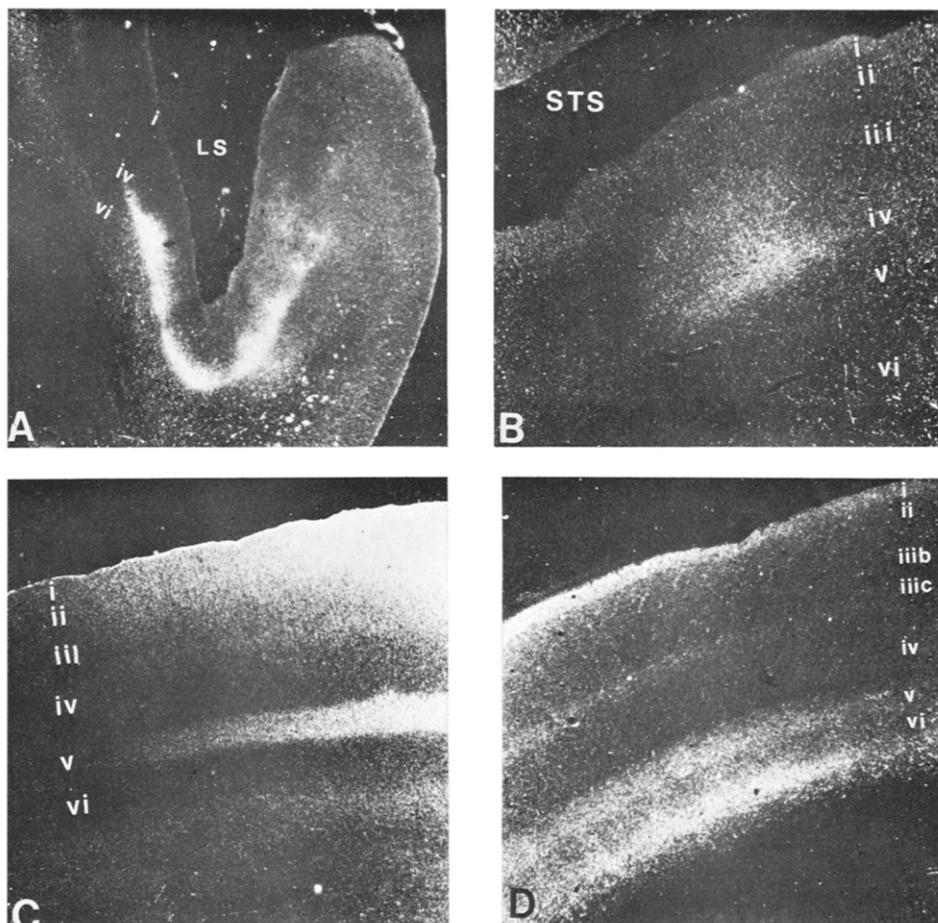


Fig. 2. Dark-field photomicrographs to show the distribution of silver grains following isotope injections in area 17 (cases 1 and 2). A: grains are seen in and around layer IV of area 18 in the lunate sulcus ($\times 9$) and in B in layer IV of the superior temporal sulcus ($\times 30$). C: there is a band of silver grains in layer V subjacent to a superficial injection in area 17 involving layers I to III ($\times 24$). D: grains near an injection site within area 17 in layers I, IIIc, and V ($\times 24$).

efferents directed mainly to layer IV within area 19 and in STS, in area 17 dense grains occurred mainly in layer I (Fig. 3B). In area 17 silver grains were also evident over layers IIIc and V, but were less abundant and more axonal in appearance than the grains over layer I. In addition to these extrinsic connections, several patterns of intrinsic connections within area 18 were discerned. Thus, when injections were confined to the supragranular layers only, a dense band of labeled grains occurred over layer V. Additionally, within 2–3 mm of an injection site, dense grains occurred in 2–3 vertical bands or ‘columns’ extending through layers I to IV (Fig. 3C).

Distribution of efferents from area 19

Injections were made in different parts of area 19 in six animals (cases 10–15) as

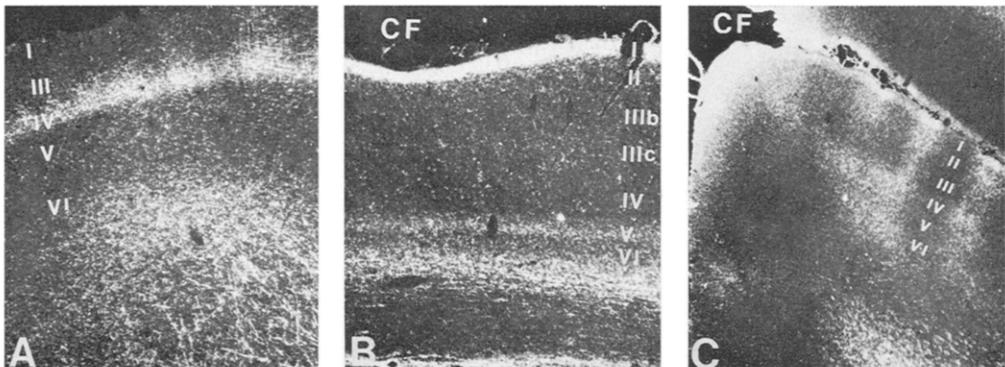


Fig. 3. Dark-field photomicrographs to show the distribution of silver grains after isotope injections in area 18 (case 6). A: grains appear in layer IV of area 19 in the preoccipital gyrus ($\times 24$). B: a dense band of silver grains is seen in layer I of area 17. Note smaller amount of grains in layer V ($\times 24$). C: grains are seen in layers I through IV in the calcarine fissure, in area 18 near the injection site. Note the bandlike distribution of grains ($\times 9$).

