Projections to the Superior Temporal Sulcus From the Central and Peripheral Field Representations of V1 and V2

LESLIE G. UNGERLEIDER AND ROBERT DESIMONE
Laboratory of Neuropsychology, National Institute of Mental Health, Bethesda, Maryland 20892

ABSTRACT

In a series of three studies, we have begun to explore the sequence of visual information processing along the pathway from striate cortex (V1), through MT, into the parietal lobe. In this first study, we sought to establish the relationships among MT, the heavily myelinated zone of the superior temporal sulcus (STS), and the V1 and V2 projection fields in the STS.

Autoradiographic material from seven hemispheres of six macaques injected with tritiated amino acids into either V1 or V2 was analyzed in detail, and the results were plotted onto two-dimensional reconstructions of the STS. Autoradiographic material from eight additional macaques with V2 injections was also examined.

The results indicate that the central visual field representations of both V1 and V2 project into the heavily myelinated zone in the lower bank and floor of the STS, confirming prior studies, whereas the far peripheral representations of both V1 and V2 project into the cortex medial to this zone on the upper bank of the sulcus. There is no evidence that this medial cortex is a separate area that receives projections from V1 and V2 in parallel with the projections these areas send to the heavily myelinated zone. Rather, there seems to be a single projection field of V1 and V2 whose central representation lies within the heavily myelinated zone and whose most peripheral representation lies medial to it.

Because of the difference in myelination between the central and peripheral field representations as well as visuotopic anomalies between them, we retain the term "MT" for the heavily myelinated zone and apply the term "MTp" to the far peripheral projection zone. Both MT and MTp are required to process the complete outputs of V1 and V2 within the STS and thus should probably be regarded as two distinctive parts of a single visual area. The difference in myelination between MT and MTp suggests that there is a difference in visual processing between the central and peripheral visual fields. The average size of MT is estimated to be 62 mm², and the average size of MT and MTp combined to be 76 mm², which is consistent with estimates derived from several other studies.

Key words: striate cortex, extrastriate cortex, area MT, visual system, macaque

In the macaque, one of the major cortical pathways out of striate cortex (V1) is directed into the parietal lobe through area MT. In a series of three studies, we have begun to explore the sequence of information processing along this pathway. As a first step, we sought to establish the relationship between MT and the V1 and V2 projection fields in the superior temporal sulcus (STS).

Several previous studies have shown that both V1 and V2 project to an area within the STS that is characterized by heavy myelination and a high proportion of directionally sensitive neurons. In this study, we sought to establish the relationship between MT and the V1 and V2 projection fields in the STS.

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selective cells (Zeki, '74, '76, '78; Ungerleider and Mishkin, '79; Van Essen et al., '81; Weller and Kaas, '83). It is not yet clear, however, whether projections from the peripheral visual field representations of either V1 or V2 are limited to the heavily myelinated zone or whether they extend into surrounding areas in the STS. The question bears on the issue of whether area MT in the macaque is coincident with the heavily myelinated zone, the V1 projection field, or both. Besides establishing the limits of MT, an answer to this question would also help clarify whether areas outside the heavily myelinated zone in the STS receive their visual input only by way of MT or whether they receive direct inputs from V1 or V2.

In the present study, we examined the projections to the STS from V1 and V2, with particular regard to the location of the representation of the peripheral visual field. In the second study of this series, we examined the visuotopic organization of the caudal STS physiologically, and in the third study, we sought to determine all of the cortical inputs and outputs of area MT.

METHODS

Autoradiographic material from three Macaca fascicularis (four hemispheres), weighing 3.2–4.5 kg, and three Macaca mulatta (three hemispheres), weighing 4.3–5.0 kg, was analyzed in detail, and the results were plotted onto two-dimensional reconstructions of the STS (see below). In all monkeys except one Macaca mulatta, injections of tritiated amino acids were made into V1 or V2 following electrophysiological determination of the receptive field at the injection site. Autoradiographic material from eight additional Macaca mulatta with V2 injections made under electrophysiological control was also examined, but the results of these cases will only be summarized here.

Animal preparation

At least 4 days prior to the recording session, a stainless-steel recording chamber and a bolt for holding the animal in a stereotaxic machine were implanted under aseptic conditions while the animal was under pentobarbital anesthesia. The treatment of the animal in the recording session has been described in detail elsewhere (Desimone and Gross, '79). Briefly, the animal was anesthetized with halothane in a mixture of 70% nitrous oxide and 30% oxygen and fixed in the stereotaxic machine by the head bolt. The bone underlying the recording chamber was removed. After all surgical procedures were completed, the animal was paralyzed with pancuronium bromide and maintained under 70% nitrous oxide and 30% oxygen anesthesia. End-tidal CO₂ and body temperature were continuously monitored and maintained within the normal physiological range. The pupil of the contralateral eye was dilated with cyclopentolate hydrochloride and the cornea was covered with a contact lens selected to focus the eye on an 85-cm-diameter translucent hemisphere. The ipsilateral eye was occluded. Recording sessions generally lasted 8–12 hours. Following the isotope injection, infusion of the paralyzing agent was terminated, and the animal was returned to its cage after recording.

