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Evidence regarding the integrity of the posterior medial lateral suprasylvian visual area in the cat¹

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Abstract

Among the areas of lateral suprasylvian visual cortex in cats defined by Palmer and colleagues (1978), PMLS (posterior lateral suprasylvian area) has been the most studied. Although PMLS has strong and well documented connections with area 17, it is unclear whether these connections extend to its upper visual field representation. We asked what cortical areas send input to the upper field representation in PMLS by making tracer injections in areas 17, 19, and posterior suprasylvian cortex. Tracer injections made in area 17's upper field representation in 15 cats failed to label the corresponding region in PMLS. Instead, they showed that area 17 is strongly connected with the posterior bank of the posterior suprasylvian sulcus (pSS), a region attributed by Palmer and colleagues to area 21a. Injections in area 19 had the same outcome. We consider this posterior upper field representation plus the lower field representation in PMLS to belong to a single area, LS (lateral suprasylvian visual area). Our data suggest that the upper field representation in PMLS belongs to a different area, most likely AMLS (anterior lateral suprasylvian area).

Keywords

PMLS; AMLS; cortical connections

INTRODUCTION

The extensive region of visual cortex located in the cat's suprasylvian sulcus has been subdivided in different ways. The prevailing view was described by Palmer et al. (1978) and Tusa and Palmer (1980), who identified eight suprasylvian visual areas based on their representations of the visual field. As these authors and others have noted, however, retinotopy in this region appears much less orderly and more complex than in areas 17, 18, and 19, and so provides somewhat ambiguous evidence for the proper delineation of cortical areas. Alternatively, one might distinguish one area from another by their cortical and thalamic connections, and on this basis we proposed that there is a single large area that can be distinguished from adjacent suprasylvian visual areas by its input from area 17 (Sherk, 1986a). This area, first referred to as the Clare-Bishop area (Hubel and Wiesel, 1969) and later as LS (lateral suprasylvian visual area: Grant and Shipp, 1991; Sherk and Mulligan, 1993), cuts across several areas as defined by Tusa, Palmer, and Rosenquist.

Although the issues regarding the proper subdivision of suprasylvian cortex remain unresolved, one of the areas described by Palmer et al. (1978), PMLS (posterior medial

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lateral suprasylvian area), has been the focus of more than 100 studies during the past two decades. Thus it is of some interest to determine whether PMLS is in fact a unitary area of visual cortex. Van Essen (1979) listed several criteria that can be used to identify such an area. A discrete area can be defined by 1) a distinctive cortical architecture, 2) a “well-defined representation of the visual field” (p. 228), and 3) connectional uniformity. The first criterion is not useful for subdividing suprasylvian visual cortex because no cyto- or myeloarchitectonic features distinguish different areas. The second criterion, that an area should have a relatively complete retinotopic representation of much or all of one hemifield, is one that PMLS clearly meets. Fig. 1B shows the retinotopic map in PMLS as described by Palmer et al. (1978). The third criterion is more problematic. A multitude of studies have shown that area 17 sends a strong projection to PMLS (see Discussion for references). But whether all of PMLS receives this projection is uncertain. Our early experiments failed to show any input from area 17 to the upper field representation (Sherk, 1986a), consistent with Montero’s report (1981), but Symonds and Rosenquist (1984) apparently found no discrepancy between inputs to different parts of PMLS.

Recent electrophysiological experiments in our laboratory have renewed our interest in the upper field representation in PMLS. We have recorded from this region in awake, behaving cats (Sherk and Wilkinson, unpub. observ.), and have found that many receptive fields extend well into the upper field, as predicted by Palmer et al.’s mapping (1978). The question is whether this representation belongs to the same area as does the lower field representation in PMLS. If so, the upper field representation of PMLS should receive strong input from area 17. To answer this question we examined data from a large set of experiments in which we injected tracer in the upper field representations of areas 17 or 19. We also looked at the outcome of tracer injections in two regions of suprasylvian cortex: first, in the upper field representation of LS, located in the pSS (labeled in Fig. 1A), and second, in PMLS itself.