shown in Fig. 1. The laminar terminations of silver grains were basically identical in all cases. After these injections, rostrally directed efferents were observed in several adjoining cortical areas; namely, the inferotemporal region (areas TE and TF), the caudal portion of the STS, and an architectonically distinct zone in the lower bank of the intraparietal sulcus (IPS; see ref. 32). The efferents to areas TE and TF terminated in and around layer IV, with intermittent extensions of grains up to layer IIIb (Fig. 4A). This was similar to the laminar pattern of connections from area 17 and from area 18. The efferents from area 19 to the STS also terminated densely in layer IV; but, except at the margins of a projection zone, vertical bands of silver grains consistently extended up to layer I as seen in Fig. 4B. Typically, there were 2–3 bands or ‘columns’, 500–800 μm in width, per section. Likewise, efferents to the intraparietal sulcus terminated in several vertical bands (Fig. 4C). These vertically organized terminations in layers I to IV were especially prominent after injections in the dorsal part of the preoccipital gyrus.

Injections in area 19 also revealed caudally directed efferents to area 18 which, like the projections from area 18 to 17, terminated mainly in layer I. Silver grains additionally occurred over layers V and VI, but were less extensive and more axonal in appearance than the grains over layer I (Fig. 4D). Finally, within 2–3 mm of an injection site in area 19, silver grains formed several vertical bands extending through layers I to IV (Fig. 4E). This pattern was similar to the vertical terminations seen within area 18, as noted above.

Isotope injections of the inferotemporal region (areas TE and TF)

Only efferents to area 19 are described here (cases 16 and 17, not illustrated). Both areas TE and TF sent caudally directed efferents to area 19, which terminated mainly in layer I. Once again, as in caudally directed projections from areas 19 to 18, there were silver grains in layers V and VI, but these were more axonal in appearance and less dense than those in layer I.

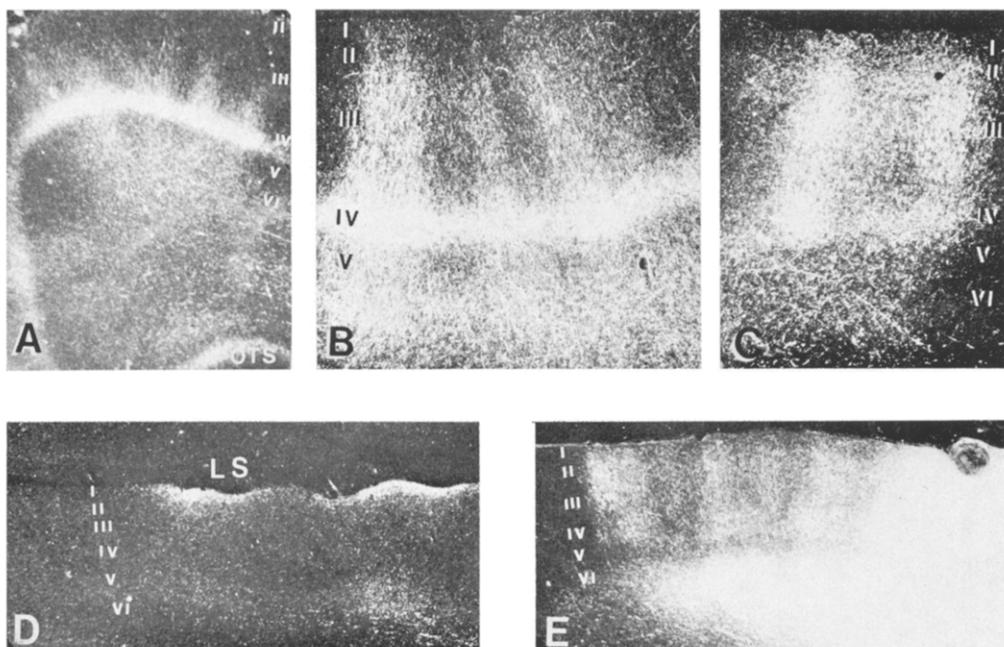


Fig. 4. Dark-field photomicrographs showing the distribution of silver grains after isotope injections in area 19 (case 13, A-C, E; case 12, D). Grains in A are in layer IV of the inferotemporal cortex. Note, however, clusters of silver grains extending into layer IIIb ($\times 9$). B ($\times 24$) and C ($\times 30$): the distribution of silver grains in the layers I through IV of the superior temporal (B) and intraparietal (C) sulci. D: grains are distributed in layer I of area 18 ($\times 24$). E: grains are seen in layers I through IV near the injection site in area 19 in the preoccipital gyrus ($\times 9$). Note the similarity of vertical terminations in B, C, E and also Fig. 3C.