Receptive field recording

The locations of the fovea and the center of the optic disc were projected onto the translucent hemisphere. The horizontal meridian was taken to be a line passing through both of these points, and the vertical meridian as an orthogonal line passing through the fovea. Action potentials from several neurons or “multiunits” were recorded with varnish-coated tungsten microelectrodes with exposed tips of 20–30 μm. Receptive fields were mapped with a handheld projector. Exploratory recordings in V1 and V2 were guided by maps of the visuotopic organization of each area (Daniel and Whitteridge, '61; Gattass et al., '81; Van Essen et al., '84) and were continued until the desired visual field representation for the injection was located.

Injections of V1 and V2

Following recording, injections were made with 1-μl Hamilton syringe with a beveled 27-gauge needle. A 21-gauge guide tube was first lowered to within 2 mm of the intended injection site, and an electrode was advanced through the guide tube to verify the location of the receptive field. The electrode was then withdrawn, the syringe was inserted in the microdrive, the syringe needle was advanced through the guide tube to the same depth as the electrode, and the injection was made as described below. Twenty minutes after the injection, the syringe needle was withdrawn into the guide tube and the guide tube was removed from the brain. This procedure assured accurate placement of the injection and also prevented any leakage of label up the track.

In each of the monkeys, an equal-parts mixture of tritiated proline (New England Nuclear L-[2,3,4,5-3H], specific activity 100–140 Ci/mmol) and tritiated leucine (New England Nuclear L-[3,4,5-3H(N)], specific activity 100–140 Ci/mmol) was injected. The labeled amino acids, which had been evaporated and then reconstituted in 0.9% saline to give a final concentration of 50 μCi/μl, were injected at a rate of 0.02 μl/2 minutes for a total volume per injection of 0.15 μl in the Macaca fascicularis (cases 2–4, 6) or 0.30 μl in the Macaca mulatta (cases 1, 5, 7). Four of the six monkeys received unilateral injections into either V1 (cases 1, 3, 4) or V2 (case 7). One monkey received an injection into V1 of one hemisphere (case 2) and V2 of the other (case 6). The remaining monkey received an injection into V2 of both hemispheres, but the results from only one of these are reported here (case 5). Since we have never seen a projection to the contralateral STS in any of 17 cases with unilateral injections or lesions of V1 or V2, we felt confident that no ambiguity was introduced by injection of tracers into both hemispheres in two of our animals.

Histological processing

After a 6-day survival period, the brains were fixed by perfusion with 0.9% saline followed by 10% formol-saline. Thereafter, they were blocked stereotaxically, removed from the skull, photographed, and stored in 30% sucrose in 10% formol-saline until they sank. Frozen sections, 30 or 33 μm in thickness, were then cut in either the frontal plane or at 20° from the frontal plane, and every fifth section was processed for autoradiography according to the procedures of Cowan et al. ('72). The sections were mounted, dipped in Kodak NTB2 emulsion, and exposed at 4°C for 12 weeks. Subsequently, the autoradiographs were developed in Kodak D19, fixed, and counterstained with thionin. Parallel series of sections 0.9 or 1.0 mm apart were stained for myelin by the Gallyas ('79) procedure or, in one case (case 1), by the Spielmeyer method (Lillie, '65). For purposes of analysis, the locations of concentrations of silver grains...
were charted onto enlarged photographs of the myelin-stained sections.

**Two-dimensional reconstructions of the superior temporal sulcus**

A two-dimensional reconstruction of the STS was made for each of the seven cases presented here. For the first few cases, we made wire models of the STS from enlarged serial sections and then physically flattened them (Gattass and Gross, '81). The wires were bent around layer IV of sections taken at 1-2-mm intervals, and marks were made on the wires at myeloarchitectural borders and other landmarks. We found that if the alignment and spacing of the wires were accurate, it was not necessary to cut any wires to flatten the sulcus. After constructing several maps in this way, we found it possible to apply the "pencil-and-paper" technique of Van Essen and Maunsell ('80) to flatten the STS in the remaining cases. The two methods appeared to yield equivalent results.

In these maps and in the descriptions to follow, we use the terms "upper" and "lower" to refer to the two banks of the STS. "Lateral" in the STS means closer to the lip of the lower bank, and "medial" means closer to the lip of the upper bank. "Posterior" in the STS means closer to the tip of the sulcus in the parietal lobe and "anterior" means closer to the portion of the sulcus in the temporal lobe.

