Functional implications of the anatomical organization of the callosal projections of visual areas V1 and V2 in the macaque monkey*

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The efferent and afferent connections of the V1/V2 border with the contralateral hemisphere have been examined using anatomical tracers. The V1/V2 border was found to exchange connections with the contralateral V2 area as well as a restricted strip of V1 lying adjacent to the V1/V2 border. Besides these homotopic projections, two heterotopic projections were found to V3/V3A and V5. Anterograde tracing of callosal connections showed that terminals in these heterotopic sites were focused in layer 4, the recipient layer of projections originating from the ipsilateral V1/V2 border. Bilateral injections of fluorescent dyes showed that these heterotopic targets of the V1/V2 border are connected to the homologous ipsilateral V1/V2 border region. The laminar location of callosal projecting neurons as well as their terminals were characteristic for each cortical region. The laminar pattern of callosal connectivity was found to differ markedly from that of associational visual pathways. Two principal hypotheses are suggested by these results. First, the fact that V1 in part is reciprocally callosally connected in all mammals supports the notion that this interhemispheric pathway completes long-range intrinsic cortical connections. Second, the convergence of inter- and intrahemispheric pathways could provide the anatomical basis for the modulation of the sensory processing within one hemisphere by ongoing activity in the contralateral hemisphere.

INTRODUCTION

The visual system of primates is organized in such a way that the representation of visual space in each hemisphere is almost entirely restricted to the contralateral visual hemifield. As it is commonly believed that corticocortical connections link regions subserving a common part of the visual field, one would predict that interhemispheric connections would uniquely concern cortex representing the vertical meridian.

Studies to date on the callosal connectivity of extrastriate cortex of the macaque show that up to 70% of extrastriate cortex exchanges connections with the contralateral hemisphere. Since electrophysiological mapping studies have not shown that the vertical meridian has an enormously expanded representation in monkey extrastriate cortex, one must presume that the topographical organization of callosal connections differs from that of associational connections. In view of this peculiarity of interhemispheric connections, it

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is important to determine if they differ from associational connections in other respects, and if they do, whether the particularities of this pathway can give a clue to its functional role.

Anatomical studies in non-primates have shown that although callosal projecting neurons are concentrated along the V1/V2 border, they are found, to a lesser extent, within area V1\(^{5,10,15,37,40,44,46,47,50,51,62}\). Early studies in primates had suggested that area V1 was devoid of callosal connections\(^{3,6,11,19,34,56}\), so that it appeared that an acallosal area V1 was a unique primate feature. Although it was subsequently shown by Zeki that callosal terminals were found in a narrow strip of V1 lying adjacent to V2\(^{57,63}\), the absence of callosal projecting neurons in this region would suggest that the interhemispheric pathway of V1 is not reciprocal. In a recent study on prosimian and New World primates, Cusick et al.\(^{8}\) have shown that callosal projecting neurons and terminals extend several millimeters into area V1 in these species. These authors concluded that the reciprocal callosal connectivity of these lower primates conforms to a common mammalian pattern. It would seem therefore that the claim that Old World monkeys do not have callosal projecting neurons in area V1 places these primates in a category apart from other mammals including lower primates. However, previous studies on the callosal connectivity of Old World primates had been carried out with non-optimum horseradish peroxidase (HRP) techniques. We have rectified this by using the more sensitive Mesulam procedure\(^{32}\). Under these conditions, HRP histochemistry reveals that a restricted region of area V1 of the macaque is reciprocally callosally connected\(^{22}\). Examination of the laminar distribution of cell bodies projecting into the corpus callosum as well as their terminals shows that there are important differences with the distribution of associational connections. In the present paper we shall briefly describe these findings and discuss some of the implications for the functional role of interhemispheric projections of areas V1 and V2.