We could find no input to PMLS from upper field injections in either area 17 or area 19. However, we did find a reliable projection from the upper field representation in LS to PMLS. These results suggest that PMLS is not a unitary area of visual cortex: the portion representing the upper visual field apparently belongs to a different area.

METHODS

All methods were approved by the Institutional Animal Care Committee of the University of Washington. Twenty-six outbred cats were obtained from commercial breeders. Most of the cases described here are drawn from four prior studies (Sherk, 1986a; Sherk, 1986b; Ombrellaro and Sherk, 1988; Sherk and Mulligan, 1993). Detailed descriptions of the procedures are given in these references. These studies were devoted to different issues, and do not describe the data presented here, except for four experiments mentioned in Sherk (1986a). For comparison with tracer injections made in upper field locations, we examined data from 20 additional experiments in which tracer was injected in area 17 at 26 lower field locations.

Tracers were injected in acute electrophysiological recording experiments in which cats remained under general anesthesia throughout (sodium pentobarbital, 2.5 mg/kg/hr). For all but two injections, either of two kinds of tracer were used: a mixture of ^3H -amino acids (proline and leucine), and HRP conjugated to wheatgerm agglutinin (WGA-HRP). Two injections were made of rhodamine conjugated to dextran (Vector Labs). Prior to an injection into visual cortex, receptive fields were plotted at the injection site by recording with a tungsten microelectrode. The electrode was replaced with a glass micropipette containing tracer and an etched wire that permitted recording in order to confirm the

location of receptive fields. Tracer was injected gradually, to a final volume of about 0.3 microliters. After transport times of 24–48 hours, the cat was perfused with mixed aldehydes while deeply anesthetized. All brains were sectioned coronally, and sections were processed for HRP using tetramethylbenzidine, or were processed for autoradiography. When fluorescent tracer was used, sections were mounted on slides with no processing.

Autoradiographic label and anterograde peroxidase label were charted with dark field illumination using a camera lucida. Examples of typical labeling are illustrated in Fig. 2. Autoradiographic label is shown in dark field (Figs. 2A, B, and D), and peroxidase labeling is shown in bright field (Fig. 2C). All label, including injection sites, was photographed using a conventional film camera with the lens mounted on a bellows to permit capture of whole sections with uniform dark field illumination. The film used was T-Max 100 (Kodak), and prints were made on Multigrade IV RC paper (Ilford). Images were digitized; contrast for some dark field images (Figs. 2A, B, D) was enhanced using Photoshop software (Adobe Inc.).

After tracer injections in areas 17, 18, or 19, label was charted at 200 μ m intervals throughout lateral suprasylvian cortex. After lateral suprasylvian injections, peroxidase-labeled cells were charted in other cortical areas at 200–400 μ m intervals. For simplicity, in the figures presented here all labeling and all receptive field data have been drawn as though injections were made in the right hemisphere. In actuality, about half of our injections were made in the left hemisphere. A total of 21 injections were made in areas 17 and 19 (or on the 17/18 border) at upper field locations, seven injections were made in PMLS, and three injections were made in the posterior bank of the pSS.

In order to determine the borders between areas 17, 18, and 19, in most experiments a set of sections was reacted for cytochrome oxidase. As described elsewhere (Sherk, 1986a), the characteristic pattern of reactivity in layer 4 in each of these areas provides a useful way of distinguishing them. To estimate the borders of LS, we pooled data from a number of different experiments in which anterograde tracer was injected in area 17. Lower field injections yielded label on the medial bank of the main limb of the suprasylvian sulcus (mSS, see Fig. 1A), sometimes extending into the sulcal fundus. Depending on the retinotopic elevation of the injection site, this label might be found as far anterior as AP +10.5 (six cases with very inferior locations). More central injections in area 17 produced label on the banks and fundus of the mSS more posteriorly. Finally, the set of 19 upper field injections in area 17 yielded label still further posterior and lateral, in the pSS.