**RESULTS**

**Myeloarchitecture of the caudal STS**

Allman and Kaas ('71) first reported in the owl monkey that most area of MT is characterized by a dense band of myelinated fibers occupying mainly the lower cortical layers. There is now convincing anatomical and physiological evidence that the region homologous to MT in the macaque is the V1 projection zone in the STS; at least a portion of the V1 projection zone is also heavily myelinated (Ungerleider and Mishkin, '79; Van Essen et al., '81; Weller and Kaas, '83). To refer to this heavily myelinated region without prejudging whether it corresponds to area MT, to the complete V1 projection zone, or to both, we will use the term MT*. Surrounding MT* are several other myeloarchitecturally distinct regions, some of which appear to constitute distinct visual areas. These myeloarchitecturally distinct regions are best seen in sections stained with silver by the Gallyas ('79) method, although they can occasionally be visualized in sections stained with hematoxylin.

Immediately lateral to MT* lies area V4t (Desimone and Ungerleider, '86), which is a narrow area (1-3 mm wide) characterized by light myelination in all cortical layers. The distinct myelination of V4t was first noted by Schein et al. ('82), and subsequently Maguire and Baizer ('84) reported that this area provides a transition between the visuotopic organizations in V4 and MT. Adjacent to V4t lies area V4, which is intermediate in density of myelination between MT* and V4t and has distinct inner and outer bands of Baillarger (see Ungerleider and Desimone, '86: Fig. 4).

The cortex immediately medial to MT* in the floor and upper bank of the STS is only lightly myelinated (although not so light as V4t), but it does not stand out as a distinctive myeloarchitectural zone. Further medially, in the upper bank of the STS, is a second densely myelinated strip, nearly as dark in a myelin stain as MT*. We shall refer to this strip of cortex in the upper bank of the STS as the "densely myelinated zone," or DMZ. This myeloarchitectural zone was originally described by Newsome and Wurtz ('82), and we have included it as part of a larger visual area termed "MST" (Desimone and Ungerleider, '86). Although the functional significance of the DMZ is unclear at present, it serves as a useful landmark. The anterior and posterior borders of both V4t and the DMZ are indistinct, especially in sections cut in the coronal plane. This is sometimes also true of the borders of MT*, as noted previously by Weller and Kaas ('83).

Anterior to MT* in the floor of the STS lies area FST (Desimone and Ungerleider, '86), which is characterized by a plexus of thick radial fiber bundles running vertically from the white matter into the supragranular layers. The posterior border of FST appears to be coincident with the anterior border of MT*, although the precise border between them is sometimes difficult to discern. Anteriorly, FST loses its distinctive appearance as the floor of the STS narrows. The appearance of each of the distinctive myeloarchitectural regions in the STS is shown in Figures 4 and 9 and in Figure 4 of Ungerleider and Desimone ('86).

There is a loose relationship between the myeloarchitectural zones we have described in the STS and the cytoarchitectural zones described by Seltzer and Pandya ('78), MT* composes the largest part of their area OAa, while V4t and V4 are both located within their area OA. The cortex between MT* and the DMZ appears to form a part of Seltzer and Pandya's area PGa, and area FST may be located within the posterior portion of their area IPa (see their Fig. 1).