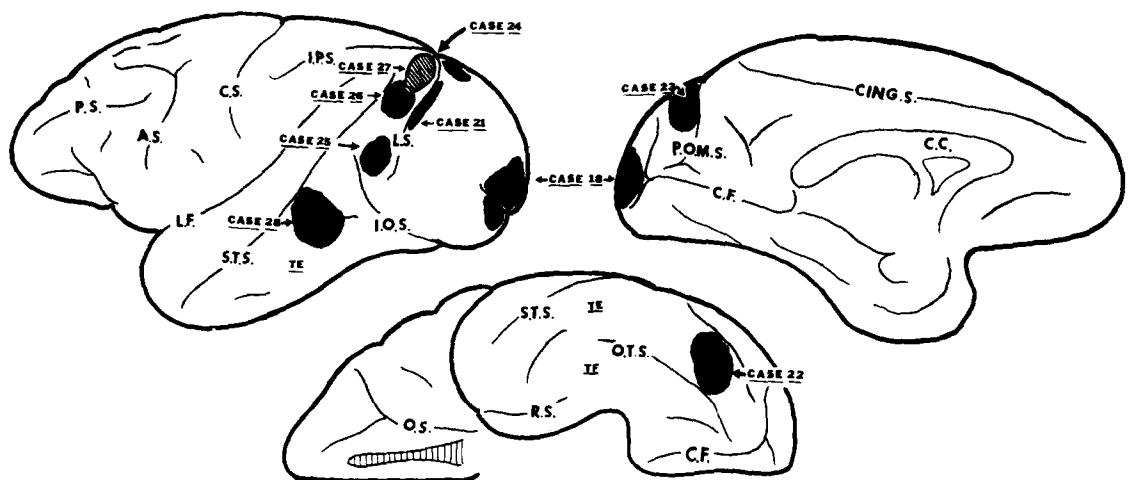


Fig. 5. Composite diagram showing the site of HRP injection in areas 17 (case 18), 18 (cases 21-24), 19 (cases 22, 24, 27) and area TE (case 28). Cases 19 and 20 (injection in area 17) and 29 (injection in areas TE and 19) are not illustrated.

(II) Horseradish peroxidase injections

Neuronal origin of afferents to area 17

In three animals (cases 18–20), HRP injections were made in different parts of area 17 (only case 18 is illustrated, see Fig. 5). One of these injections (case 20) also extended into adjoining area 18. Following these injections, HRP-labeled neurons were found in area 18 and in the caudal part of the superior temporal sulcus. In both these regions, labeled neurons were most numerous in the infragranular layers (Vb and VI). However, there was a smaller number of neurons in the supragranular layers, especially layer IIIa (Fig. 6A). In layer IIIa, labeled neurons occurred either singly or in small groups, whereas in the infragranular layers, labeled neurons were densely and evenly distributed. In the vicinity of an injection, HRP-labeled neurons were seen in layers IIIb, IIIc, and VI of area 17. In layer VI, scattered neurons (4–8 per section) were found as far as 3–4 mm from the injection site. On the basis of their isolated occurrence and large size (30–45 μm), these neurons resembled solitary cells of Meynert¹⁸ (Fig. 6B).

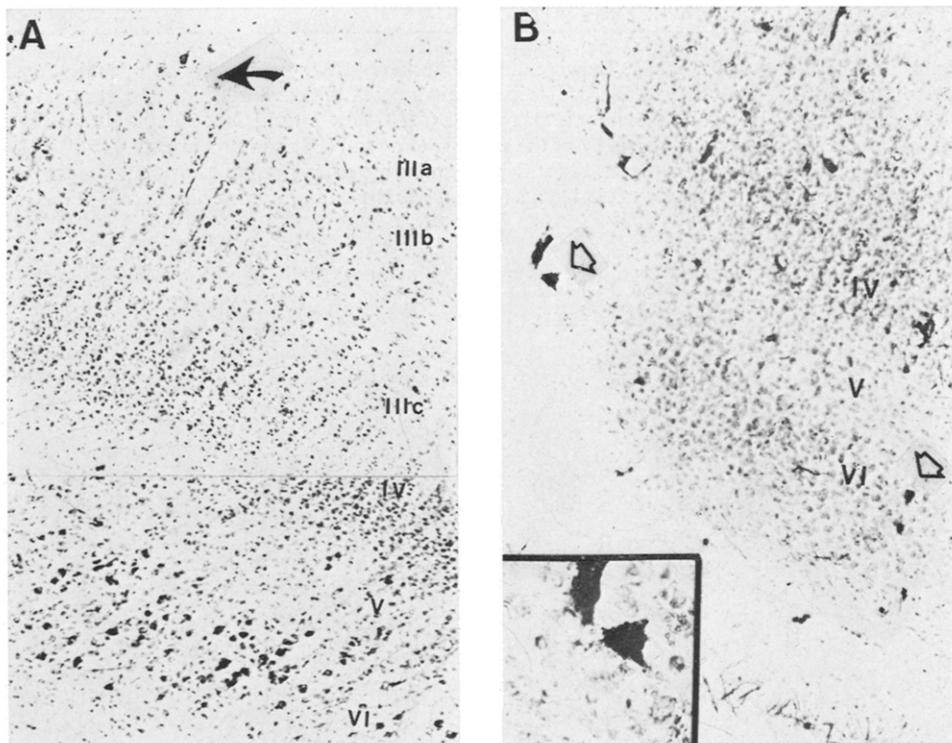


Fig. 6. Photomicrographs showing the distribution of HRP-positive neurons after an HRP injection in area 17 (case 18). A: labeled neurons in area 18 are seen in layers Vb and VI, as well as in IIIa (see arrow) ($\times 120$). B: two HRP-positive neurons (Meynert cells) are seen in area 17 ($\times 120$). Inset depicts one of these neurons at higher magnification ($\times 480$).