To estimate the extent of the retinotopic spread of tracer after injections in area 17, label was charted in the LGN, and then compared to Sanderson's (1971) maps of geniculate retinotopy. The method is illustrated in Fig. 3. In this coronal section, dots show peroxidase-labeled cells, gray represents autoradiographic label, and dashed lines show azimuth and elevation from Sanderson's (1971) study. In cases with injections in the medial or posterior bank of the suprasylvian sulcus, geniculate cell labeling was sparse and scattered compared to that after injections of area 17, and thus less useful for estimating the retinotopic extent of tracer spread. However, we also charted labeled cells in area 17, and then compared their distribution with Tusa et al.'s (1978) mapping data for area 17.

RESULTS

Tracer injections in areas 17 and 19

PMLS occupies the medial bank of the mSS, from AP -2 to AP +8 (Palmer et al., 1978), as shown in Fig. 1B. The first question we addressed is whether tracer injections in the upper field representations of either area 17 or area 19 produce anterograde label in PMLS. We

made 19 tracer injections in area 17's upper field representation, with visual field locations shown by the light gray circles in Fig. 1C. All injections resulted in patches of anterograde label in lateral suprasylvian cortex, primarily in layers 3 and 4. The complete pattern of labeling in suprasylvian cortex is illustrated for four injections in Figs. 4 and 5; these cases were chosen to show the range of labeling patterns that occurred with injections at different retinotopic locations in the upper field.

After injections in area 17's peripheral upper field, label was confined to the posterior bank and fundus of the pSS. In the case illustrated in Figs. 2A and 4, WGA-HRP was injected at 25 deg eccentricity, and ^3H -amino acid at 60 deg eccentricity, yielding adjoining injection sites (see bottom of Fig. 4). Patches of label were concentrated far laterally on the posterior bank of the pSS, extending down into the fundus and medially to the middle of the posterior bank. The pattern of labeling was strikingly patchy, a phenomenon that is particularly clear in the near-tangential sections through the posterior bank of the pSS. Patches labeled with different tracers were interspersed, often adjoining each other but showing almost no overlap, as can be seen more clearly in reconstructions in flattened cortex (Fig. 7, Serk and Mulligan, 1992). The only additional cortical labeling was in areas 18 and 19, in sections posterior to those illustrated in Fig. 4.

Upper field injections closer to the center of gaze yielded patches of label on the posterior bank of the pSS that were located more medially and wrapped around to the extreme posterior end of the medial bank of the mSS. This pattern is illustrated in Figs. 2B, C and Fig. 5, which show labeling arising from different tracer injections in area 17. The two injections in Fig. 5 had eccentricities of 4 deg (WGA-HRP) and 9 deg (^3H -amino acid). In addition to patches on the posterior bank of the pSS, labeling continued down to the floor of the pSS, and slightly up onto its anterior bank (see section at AP -3.1 in Fig. 5). Injections at the same retinotopic locations in other experiments yielded labeling that extended half way up the anterior bank, reflecting variability in the retinotopic map (see Discussion). As in the case described above (Fig. 4), patches of label arising from the two injections shown in Fig. 5 were intermixed but almost entirely non-overlapping. Additional labeling was visible in areas 18 and 19, posterior to the illustrated sections, but nowhere else in cortex.

There appeared to be some variability among cats. In one cat a tracer injection in area 17's upper field representation (azimuth 10 deg, elevation +4 deg) yielded both strong label on the posterior bank and fundus of the pSS (shown in Fig. 2C), and small patches in the fundus of the mSS at AP +1.2. We believe that this label reflected a small anomalous representation of part of the upper quadrant in this cat. It could not have resulted from accidental tracer spread to some other part of area 17 because an injection of a different tracer at the same retinotopic site in the C layers of the LGN yielded patches of label at the identical location in the mSS.

We also made tracer injections into area 19's upper field representation in two cats. Just as with area 17 injections, we found strong label on the posterior bank and fundus of the pSS, and no label on the medial bank of the mSS. Fig. 6 illustrates one of these cases. Additional anterograde label was found in two other locations: the crown of the suprasylvian gyrus (presumably area 7), and the lateral bank of the mSS (both visible in section at AP +2, Fig. 6). These sites were never targets of projections from area 17. This assertion was confirmed in this experiment by an injection of ^3H -amino acid in area 17 at the same retinotopic location as the area 19 injection. Dense label was visible on the posterior bank and fundus of the pSS (see dark field photograph in Fig. 6), but no label was found at more anterior levels in any cortical area.