**Projections of V1 to STS**

In all previous studies, the projections from the central visual field representation of V1 to the STS have been found to be confined to MT*, i.e., the heavily myelinated zone (Ungerleider and Mishkin, '79; Van Essen et al., '81; Weller and Kaas, '83). To reexamine this finding, we injected the lateral surface of striate cortex in one monkey, case 1. We placed the injection as close as possible to the V1/V2 border to maximize the possibility of observing a V1 projection lateral to MT*, if one existed. We did not record the receptive field at the injection site in this case, but from published maps of V1 (Daniel and Whitteridge, '61; Gattass et al., '81; Van Essen et al., '84) and the location of label in the lateral geniculate nucleus (Malpeli and Baker, '75) we estimate that the injection was placed adjacent to the representation of the vertical meridian at about 0.5" into the upper visual field. Figure 1 shows that, as expected, the label in the STS in this case was completely restricted to the heavily myelinated zone and was located in its anterior portion where the central visual field is represented (Ungerleider and Mishkin, '79; Gattass and Gross, '81; Van Essen et al., '81; Weller and Kaas, '83). Consistent with previous reports (Ungerleider and Mishkin, '79; Rockland and Pandya, '79; Montero, '80; Weller and Kaas, '83), the label was concentrated in layer IV and the deep part of layer III. Although the injection in V1 was nearly at the representation of the vertical meridian, the location of label was not at the border of the heavily myelinated zone, confirming the observations of both Van Essen et al. ('81) and Gattass and Gross ('81), who found that the representation of the vertical meridian in MT is not always at the border...
Fig. 1. Case 1: Location of label in the superior temporal sulcus (STS) following injection in central visual field representation of the striate cortex (V1). Upper right: Two-dimensional reconstruction of caudal STS indicating borders of heavily myelinated zone (MT*). Note that the projection is confined to MT*. Dashed lines demarcate the boundaries of the upper bank, floor, and lower bank of the sulcus. Heavy line crossing sulcus indicates the layer IV contour line of section 70, shown below. Upper left: Lateral view of hemisphere, with injection site shown in black. Dashed line indicates the border of V1, and arrows demarcate the portion of STS that has been reconstructed in upper right. Bottom: Cross sections through injection site (black) and projection in STS. V1 is indicated by the dashed lines in the sections. Arrows in cortex indicate limits of myeloarchitectural zones. Scale marker applies to both the sections and the reconstruction of STS. In this and the following figures, all brains are shown as a right hemisphere even though some experiments were performed in the left hemisphere, and distance between sections numbered consecutively is 300 or 330 μm. Abbreviations: ca, calcarine fissure; io, inferior occipital sulcus; ip, intraparietal sulcus; 1, lunate sulcus; la, lateral sulcus; ot, occipitotemporal sulcus; st, superior temporal sulcus.
Fig. 2. Case 2: Location of label in STS following injection in upper peripheral field representation of V1. The receptive field recorded at the injection site is illustrated in the lower left. Note that the projection in STS is located medial to MT*. See Figures 3 and 4 for corresponding photomicrographs of injection site and projection in STS. Abbreviations: DMZ, densely myelinated zone medial to MT* in upper bank of STS; V4t, lightly myelinated area lateral to MT* in lower bank of STS; FST, area with distinctive radial myelination anterior to MT* in floor of STS; HM, horizontal meridian; VM, vertical meridian; pmt, posterior middle temporal sulcus. See Figure 1 for other conventions and abbreviations.
In cases 2 and 3, the injections were centered in the representation of the upper visual field, and in case 4 the injection was centered in the lower visual field. Because we wanted to avoid any possibility of spread into V2, the injections in all three cases were placed far from the V1/V2 border, near and possibly within the representation of the horizontal meridian in V1. In case 4, with a nominally lower visual field injection in V1, there was almost certainly involvement of the horizontal meridian, because there was a projection not only within the lower visual field representation of V2, but also at the anterior boundary of the upper field representation in V2. Similarly, in cases 2 and 3, with nominally upper visual field injections in V1, there was label not only in the upper field representation of V2, but dorsally in the hemisphere as well, in what may be the lower field representation of V2. Thus, the conservative interpretation is that in all three cases the injections were centered within, but not confined to, the intended upper or lower field representations in V1. In none of the cases was there any detectable spread of label from the injection site to area V2, and in none of the cases was there any label in visual areas that receive V2 but not V1 projections.

In all three of these cases involving the far peripheral representation of V1, the label in the STS was located medial to the border of MT*. In case 2 (Figs. 2, 4), the label extended from 2.6 to 4.4 mm beyond the heavily myelinated border, in case 3 (Fig. 5), from 0.9 to 3.0 mm beyond the border, and in case 4 (Fig. 6), from 0.7 to 5.0 mm beyond the border. The label in cases 2 and 3, the upper field injection cases, was located more anteriorly in the STS than in case 4, the lower field injection case. In all three cases, the label extended into the upper bank of the STS as much as 0.7–1.8 mm inside the densely myelinated zone (DMZ). As was true of the V1 projection to MT*, the V1 projection medial to MT* was concentrated in layer IV and the deep part of layer III.

The results from our cases with V1 injections in the representation of the far peripheral visual field indicate clearly that the projection field of V1 in the STS extends medial to MT*. Maunsell and Van Essen ('83a) include this medial cortex within a separate visual area termed "MST." Van Essen et al. ('81) suggested that the cortex medial to the heavily myelinated zone might receive a projection from V1 or V2 in parallel with the one V1 and V2 send to MT. If so, then the cortex just medial to MT* would have to be considered a separate visual area. Although we saw no evidence of dual projections from V1 to MT* and the cortex medial to it, it remained a possibility that each of these two regions might receive a separate projection from V2. To examine this possibility, we investigated the projections of V2 to the STS.