Neuronal origin of afferents to area 18

In four animals (cases 21–24, Fig. 5), HRP was injected into dorsal or ventral portions of area 18. In one case, the injection was confined to the lateral juxtastriate region (case 21); but in another case there was diffusion into adjacent area 17 (case 23), and in the remaining two cases HRP also extended into area 19 (cases 22 and 24). In all these cases, HRP-labeled neurons appeared in area 17, in area 19, in the caudal part of the superior temporal sulcus (STS), and within area 18. In area 17, labeled neurons were confined to layer III, primarily within two sublaminae, IIIa and IIIc. Neurons in layer IIIc were clustered in groups of 3–7 cells (Fig. 7A). In contrast, labeled neurons in area 19 and the STS occurred predominantly in the infragranular layers (Vb and VI), with a smaller number of neurons in layer IIIa (Fig. 7B–D). Thus from area 19 and the STS, the laminar distribution of caudally directed efferents to area 18 was similar to that of efferents from area 18 to 17. Near the injection site in area 18, HRP-positive neurons were present in layers III and V, particularly in IIIc and Va, and seemed to be organized in 2–3 discrete groups per section.

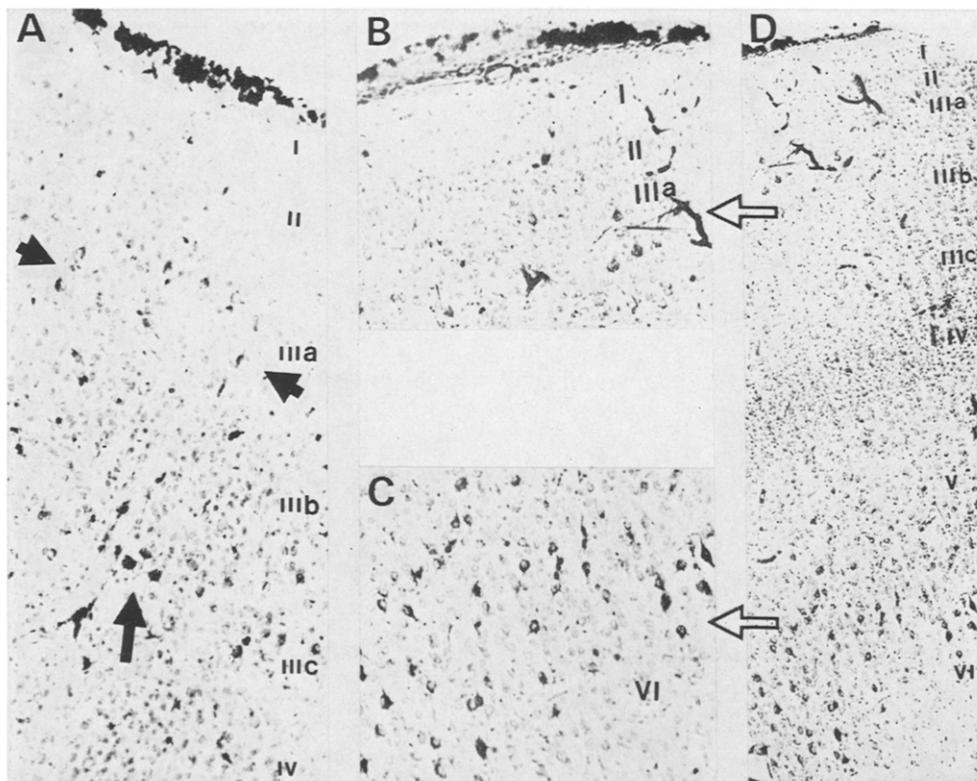


Fig. 7. Photomicrographs showing the distribution of HRP-positive neurons after an HRP injection in area 18. A: labeled neurons are in area 17, in layers IIIa and IIIc (case 24), ($\times 120$). D: neurons are seen in area 19, in layers Vb and VI, with a few neurons in layer IIIa (case 23) ($\times 120$). B and C: these neurons at higher magnification ($\times 480$).

Neuronal origin of afferents to area 19

HRP was injected into different parts of area 19 in five animals (cases 22, 24–27, Fig. 5). Two of these injections also involved adjoining area 18, (cases 22 and 24). In all these cases, HRP-labeled neurons were found in area 18, in the caudal part of the STS, and in the inferotemporal cortex (areas TE and TF), as well as within area 19. In area 18, labeled neurons were mainly in layer IIIc and, to a lesser extent, in layers IIIa and IIIb (Fig. 8A). In contrast, in both areas TE and TF, as well as in the STS, labeled neurons were in both the supra- and infragranular layers. In areas TE and TF, labeled neurons occurred in layers Vb and VI, with a smaller number of neurons in layers IIIb and IIIc (Fig. 8B–D). In the STS, HRP-positive neurons were more evenly distributed in the supra- and infragranular layers. Within area 19, both near the injection site as well as in more distant parts of area 19, labeled neurons were identified mainly in layers IIIc and Va (Fig. 8E).