In contrast to upper field tracer injections in areas 17 or 19, 26 injections in the lower field produced labeling only on the medial bank and fundus of the mSS. As expected from mapping studies, there was a tendency for more inferior locations to yield more anterior label. A lower field injection in area 17, at 26 deg eccentricity, is illustrated in Figs. 2D and 7. Patches of anterograde label were found on the medial bank and fundus of the mSS, extending from AP +4.5 to +10.5. Some of these patches fell within PMLS, and the remainder were more anterior. In addition, strong labeling was visible in areas 18 and 19, as well as one patch lateral to area 19, in a visual area identified by Marcotte and Updyke (1982). As with upper field injections, the labeling pattern in suprasylvian cortex was remarkably patchy. In the coronal sections shown in Fig. 5 it is difficult to tell whether these scattered patches were joined to form bands, but when the complete pattern of labeling was reconstructed in a flattened view of the cortex, we found that the patches were unconnected (Fig. 6 of Mulligan and Sherk, 1993). Other lower field injections also yielded patchy labeling on the medial bank and fundus of the mSS, differing primarily in anteroposterior location from that in Fig. 7. Less inferior visual field locations tended to result in labeling that was shifted further posterior.

Tracer injections in areas LS

We might interpret these results in two ways. First, it is possible that PMLS occupies the entire region of medial bank of the mSS as described by Palmer et al. (1978), but contains no representation of the upper visual field. Second, it is possible that the upper field is present as these authors described, but that it does not receive input from areas 17 and 19. The next set of experiments provided evidence supporting the second possibility. In three cats we injected tracer into the upper field representation of LS (the posterior bank of the pSS; see Fig. 1C, white circles). In all three cases patches of label were found on the medial bank of the mSS, both in PMLS and beyond its presumptive borders. Fig. 8 shows an injection of WGA-HRP and the resulting distribution of labeled cells. Anterograde label was found at corresponding locations, but it was lighter than after injections of areas 17 or 19. In addition to a substantial patch of labeled cells on the medial bank of the mSS, there was a still larger patch on the lateral bank, and small patches on the crown of the suprasylvian gyrus, in area 7, and further anterior in the fundus of the mSS, extending anteriorly to AP +9.2. Posteriorly, there was a dense zone of labeled cells in the depths of the pSS, below the ectosylvian gyri, and smaller patches of label situated lateral to suprasylvian cortex. The largest number of labeled cells was found in area 17's upper field representation (see most posterior section in Fig. 8), and substantial numbers were also found in areas 18 and 19, in sections posterior to those illustrated in Fig. 8. The patterns of labeling in the other two cases were similar, with the most anterior label on the medial bank of the mSS occurring at AP +11.2. These experiments confirmed that there is a representation of the upper visual quadrant on the medial bank of the mSS, as reported by Palmer et al. (1978).

Based on these findings, we predicted that tracer injections made in the upper field representation on the medial bank of the mSS should label cells on the posterior bank of the pSS but *not* cells in area 17's upper field representation. The final set of experiments tested this prediction. We made seven injections in PMLS, shown in Fig. 10A. Receptive fields plotted at the injection sites were all in the lower field, at elevations from -2.5 to -8.3 deg (see hemifield plot in Fig. 10A). However, for the cluster of five relatively anterior injections, at AP +2 to +4, tracer apparently spread into the upper field representation (a region of cortex that was not visually responsive at the time of recording). These five injections yielded patches of label on the posterior bank of the pSS, but no labeling in the upper field representations of areas 17, 18, or 19. Fig. 9 shows this pattern for the largest injection. A substantial patch of labeled cells is visible on the posterior bank of the pSS (see arrow in Fig. 9). Labeled cells were also found in areas 17, 18, and 19 in the representation

of the lower field, consistent with the receptive fields plotted at the injection sites. The same pattern was found in the C layers of the LGN: labeled cells were present in the lower but not upper field representation.

The more posterior two PMLS injections shown in Fig. 10A failed to label cells on the posterior bank of the pSS, although they did label abundant cells in area 17, and some cells in the geniculate C layers. We concluded that these two injection sites were located within PMLS but posterior to its upper field representation.