Projections of V2 to STS

In case 5 (Fig. 7), we placed an injection in V2 at the representation of 6.5° eccentricity on the horizontal meridian of the lower visual field. It is likely that the injection in this case also involved V3 just beyond the V2/V3 border. As with our central field V1 cases, there was label in the STS...
**Fig. 4.** Case 2: Relationship between location of label in STS and borders of myeloarchitectural zones. Injection site in this case involved the upper peripheral field representation of V1. A. Enlargement of STS shown in section 70, Figure 2, stained for myelin. Box indicates the region enlarged on right in B and C. Scale marker indicates 1 mm. B, C. Brightfield and darkfield photomicrographs, respectively, of adjacent autoradiographic section stained with thionin. Note that the projection is beyond MT*, within the DMZ. Scale marker indicates 500 μm. D, E. Enlargements of DMZ and FST shown in A, illustrating distinctive myeloarchitecture of these regions. Scale marker indicates 250 μm. See Figures 1 and 2 for conventions and abbreviations.
Fig. 5. Case 3: Location of label in STS following injection in upper peripheral field representation of V1. Note that both the injection site and the projection zone are very similar to those in case 2. Dotted line at the posterior end of MT* indicates a region of uncertainty in the location of MT*'s border. See Figures 1 and 2 for conventions and abbreviations.
Fig. 6. Case 4: Location of label in STS following injection in lower peripheral field representation of V1. Note that the location of the projection beyond the heavily myelinated zone is somewhat more posterior than in cases 2 and 3, consistent with the more posterior representation of the lower visual field in area MT. See Figures 1 and 2 for conventions and abbreviations.
Fig. 7. Case 5: Location of label in STS following injection in central visual field representation of V2. In contrast to the single projection zone seen after injections in the central field representation of V1, there are two patches of label in STS, one within MT* and another lateral to it. See Figures 1 and 2 for conventions and abbreviations.
within MT* but not in cortex medial to it. Table 1 shows that in five other cases with injections of V2, at eccentricities ranging from about 2° to about 15°, we have seen projections to MT* but never to the cortex medial to it. In case 5 (and in all of our V2 cases involving the central 15° in the lower visual field) there was, however, a separate projection to the cortex lateral to MT*. This projection always involved area V4 and in some cases, as in case 5, extended into area V4t as well. Our V2 cases with projections to area V4t were commonly those with injections near the V2/V3 border. Thus, the projection to V4t may reflect involvement of either area V3 or the representation of the horizontal meridian at the V2/V3 border.

In cases 6 and 7 we examined the projections to the STS from the far peripheral representation of V2. In case 6 (Figs. 8, 9), we injected V2 at an eccentricity of 48° in the upper visual field, and in case 7 (Fig. 10), at an eccentricity of 39° in the lower visual field. The injections in each case were confined within the borders of V2, based on both myeloarchitecture (Gattass et al., '81; Ungerleider and Desimone, '86) and electrophysiological recordings. A photomicrograph of the injection site in case 6 is shown in Figure 3.

In both cases 6 and 7 there was a single projection to the STS that began just inside the border of MT* and extended into the cortex medial to it. In case 6 (Fig. 8), the projection extended approximately 5 mm medial to the border of MT*, into the DMZ in the upper bank of the STS. Although the injection in case 6 (the other hemisphere of case 5) was made with the same volume of isotope and at a comparable eccentricity to that in case 2, the projection in case 6 was considerably more extensive. This finding may reflect the fact that projections from V2 to the STS are stronger than those from V1 (Maunsell and Van Essen, '83a; Ungerleider and Desimone, '86).

In case 7 (Fig. 10), the projection to the STS extended approximately 4.5 mm medial to the border of MT* and, like that in case 6, also included a part of the DMZ in the upper bank of STS. However, unlike the projection in case 6 (which involved the upper visual field), the projection in case 7 (which involved the lower visual field) wrapped around the posterior end of MT*. This portion of the projection in case 7 is probably located within the lower peripheral field representation of V4, which extends into the posterior tip of the STS (Ungerleider et al., '83; Desimone and Ungerleider, '86).

As shown in Table 1, two additional cases with injections in the far peripheral field representation of V2 had projections in the STS that were continuous from MT* into the cortex medial to it, and in a third case the projection was located entirely within the cortex medial to MT*. In all V2 cases, both central and peripheral, the laminar pattern of labeling in the STS was similar to that seen following V1 injections.

In summary, the central representations of both V1 and V2 send projections into MT*, and the far peripheral representations of both V1 and V2 send projections into the cortex medial to MT*. Although the lower visual field representation of V2 sends projections to the cortex lateral to MT* as well, V1 does not, indicating that area MT does not extend lateral to the heavily myelinated zone. There is no evidence that any portion of either V1 or V2 sends separate projections to both MT* and an area medial to it. Rather, V1 and V2 each seems to have a single projection field in the STS, consisting of a central visual field representation within the heavily myelinated zone and a far peripheral representation medial to it.