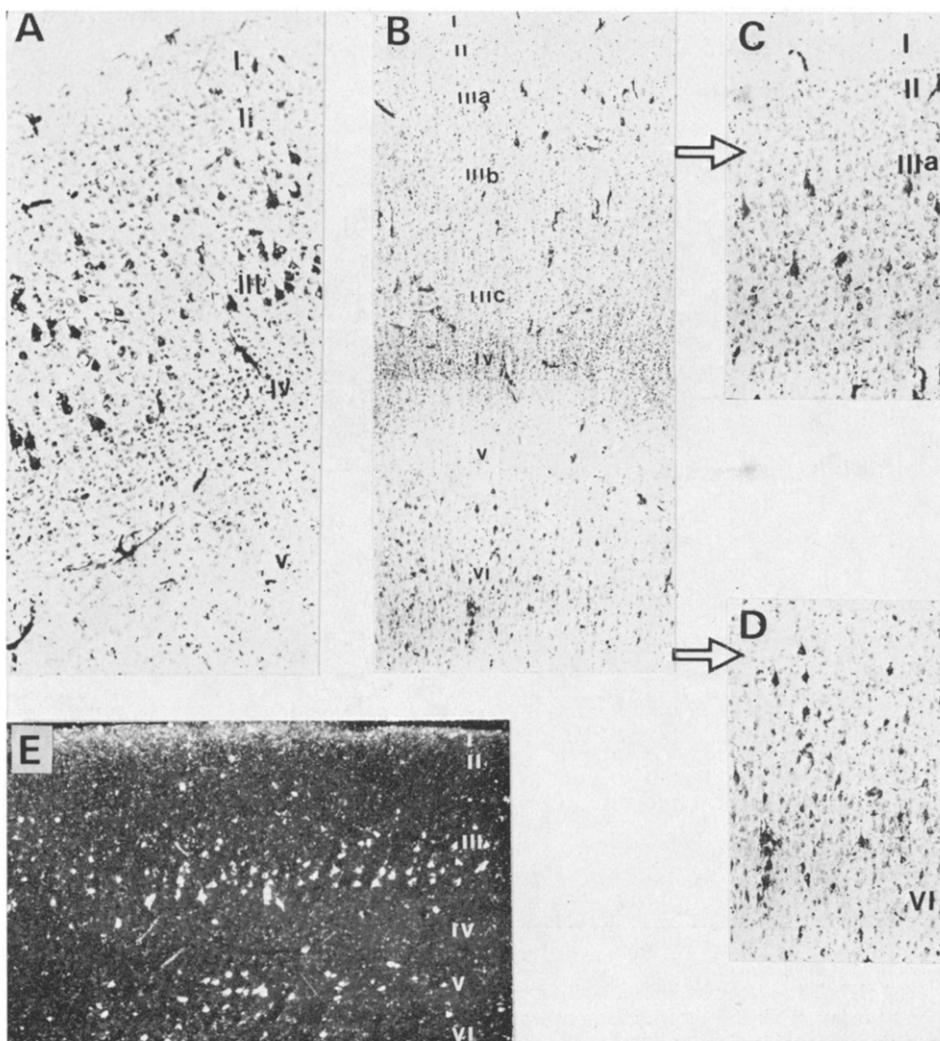


Fig. 8. Photomicrographs showing the distribution of HRP-positive neurons after an HRP injection in area 19. A: neurons are seen in area 18 in layer III. Note that both medium and small as well as large-sized pyramidal cells are labeled (case 25) ($\times 120$). B: neurons are in area TE in layers Vb and VI and, to a lesser extent, IIIa (case 27) ($\times 80$). C and D: same at higher magnification ($\times 120$). E: neurons are seen in area 19 in layers IIIc and Va; dark-field illumination (case 24) ($\times 120$).