DISCUSSION

Upper field representation in PMLS

The outcome of these experiments indicated that PMLS contains two distinctly different regions. The larger region, representing the lower hemifield and horizontal meridian, receives strong input from area 17, as demonstrated in previous tracer studies (Maciewicz, 1974; Gilbert and Kelly, 1975; Kawamura and Naito, 1980; Montero, 1981; Bullier et al., 1984; Symonds and Rosenquist, 1984; Sherk, 1986a; Sherk, 1986b; Grant and Shipp, 1991; Sherk and Mulligan, 1992; Sherk and Mulligan, 1993). The smaller region in PMLS, reported by Palmer et al. (1978) to map the upper visual field, we found receives no input from area 17 (see also Montero, 1981). We also failed to find input from area 19, though our evidence is more limited. Because of the difference in their cortical inputs, the upper and lower field representations seem unlikely to belong to a single unitary area, PMLS.

We assume that if a part of one cortical area receives input from another cortical area, the rest of this cortical area likewise receives such input. In macaque monkeys, the three areas that receive strong input from V1 (V2, V3A, and MT) support this assumption (for V2, see Gattass et al., 1997; for V3A, see Burkhalter et al., 1986, and Lyon and Kaas, 2002; for MT, see Van Essen et al., 1981, and Ungerleider and Desimone, 1986). MT (middle temporal area) is of particular interest. Its extent as defined by myelo-architecture differs from its extent as defined by its connections with V1. Ungerleider and Desimone (1986) concluded that the connectional evidence provided the best means of determining MT's extent; connectional homogeneity is more important than architectonic homogeneity.

At least one example in macaque monkeys does not completely conform to our assumption of homogeneous connections between cortical areas. V4 receives an input from V1 that is modest to its central and mid-field representations, but weak and variable to its peripheral representation (Ungerleider et al., 2008). However, we consider that the areas noted above – V2, V3A, and MT – are better models for striate-recipient suprasylvian cortex in cats because of the latter area's massive input from area 17. Indeed, this area has long been thought to be analogous to primate MT (Zeki, 1974).

There is some variability from cat to cat in how the visual field is mapped in suprasylvian visual cortex, as noted here and as observed previously (Djavanian and Harutiunian-Kozak, 1983; Zumbroich et al., 1986; Sherk and Mulligan, 1993; Olman et al., 2003); there may also be some variability among cats in the strength of connections to suprasylvian visual areas (MacNeil et al., 1997; Hilgetag and Grant, 2000). Is it possible that the upper field representation in PMLS receives strong input from area 17 in some cats, and none in others? We think this unlikely because we found the same result for all 15 cats with upper field tracer injections in area 17: there was no evidence of connections with PMLS.

If the upper field representation is eliminated from PMLS, the area would be only somewhat reduced in size since this representation is small. However, the map in PMLS would suffer a major loss of retinotopic completeness, being reduced to the lower visual quadrant. A

complete map of the visual field can be regained by uniting the striate-recipient part of PMLS with the upper field representation on the posterior bank of the pSS, shown in orange in Fig. 10B. This upper field map is a major target of area 17 (Montero, 1981; Symonds and Rosenquist, 1984; Sherk, 1986a; Grant and Shipp, 1991; present results). Moreover, the complete set of cortical and thalamic connections of this upper field representation are the same as the connections of the lower field in PMLS (Sherk, 1986a), suggesting that the two regions belong to a single area, LS.

The upper field representation in PMLS remains mysterious. What area does it belong to? Because of its small size and limited retinotopic extent, we think it unlikely to be a distinct area. It might belong to either of the two adjoining areas, area 7 or AMLS (anterior medial lateral suprasylvian area (Palmer et al., 1978)). Inclusion in area 7 seems unlikely. Pigarev and Rodionova (1998) found that, in awake cats, response properties in area 7 are quite different from those in PMLS and AMLS; for example, they have strikingly elongated receptive fields and lack clear direction selectivity.