### Size and shape of MT*

Table 2 lists for each case the size of MT* and the estimated size of the complete projection zone of V1 and V2, including the far peripheral portion. We estimated the complete projection zone in each case by expanding the boundary of MT* to incorporate any projections located medial to it. The area of MT* ranges from 36 mm² to 82 mm² and the far peripheral projection zone adds another 8 mm² to 20 mm². On the average, the far peripheral projection zone appears to contain about 20% of the complete projection zone.

Figure 11 summarizes the relationship between MT* and the far peripheral projection zone in our five cases with peripheral field injections. To facilitate comparison, we superimposed projected drawings of the flattened maps of the STS from each of the cases and adjusted their sizes so that MT* would be about the same size in all cases. The locations of the projections from the far peripheral representations of V1 and V2 were very similar across cases and, except in case 7, were limited to the cortex just medial to the border of the posterior half of MT*. In case 7, as indicated earlier, the projection from the far peripheral representation of V2 extended not only medial to MT* but also posterior to it, into cortex we regard as the far peripheral representation of V4 (Ungerleider et al., '83; Desimone and Ungerleider, '86). Although MT* is roughly oval in shape, the far peripheral projection zone gives the complete projection field of V1 and V2 the shape of a kidney bean.

### DISCUSSION

#### Defining area MT

The first description in the macaque of the complete V1 projection zone in the STS was provided by Ungerleider and Mishkin ('79). Based on degeneration following large lesions of V1, they reported that the central visual field representation of the projection zone was located in the lower bank of the STS, the midperipheral field was located more medially in the sulcal floor, and the far peripheral field was located still more medially in the floor and even extended a short distance into the upper bank of the sulcus. Furthermore, they reported that the portion of the projection zone located in the lower bank and floor of the sulcus,
Fig. 8. Case 6: Location of label in STS following injection in upper peripheral field representation of V2. Note that the projection begins just inside MT* and extends into the cortex medial to it. See Figures 3 and 9 for corresponding photomicrographs of injection site and projection in STS. See Figures 1 and 2 for conventions and abbreviations.
Fig. 9. Case 6: Relationship between location of label in STS and borders of myeloarchitectural zones. Injection site in this case involved the upper peripheral field representation of V2. Left: Enlargements of STS shown in sections 67 (A) and 73 (D), Figure 8, stained for myelin. Boxes indicate the regions enlarged on right. Scale marker, which applies to A and D, indicates 1 mm. Right: Brightfield and darkfield photomicrographs of adjacent autoradiographic sections stained for thionin. Note that the projection extends medial to MT* into the DMZ. Scale marker, which applies to B, C, E, and F, indicates 500 μm. See Figures 1 and 2 for conventions and abbreviations.
Fig. 10. Case 7: Location of label in STS following injection in lower peripheral field representation of V2. Note that the projection begins within MT* and extends both medially and posteriorly. The most anterior portion of the projection is connected to the remainder of the projection zone by a region of light label. The most posterior portion of the projection may lie within area V4. See Figures 1 and 2 for conventions and abbreviations; pom, medial parieto-occipital sulcus.
the visual field beyond about 25°, however, appeared to extend beyond the heavily myelinated zone. Ungerleider characterized by heavy myelination. The representation of containing the central 20°-30°, was characterized by heavy myelination. The representation of the visual field beyond about 25°, however, appeared to extend beyond the heavily myelinated zone. Ungerleider and Mishkin suggested that the complete V1 projection zone in the STS corresponded to area MT but that the borders of MT were not coincident with those of the heavily myelinated zone. This description of MT in the macaque was similar to that of area MT in the owl monkey, which was reported to be thicker and somewhat more heavily myelinated in the central than in the far peripheral visual field (Allman and Kaas, '71), and virtually identical to that of area MT in the Galago, in which the far peripheral visual field was found to be represented beyond the heavily myelinated zone (Allman et al., '73: Fig. 3; Allman, personal communication).

The description of MT by Ungerleider and Mishkin was subsequently brought into question by Van Essen et al. ('81), whose data suggested that MT might indeed be completely coincident with the heavily myelinated zone in the lower bank and floor of the STS. This interpretation was based on both their autoradiographic findings that projections to the STS from V1 (mainly from the central visual field representation, but in one case from the peripheral field at an eccentricity of about 40°) were restricted to the heavily myelinated zone and their physiological results that receptive fields in the upper bank of the STS were much larger than those within the heavily myelinated zone and were in an inappropriate location. They favored the view that the projection medial to the heavily myelinated zone observed in the Ungerleider and Mishkin ('79) study was due to inadvertent damage to the far peripheral representation of area V2, a possibility considered but rejected by Ungerleider and Mishkin. More recently, Maunsell and Van Essen ('83a) have included the cortex medial to the heavily myelinated zone within a separate visual area termed "MST," which receives projections from MT and, presumably, V2.