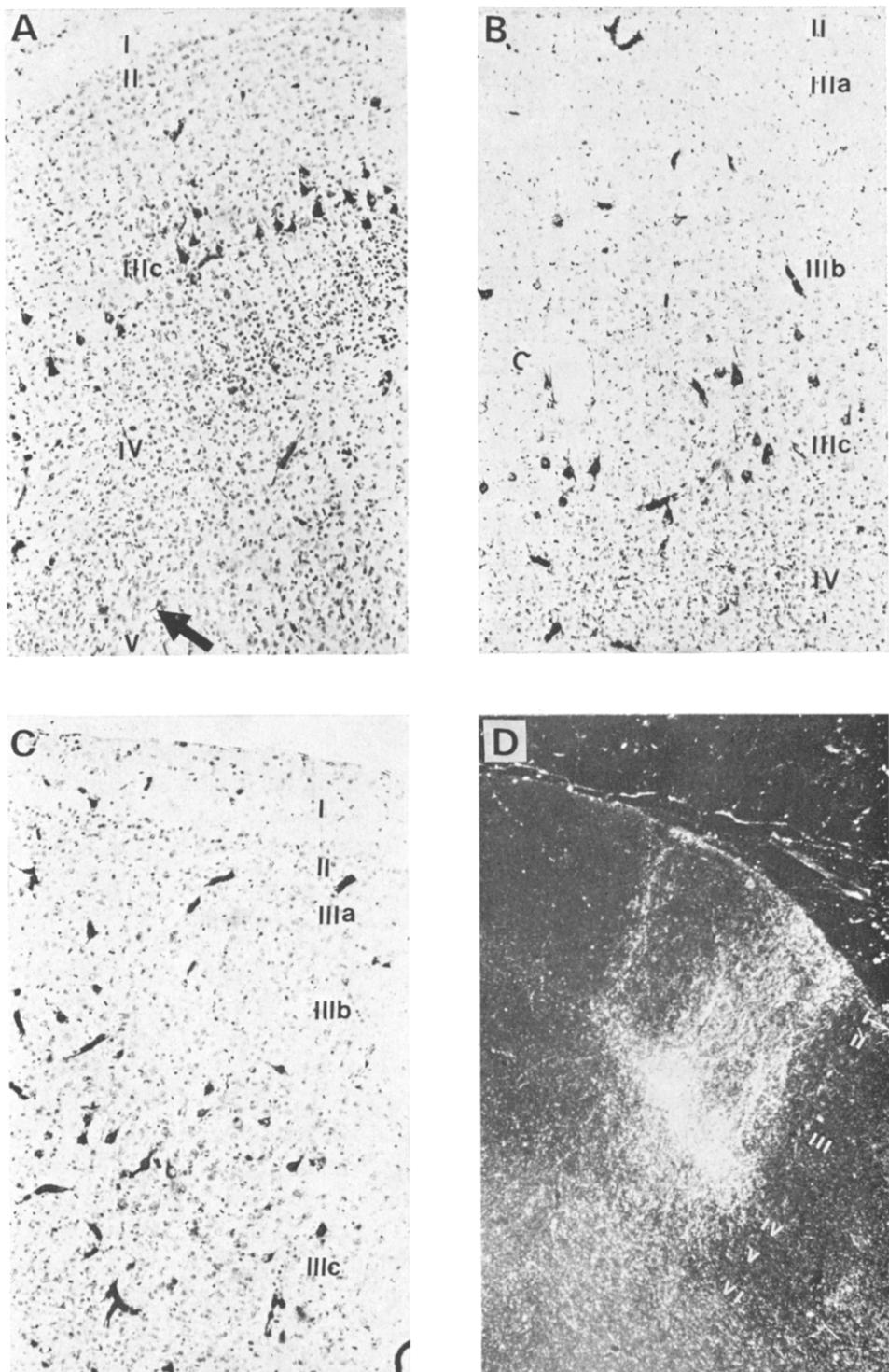


Fig. 9. Three photomicrographs (A–C) showing the distribution of HRP-positive neurons in the opposite hemisphere after HRP injections in areas 18, 19, or TE. A: neurons occur in layer III of area 18. Arrow indicates the border of areas 17 and 18 (case 22) ($\times 120$). B: neurons occur in layer III of area 19 (case 26) ($\times 120$). C: neurons in layer III of area TE (case 28) ($\times 120$). D: a dark-field photomicrograph showing the distribution of silver grains in area 19 after an isotope injection in the opposite hemisphere (case 14). Note the vertical bands or 'columns' of silver grains in layers I through IV ($\times 24$).

Neuronal origin of occipital afferents to area TE

In two animals (cases 28 and 29, Fig. 5, case 29 is not illustrated), injections of area TE produced labeled neurons mainly in layer IIIc of area 19. Unlike rostrally directed efferents from area 17 to 18, and from area 18 to 19, however, some labeled neurons were also present in layer Va of area 19.

Origin and termination of callosal connections

In some of the HRP and autoradiographic cases described above, the opposite hemisphere was available for analysis of the laminar distribution of callosal connections. The HRP cases (cases 21, 23, 26 and 28, Fig. 5) revealed callosally projecting neurons principally in layer IIIc of the juxtastrate region, area 18, area 19, and the caudal part of area TE (Fig. 9A–C). A few HRP-positive neurons were also found in other sublaminae within layer III. Labeled neurons were most numerous in the juxtastrate area, with progressively fewer filled neurons appearing in each of the more rostral cortical fields; i.e. in areas 18, 19 and TE. The autoradiographic cases (cases 5, 6, 11 and 14, Fig. 1) showed callosal efferents from areas 18 and 19 densely concentrated in layer IV of the homotopical area in the opposite hemisphere. From layer IV, these terminations extended toward the molecular layer in several vertical bands (Fig. 9D).

DISCUSSION

The above experiments indicate a clear duality in the laminar organization of rostrally as opposed to caudally directed occipital lobe connections. In addition, there is a distinct laminar organization of intrinsic and callosal connections of the same area. As summarized in Fig. 10, each of these different connections originate from and terminate in different cortical laminae.

Rostrally directed connections

Rostrally directed efferents from areas 17, 18, and 19 originate from neurons mainly in the supragranular layers and terminate primarily in layer IV of areas 18, 19, and TE, respectively. Similar laminar distributions were previously reported by several anterograde studies of the visual areas in New World monkey^{21,36,38,44}. While this pattern thus appears to be general for the visual system, different laminar arrangements have been reported in the somatosensory cortex^{9,10}. That is, cortico-cortical efferents from the primary somatosensory area to the parasensory and contralateral regions terminate in vertical bands or ‘columns’ in layers I through IV. In the visual cortex, only rostral efferents from area 19 to the superior temporal and intraparietal sulci terminate in this distinct columnar fashion with distribution of terminations in layers I through IV. Although other visual efferents (i.e. from area 17 to area 18, and area 19 to inferotemporal area TE) appear to resemble this columnar pattern of termination, a closer analysis reveals that terminations are mainly directed to layer IV with periodic extensions into layer III. These intermittent ‘sprays’ of silver grains are different from and less pronounced than the classical ‘columns’, as seen in the