Furthermore, these authors have identified a representation of the upper visual field on the crown of the posterior suprasylvian gyrus, remote from the upper field in PMLS, that they conclude is functionally the upper field component of area 7 (Rodionova et al., 2004).

We think that the upper field representation in PMLS is functionally part of AMLS (see Fig. 10B). Our reasons are three-fold. First, the upper field representations in PMLS and in AMLS adjoin each other, and could form a single upper field zone. Palmer and colleagues assigned them to different areas because their putative border mapped the vertical meridian, a common criterion for the transition from one cortical area to another. However, Palmer et al.'s data were obtained from only two cats, and subsequent authors have not confirmed this retinotopic boundary (Ouellette et al., 2004). Moreover, the presence of a vertical meridian representation does not always coincide with the border between different cortical areas: in both LS and in the macaque monkey's area MT, the vertical meridian is partially embedded inside the area (Maunsell and Van Essen, 1987; Sherk and Mulligan, 1993; Pigarev and Rodionova, 1998). Second, the response properties of single neurons in awake cats are not obviously different on either side of the AMLS/PMLS border (Sherk and Wilkinson, unpub. observ.). They do differ sharply, however, from response properties recorded in LS in the same experiments; almost no AMLS cells respond consistently to repeated stimulus presentations, many have a strong gaze shift contribution, and they are particularly sensitive to sudden changes in stimulus behavior (Wilkinson, 2009). Third, the upper field representations described by Palmer et al. (1978) in PMLS and AMLS have similar connections. In contrast to the lower field representation in PMLS, the upper field representations in both AMLS and PMLS lack input from areas 17 and 19 (for AMLS, Montero, 1981; Symonds and Rosenquist, 1984; Sherk, 1986a; present results), and they both lack input from the LGN (for AMLS, Updyke, 1981; Tong et al., 1982; Raczkowski and Rosenquist, 1983; Kawano, 1998; present results).

The conclusion that the upper field representation in PMLS actually belongs to AMLS might explain one puzzle: electrophysiological mapping experiments carried out since that of Palmer et al. (1978) have almost never encountered receptive fields in the upper field on the medial bank of the mSS (Turlejski and Michalski, 1975; Djavadian and Harutiunian-Kozak, 1983; Zumbroich et al., 1986; Sherk and Mulligan, 1993). In anesthetized cats most cells in AMLS are unresponsive or nearly so (Ouellette et al., 2004). In recording from PMLS in anesthetized cats, Hubel and Wiesel (1969) often did not encounter visually responsive cells until their electrode had traversed the upper one third of the medial bank of the mSS, and we think that this unresponsive zone corresponded to AMLS.

Patchy cortical projections to suprasylvian cortex

Every tracer injection in areas 17 and 19 yielded multiple patches of anterograde label in the suprasylvian sulcus. Montero (1981) first observed this striking phenomenon, and we subsequently investigated it in both electrophysiological and anatomical experiments (Sherk, 1986b; Sherk and Ombrellaro, 1988; Sherk and Mulligan, 1992; Sherk and Mulligan, 1993). We found that similar patchiness occurs no matter what the retinotopic location of the injection site. Three explanations seem likely. First, all of the patches arising from a single injection might fall within a single area that has a very disorderly retinotopic map. Second, each distinct patch might belong to a different cortical area within the suprasylvian sulcus. Third, all patches might lie within a single area that has an orderly retinotopic map that contains duplications of parts or all of the visual field. The third explanation, we believe, is correct.