Simultaneously with the study of Van Essen et al. ('81), a third description of MT was provided by Gattass and Gross ('81). On the basis of electrophysiological mapping of the STS, they reported that the peripheral visual field representation in MT extended beyond the heavily myelinated zone both medially, as proposed by Ungerleider and Mishkin, and possibly posterolaterally as well. Their estimate of the size of MT was over twice that reported by Van Essen et al. Still more recently, in an anatomical study of projections from the central and midperipheral visual field representations of V1, Weller and Kaas ('83) estimated the size of MT to be about the same as that reported by Gattass and Gross, yet found V1 projections to be limited to the heavily myelinated zone, as had Van Essen et al.

The results of the present study, in conjunction with our physiological results in a companion study (Desimone and Ungerleider, '86), support all of the previous interpretations in part, but none completely. First, we have confirmed the original finding of Ungerleider and Mishkin ('79) that the far peripheral representation of V1 projects beyond the heavily myelinated zone, and we have ruled out inadvertent involvement of V2 as a factor. In addition, we have found that the far peripheral representation of V2 projects to this same region, indicating that there is a convergence

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**TABLE 2. Comparison of Size of Heavily Myelinated Zone in STS (MT*) With Estimated Size of Complete V1 and V2 Projection Zone**

<table>
<thead>
<tr>
<th>Case</th>
<th>Species</th>
<th>Size of MT* (mm²)</th>
<th>Size of complete projection zone (mm²)</th>
<th>% of visual field representation beyond MT*</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Macaca mulatta</td>
<td>52</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
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<td>36</td>
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</tr>
<tr>
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<td>71-78</td>
<td>24</td>
</tr>
<tr>
<td>5</td>
<td>Macaca mulatta</td>
<td>52</td>
<td>?</td>
<td>?</td>
</tr>
<tr>
<td>6</td>
<td>Macaca fascicularis</td>
<td>41-45</td>
<td>60-65</td>
<td>31</td>
</tr>
<tr>
<td>7</td>
<td>Macaca mulatta</td>
<td>82</td>
<td>102</td>
<td>20</td>
</tr>
</tbody>
</table>

*In cases 3, 4, and 6, the range of sizes shown indicates the uncertainty in determining the myeloarchitectural border. In cases 1 and 5, the question marks (?) indicate that the value could not be calculated as the injections involved the central visual field representation of V1 and V2, respectively. Values shown are not corrected for tissue shrinkage. STS, superior temporal sulcus.
of inputs in the STS from the far peripheral representations of V1 and V2, just as there is a convergence of inputs in the STS from the central field representations of V1 and V2 (Zeki, '76). Furthermore, consistent with both these anatomical findings and the physiological findings of Gattass and Gross ('81), we found in our companion physiological study (Desimone and Ungerleider, '86) that the central and midperipheral portions of the visual field are represented within the heavily myelinated zone, but the far peripheral field is represented in cortex medial to it. Not only do both these regions receive inputs from V1 and V2, but both are characterized by a high proportion of directionally selective neurons, and both share a common relationship between receptive field size and eccentricity (Desimone and Ungerleider, '86).

Yet our physiological data also support the observation of Van Essen et al. ('81) that there is sometimes a discontinuity in the representation of the visual field as one crosses the medial border of the heavily myelinated zone (Desimone and Ungerleider, '86). This discontinuity, together with the abrupt change in myelination, convinces us that the central V1 projection field within the heavily myelinated zone should be distinguished in some way from the peripheral V1 projection field located beyond it. Therefore, to underscore the distinctions between the two regions as well as their commonalities, we propose that the term "MT" be restricted to the heavily myelinated zone (the region we have so far termed MT and the term "MTp" be used for the peripheral field portion of the V1 projection located medial to the heavily myelinated zone. It should be noted that MTp extends a small distance into the densely myelinated zone (DMZ) on the upper bank of the STS, but is largely located lateral to it. MT and MTp are both required to process the full output of V1 in the STS and thus should probably be regarded as two distinctive parts of a single visual area.

**Significance of myeloarchitecture**

With the advent of silver-based myelin stains (Gallyas, '79), it has been possible to observe more myeloarchitectural detail in the cortex than ever before. There are at least three distinctive myeloarchitectural zones near MT in the STS and numerous others in other parts of the extrastriate cortex (Desimone and Ungerleider, '86; Ungerleider and Desimone, '86). In some cases these zones appear to constitute complete visual areas, in some cases they may constitute only portions of areas, and in still other cases these zones may span two or more visual areas.

In the case of MT and MTp, the myeloarchitectural difference is related to the central and peripheral portions of the V1 projection field and could therefore simply reflect a difference in external connectivity. Since MT and MTp lie just above the calcarine fissure, which contains the peripheral field representation of V1, it may be that messages from peripheral V1 have less distance to travel compared to those from central V1 and can consequently be carried by less heavily myelinated fibers.