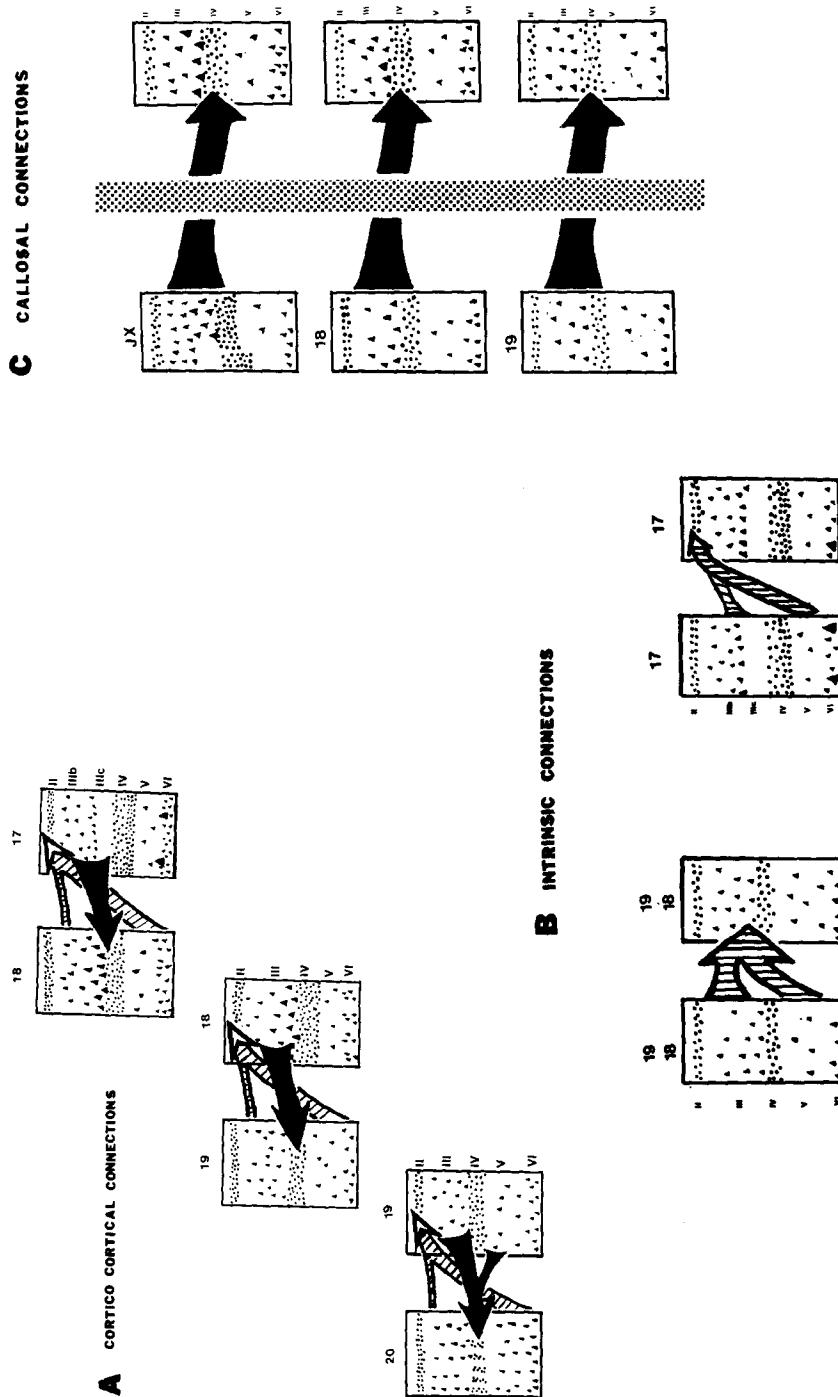


Fig. 10. Summary diagram to show: A, rostral and caudal connections of areas 17, 18 and 19. Note that rostrally directed connections, shown by dark arrows, originate from layer III of areas 17, 18 and 19 and terminate in layer IV of areas 18, 19 and 20, respectively, while caudally directed connections from areas 20, 19 and 18 (shown by hatched arrows) originate from layers Vb, VI, and terminate in layer I of areas 19, 18 and 17, respectively; B, intrinsic connections. In areas 18 and 19 these connections originate from layers IIIc and Va and terminate in layers I through IV (left). In area 17, these intrinsic connections originate from layers IIib, IIIc, and VI and terminate mainly in layer I (right); C, callosal connections of juxtastriate area, area 18 and area 19. Note that in each of these areas, callosal connections originate from layer III and terminate in layers I through IV.

somatosensory system^{9,10} and in the superior temporal and intraparietal sulci (compare Figs. 2A, 3A and 4A with 4B and 4C).

The use of HRP injections in the present study has further allowed the precise visualization of neurons giving rise to these rostrally directed cortical connections. In area 17, two spatially separated populations of neurons, in layers IIIa and IIIc, project to area 18. In area 18, however, efferents to area 19 originate from neurons in layer III, primarily IIIc, without any spatial discontinuity. Finally, neurons projecting rostrally from area 19, like those in areas 17 and 18, are mainly in the supragranular layers, but a smaller number also occur in layer Va.

Caudally directed connections

It is now well-established for the primary auditory²⁷, somatosensory⁴³ and visual^{12,17,38,39,48} cortical areas, that projections from the parasensory cortices are directed back to the primary sensory areas, where they terminate mainly in the plexiform layer. Our results indicate that, in the occipito-temporal region of the rhesus monkey, each cortical area projects back to a given 'precursor' area, not just the parasensory region (area 18) to the primary sensory area (area 17). These caudally directed connections terminate mainly in layer I and, to a lesser extent, in layers V and VI (or IIIc and V in area 17). Similar connections from area 18 to area 17 in New World monkeys appear to have a wider laminar distribution, with terminations in layers III, V, and VI, as well as in layer I^{12,39,48}.

The exact functional role of rostrally and caudally directed connections is not clear. The strikingly different laminar distribution of these two efferent systems, however, may be indicative of two quite different functional mechanisms. The rostrally directed system, for example, may relay sensory information from the primary cortical region to successively higher order sensory areas, while 'feedback' modulation may be provided by the caudally directed system. Similar reciprocal connections are known to occur in other systems, such as the cortico-thalamic^{25,26}. In this context, it is interesting that, like caudally projecting neurons, cortico-thalamic neurons are located in the infragranular layers^{11,20,40}. It is conceivable that these two pathways, which originate from similar laminae and possibly from identical neurons, may be engaged in somewhat similar operations.