We can rule out the disorderly retinotopy hypothesis because both anatomical and physiological data show that the map in LS is complex but not disorderly. Adjacent but non-overlapping tracer injections in area 17 always yield patches of label in LS that are adjacent but almost completely non-overlapping (Sherk and Ombrellaro, 1988; Sherk and Mulligan, 1992; see Figs. 4 and 5). Furthermore, the receptive fields of cells recorded in a column orthogonal to the cortical surface in LS show little scatter (Sherk and Mulligan, 1992). These two findings demonstrate that the map is locally orderly. The second explanation, that each patch belongs to a different cortical area, seems highly unlikely. Because patchiness occurs throughout LS, this explanation would result in many small areas, each representing only a fragment of visual field. Putative areas on the posterior bank of the pSS, for example, would all have maps that were fragments of the upper contralateral quadrant because the lower field and area centralis are not represented there. Moreover, there is no connectational or physiological evidence for the existence of these putative areas. Tracer injections anywhere in LS yield the same pattern of thalamic and cortical connections (Sherk, 1986a). Response properties such as direction selectivity appear to be similar whether cells are recorded in PMLS, and have inferior receptive fields, or on the posterior bank of the pSS, and have superior receptive fields (Spear and Baumann, 1975; Mulligan and Sherk, unpub. observ.). Finally, the lower field map and the upper field map in LS are globally similar: the extreme lower periphery and the extreme upper periphery are represented at opposite ends of LS, and central visual field is represented in the middle, at the junction between the mSS and the pSS (for lower field mapping, Palmer et al., 1978; Grant and Shipp, 1991; Sherk and Mulligan, 1993; for upper field mapping, Tusa and Palmer, 1980; Sherk and Mulligan, unpub. observ.).

We would conclude that LS is a single large area in which the upper field is mapped postero-laterally, the lower field anteriorly, and the area centralis in between. Throughout this global organization, the visual field appears to be duplicated in a fragmentary fashion. Retinotopic duplications within areas of visual cortex have been recognized in monkeys for some time. In the macaque's area V1, strips of visual field are duplicated in ocular dominance columns in layer 4, yielding two interdigitated maps (Hubel et al., 1974). In area V2 in macaques, there is retinotopic duplication in thick, thin, and interstripe regions, resulting in three interdigitated maps that correspond to functionally different compartments (Roe and Ts'o, 1995). Similar retinotopic duplication appears to occur in both V2 and V3 of owl monkeys (Kaskan et al., 2009). In LS, the fact that nearby regions of visual field are often mapped in an interspersed fashion, as in Figs. 4 and 5, is suggestive of interdigitated maps that might correspond to functionally distinct compartments. However, there is no physiological evidence for this hypothesis.

Conclusions

Based on the pattern of cortical connections between areas 17, 19, and suprasylvian visual cortex, we have reached two conclusions, illustrated in Fig. 10B. First, PMLS is not a unitary cortical area. The larger part of it can be united with the more posterior upper field representation to form an area, LS, that is connectionally homogeneous. Second, AMLS extends considerably further posterior than originally thought because it includes the upper field representation in PMLS.

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Figure 1.

A. Top-down view of cat's cortex with the main suprasylvian sulcus (mSS) and the posterior suprasylvian sulcus (pSS) labeled. B. Lateral view of the right cortical hemisphere, with the ectosylvian gyri removed to reveal the medial and posterior banks of the suprasylvian sulcus. PMLS (posterior medial lateral suprasylvian area) is shown with its retinotopic map color-coded. The upper visual field is orange, the lower visual field is blue, and a strip centered on the horizontal meridian, 6 deg wide, is yellow. C. Drawing of the upper left visual field showing receptive field locations at the centers of tracer injections. Most (19) injections were in area 17 or on the area 17–18 border. Two injections were in area 19, and three were on the posterior bank of the pSS.

Figure 2.

Photographs of anterograde label in coronal sections from four experiments; medial is to the left for each section. A. Dark field image of autoradiographic label on the posterior bank of the pSS after a ^3H -amino acid injection in area 17, centered 60 out in the upper field (illustrated further in Fig. 4). The halo of the injection site is visible in the lower left corner. B. Dark field image of autoradiographic label at the same anteroposterior level as panel A, after a ^3H -amino acid injection in area 17 in more central upper field (illustrated further in Fig. 5). C. Bright field image of peroxidase label at the same level as panels A and B, after a WGA-HRP injection in area 17; the retinotopic location was about the same as that of the panel B injection. D. Dark field image of autoradiographic label on the medial bank of the mSS after a ^3H -amino acid injection in area 17 in the lower field. Dense label in area 19 is also visible. Scale bar applies to all panels.