Alternatively, it is tempting to speculate that the myeloarchitectural difference between MT and MTp reflects a more functionally significant difference, such as a difference in perceptual capacities between the central and peripheral visual fields. Since neurons within at least the central field representation of MT are sensitive to disparity (Maunsell and Van Essen, '83b), the difference in myelination could relate in some way to differential involvement in stereopsis. Recent anatomical evidence indicates that the central and peripheral visual fields may be treated differently throughout the visual cortex. At least two extrastriate areas, V3A and PO, receive inputs predominantly from the peripheral field representations of other visual areas (Zeki, '80; Colby et al., '83), while other extrastriate areas, such as V4, receive inputs predominantly from the central field representations (Ungerleider et al., '83). Thus, the different processing demands of the central and peripheral visual fields may have generated, in some cases, separate extrastriate areas, and in other cases, differences in myeloarchitecture within an area. In this regard, it is interesting to note that differences in both cytoarchitecture and myeloarchitecture have been reported for different portions of the visual field representation within areas 18 and 19 of the cat (Tusa et al., '79).

**Size of MT and MTp**

As shown in Table 3, the size of the complete map of the visual field in the STS, i.e., MT plus MTp, found in the present study is roughly comparable to that of Gattass and Gross ('81), Weller and Kaas ('83), and Ungerleider and Mishkin ('79) but seems to be at variance with that of Van Essen et al. ('81). Excluding case 7, a rhesus monkey with a particularly large brain, we measured the average size of the heavily myelinated zone (MT) to be 48 mm² and the average size of the complete visual field representation (MT plus MTp) to be 59 mm². From the known spacing of electrode penetrations in our animals, we estimate that the tissue shrinkage during perfusion and histological processing was about 12% in all linear dimensions. Therefore, with a linear correction factor of 12% applied to our material, the foregoing areal values become 62 mm² and 76 mm², respectively. Based on electrophysiological mapping of receptive fields, Gattass and Gross reported an overall size of 83 mm² (corrected for shrinkage) for the complete visual field representation. Based on the pattern of projections from V1 (out to about 20° eccentricity), Weller and Kaas estimated a size of 68 mm² for the complete projection zone. Weller and Kaas did not correct their measurement for tissue shrinkage; if we assume that shrinkage in their material was also about 12%, then the size of their complete map would be 88 mm². Based on degeneration from lesions that collectively included all of V1, Ungerleider and Mishkin described the boundaries of the complete V1 projection field but did not calculate its size. From the data of Ungerleider and Mishkin, we have calculated its size to be 106 mm². This value may be an overestimate of MT plus MTp.
as their V1 lesions involved the far peripheral representation in V2, which also projects to V4 in the STS in some cases (Ungerleider et al., '83). Nonetheless, there is considerable agreement in the size of the complete V1 projection field, or visual field map, as estimated by the present study, Gattass and Gross, Weller and Kaas, and Ungerleider and Mishkin.

In their study of MT, Van Essen et al. ('81) estimated the size of the complete visual field map in the STS to be only 33 mm², less than half the size found in any other study. There are at least three factors that may account for this small size. First, Van Essen et al. derived their estimate from measurements of the heavily myelinated zone, since they considered the representation of the entire visual field to be contained within this zone. This would account for some but not all of the difference inasmuch as we measured the heavily myelinated zone to be 62 mm². Second, the animals in the Van Essen et al. study were considerably smaller than those in our own and at least two of the three other studies of MT. The animals in the Van Essen et al. study ranged from 1.5 to 3.5 kg, whereas ours ranged from 2.2 to 4.5 kg (not including the one large monkey, case 7, excluded from our average); those of Gattass and Gross ranged from 3.0 to 4.8 kg; and those of Ungerleider and Mishkin ranged from 4.5 to 6.5 kg. The weight range of the animals in the Weller and Kaas study was not specified. Thus, Van Essen et al. may have excluded from our average because of its size a 5-kg rhesus monkey with a very large brain. The size of the heavily myelinated zone in this monkey was 82 mm² or, corrected for tissue shrinkage, 106 mm² (Table 2). The exceptionally large size of MT in this animal suggests that the small monkeys used by Van Essen et al. may have contributed to the small size of MT in their study relative to the sizes calculated by other investigators. Similarly, the large monkeys used by Ungerleider and Mishkin could account in part for the particularly large size of MT in that study. Finally, and perhaps most importantly, Van Essen et al. may have used a set of criteria for defining the borders of the heavily myelinated zone that differed from that used by other investigators. Thus, Van Essen et al. may have systematically excluded cortex from the heavily myelinated zone that others have included.

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LITERATURE CITED