Unlike the cortico-thalamic system, however, the caudally directed cortical projections include an additional component from neurons in layer IIIa. These neurons, with dendritic arborizations mainly in layer I¹⁹, send efferents to layer I of their cortical projection zone. In contrast, the infragranular neurons, which also project to layer I, have dendrites which extend through several layers toward the pia¹⁹. Accordingly, these neurons in the infragranular layers appear to be strategically located for integrating information from several laminae, whereas those in layer IIIa seem to be optimally situated for forwarding information from layer I of one area to layer I of another area.

Superior temporal sulcus

Reciprocal connections between area 17 and the caudal part of the superior

temporal sulcus (STS) have been demonstrated by several investigators^{35,45}. The laminar organization of these connections closely conforms to the pattern of rostrally and caudally directed systems as discussed above. Thus, efferents from striate cortex terminate in and around layer IV of the STS^{31,35,41,45}. In New World monkeys the reciprocal connections from the STS terminate in layers I, IIIc, and VI of area 17 but not in layer IV³⁵. Like other caudally directed connections, these projections from the STS arise from neurons mainly in the infragranular layers^{35,45}. However, the projections from area 17 to the STS, unlike those from area 17 to area 18, originate from neurons in both supra- and infragranular layers^{20,33-35}.

Besides the connections between area 17 and the STS, our data indicate reciprocal connections between both areas 18 and 19 and different parts of the STS. The present results suggest that the connections linking area 18 and the STS are similarly arranged to those between area 17 and the STS. That is, efferents from area 18 terminate mainly in layer IV of the STS and are reported to originate from both the supra- and infragranular layers³⁴, while the reverse connections originate from neurons mainly in the infragranular layers of the STS. The connections between area 19 and the STS, however, have a different laminar arrangement. Thus, terminations from area 19 extend in a vertical band through layers I to IV of the STS; and the neurons in the STS which project back to area 19 occur in both the supra- and infragranular layers. This morphological diversity of laminar arrangements suggests that different parts of the STS may be differentially interconnected with the prestriate, as opposed to striate cortex. The existence of heterogeneous visual areas within the STS has also been already suggested by physiological experiments⁵¹.

Intrinsic connections

In area 17, terminations extend from the injection site in characteristic horizontal bands in layers I, IIIc and V, as observed by Fisken et al.⁶. After HRP injections in area 17, retrogradely filled neurons are seen in layers IIIb, IIIc and VI, including solitary Meynert cells at the border of layers V and VI. Since filled neurons occur selectively in these layers in the vicinity of injection sites, it is likely that they give rise to the horizontal connections observed in anterograde experiments. The labeling of Meynert cells in layer VI, after HRP injections of area 17, raises the question of whether such labeling resulted from uptake by axons traveling to the superior temporal sulcus, where these neurons are known to project^{20,32,35}. The absence of labeled Meynert cells after injections confined to areas 18 or 19, however, and their occurrence 3-4 mm rostral to the injection site in area 17, suggest that in fact these neurons also give rise to intra-striate connections.

In both areas 17 and 18, a superficial injection of isotope limited to layers I-III resulted in an interlaminar connection to layer V (see Fig. 2C). This interlaminar connection has been previously reported in several visual areas (both primary and non-primary) in New World primates^{21,36-38,44}.

Within areas 18 and 19, but not area 17, connections near an isotope injection terminate in several vertical bands in layers I through IV. Similar terminations have also been described in the primary somatosensory¹⁰ and motor¹⁶ cortices. In areas 18

and 19, the cells of origin of these intrinsic connections occur in discrete clusters in layers IIIc and Va. Once again, this type of laminar distribution has been reported for cells giving rise to intrinsic connections within the somatosensory system¹¹.

Callosal connections

Callosal connections between occipital regions are also characterized by a distinct laminar organization. In areas 18, 19 and TE, these connections originate from neurons in layer III (mainly IIIc), just as rostrally directed intracortical connections. Unlike the intracortical connections, however, callosal efferents from areas 18 and 19 regularly terminate in vertical bands in layers I through IV. These results confirm and extend previous reports concerning the laminar distribution of callosal efferents from area 18^{7,15,20,24,38,46,47,49}.

Vertical terminations

Several cortical connections within the occipital lobe terminate in vertical bands or 'columns' in layers I through IV; namely, the connections from area 19 to the superior temporal and intraparietal sulci, intrinsic connections within areas 18 and 19, and homotopical callosal connections from areas 18 and 19 (see Figs. 3, 4 and 9). The possible significance of layer I versus layer IV terminations has been discussed above. The significance of vertically organized terminations, however, is particularly unclear. It is especially unclear why certain fiber systems should terminate mainly in layer IV, while others terminate in layers I through IV. For example, efferents from areas 17 and 18 terminate in layer IV of the STS; but efferents from area 19 to the STS terminate in vertical bands. Another intriguing aspect of these vertical terminations is their apparent regularity or periodicity. A somewhat similar periodic columnar organization has been described in somatosensory^{9,10} and motor¹⁶ cortices and in some instances the morphological organization has been correlated with physiologically defined phenomena¹⁴. Possibly the vertical mode of termination serves to achieve an interdigitating arrangement of different afferent inputs to a given region. For instance, callosal and intracortical input to a given area (or intracortical connections from two different areas) may terminate in a complementary, rather than overlapping fashion. The occurrence of vertically organized terminations has been observed through many regions of the cortex¹³. The widespread occurrence of periodicity of termination implies that this type of organization might have a significant role to play in cortical functions. Further investigations, however, are necessary to clarify the functional role of this particular anatomical organization.

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