Figure 3. Drawing of a coronal section through the right LGN of C60 (illustrated in Fig. 5). Retrogradely labeled cells from the WGA-HRP injection in area 17 are shown as dots, and anterograde label from the ³H-amino acid injection in area 17 is shown in gray. Both kinds of label had their maximal extents in this section. Dashed lines indicate azimuth and elevation lines from Sanderson's (1971) retinotopic map at this level. Medial is to the left.

Figure 4.

Two tracer injections in area 17's upper field representation in one cat. Retinotopic locations, based on receptive fields at the injection sites and labeling in the LGN, are shown in a drawing of the upper left visual quadrant (stipple = WGA-HRP, gray = ^3H -amino acid). Anterograde label is charted in coronal sections that extend from the posterior bank of the pSS to the anterior limit of PMLS (numbers give AP locations of each section). The only additional cortical label found was in more posterior sections, in areas 18 and 19. Label, both peroxidase and autoradiographic, is also shown on a drawing of the right hemisphere, with PMLS outlined in black. Note the absence of label on the medial bank of the suprasylvian sulcus. Photographs through the centers of the injection sites are shown at bottom, in adjacent sections at AP -6.0.

Figure 5.

Two tracer injections in area 17's upper field representation in one cat; conventions as in Fig. 4. These injections were more central than those in Fig. 4, and cortical labeling was shifted more medially on the posterior bank of the pSS. Additional labeling occurred in areas 18 and 19, in sections posterior to those shown. In area 17, injections were centered at AP -9.9 (WGA-HRP) and AP -8.6 (^3H -amino acid) (photographs shown at bottom of figure).

Figure 6.

A WGA-HRP injection in area 19's upper field representation (conventions as in Fig. 4). Stipple shows strong anterograde label, and dots show retrogradely labeled cells (each dot indicates at least three cells). The injection site in area 19 is shown at bottom (left photograph). A dark field photograph (bottom, right) shows autoradiographic label on the posterior bank of the pSS arising from a ^3H -amino acid injection in area 17, at the same retinotopic location as the area 19 injection (injection site not illustrated). These patches were largely superimposed on the peroxidase label at the same level (AP -4.1). However, the more anterior sites that were labeled by the area 19 injection showed no autoradiographic label. On hemisphere drawing, black shows the injection site and gray shows anterograde label.

Figure 7.

A ³H-amino acid injection in area 17's lower field representation (conventions as in Fig. 4). In addition to patches on the medial bank of the mSS, there was intense label in areas 18 and 19, and modest labeling in an area lying just lateral to area 19 (Marcotte and Updyke, 1982), visible in the most anterior section.

Figure 8.

A WGA-HRP injection in the upper field representation of LS, on the posterior bank of the pSS (black patch on hemisphere drawing). Dots show labeled cells (each dot indicates at least three cells), and the injection site is black. Labeled cells were found in PMLS (see sections +3.8 and +4.6). They also were abundant on the lateral bank of the mSS, and in the depths of the pSS, below the ectosylvian gyri. The greatest number of labeled cells was found in area 17; the anterior portion of this field is visible in the most posterior section. Sections further posterior also contained many labeled cells in areas 18 and 19. In all three areas, labeled cells were located in the upper field representation.

Figure 9.

A WGA-HRP injection in the lower field representation of PMLS. Tracer was injected at about mid-depth of the medial bank, and spread to its upper end, the presumptive upper field representation. A substantial patch of labeled cells (arrow) is visible on the posterior bank of the pSS, in the upper visual field representation (section at AP -4.8), but in area 17 labeled cells were in the lower field representation (sections -4.8 through $+1.6$).

Figure 10.

Two different organizational schemes proposed for the medial bank of the mSS. A. PMLS and AMLS as described by Palmer et al. (1978). Sites of tracer injections in PMLS in seven experiments are indicated by black outlines. Their retinotopic centers are marked in the drawing of the left hemifield. B. The alternative organization proposed here. LS (orange for upper field representation, blue for lower field representation), and approximate location of AMLS (red). The anterior and lateral limits of AMLS are uncertain. The extent of the lower field representation in LS is based on numerous tracer injections in area 17's lower field representation (Serk and Mulligan, 1993). Note that Tusa and Palmer (1980) included the upper field representation of LS (orange zone) in area 21a.