**MATERIALS AND METHODS**

Anatomical tracing experiments were carried out on 5 adult cynomolgus monkeys (*Macaca irus*). In this paper we shall report on two series of experiments. In a first series of experiments, the location of callosal projecting cell bodies and their axonal terminals were determined using wheat germ agglutinin conjugated to horseradish peroxidase (WGA–HRP) or free HRP. Both tracers gave very similar results. In a second series of experiments, fluorescent dyes, Fast blue (FB) and Diamidino yellow (DY), were used to examine the relationship between ipsilateral and contralateral projecting neurons. Only a brief description of the methods will be given here as they are described in greater detail elsewhere\(^{20–22}\).

A large craniotomy was performed and the dura reflected over the full extent of the lunate sulcus. In the HRP tracing experiments, injections were made along the V1/V2 border midway from the most ventral lateral limit of the lunate sulcus, where the fovea is represented, to within 1 cm of the midline. Injections on the operculum were made at a shallow angle to the cortical surface and were largely restricted to the gray matter. Injections in V1 extended 7 mm behind the lunate sulcus. Injections in V2 were made by vertical stabs down the full depth of the posterior bank of the lunate sulcus. In all cases, injections were made with a Hamilton syringe and were placed close together to ensure complete filling of V1 and V2. Following 48 h survival, the animals were perfused with 200 ml of saline followed by 2 liters of 1% paraformaldehyde and 1.25% glutaraldehyde in phosphate buffer and 1 liter of 10% sucrose in phosphate buffer. After 12 h in a 10% sucrose solution, the brains were blocked and sections cut at 60 \(\mu m\) parasagittally or horizontally, on a freezing microtome. Adjacent sections were processed for HRP histochemistry\(^{32}\) and cytochrome oxidase histochemistry\(^{61}\).

In the fluorescent dyes studies, FB was injected in area V1 and V2 on the left side of the brain and DY was injected in the right hemisphere in V1 at a distance of up to 5 mm from the V1/V2 border. The injection of V2 was carried out as were the
HRP injections and ran about 8 mm parallel to the lunate sulcus. In the case of the DY injection in V1, the injection was made in three 8-mm stabs running parallel to the lunate sulcus. Care was taken that the region of cortex injected corresponded in both hemispheres, and was roughly midway between the midline and the most lateral extremity of the lunate sulcus. This region of the cortex is where the parafoveal representation of the visual field is to be found. After a survival period of 12 days the animal was perfused with 200 ml of 2.7% saline followed by 3 liters of 30% formalin in 0.1 M cacodylate buffer, 1 liter of 8% sucrose and 1 liter of 30% sucrose in cacodylate buffer. The brain was immediately removed, blocked and 40-µm sections were cut parasagittally on a freezing microtome.

Sections of the hemisphere contralateral to the HRP injections were traced and the position of labelled neurons and terminals recorded by means of an X–Y plotting table electronically coupled to the microscope stage. The pial border and blood vessels were outlined and served as landmarks. Histological borders were determined either from the adjacent cytochrome oxidase stained section or by counterstaining the section used for plotting.

In the fluorescent dye tracing experiment, the hemisphere contralateral to the FB injection was traced out and FB- and DY-positive neurons were observed under UV light using a Leitz fluorescence microscope equipped with a D-filter set (355–425 nm). The positions of neurons were plotted out using the X–Y plotter and allocated to cortical layers after Nissl counterstaining.

RESULTS

Callosal connections of area V1

Following all injections of V1 and V2, callosal terminals and retrograde labeled cell bodies were found in the contralateral area 17. Callosal connections were restricted in V1 to a 1–2.5 mm band of cortex lying adjacent to the V1/V2 border. This callosally connected strip of area V1 terminated abruptly so that V1 consisted of a callosal and an acallosal component. The width of the callosally connected strip in V1 was found to be influenced by eccentricity. Cortex subserving the central visual field was found to have callosal connections stretching out to 2.5 mm, whilst in cortex subserving the peripheral visual field, the maximum extent of callosal connections was about 1 mm. Callosal connections in V1 are shown in Fig. 1 which is taken from cortex subserving the parafoveal visual field. Callosal connections in V1 are not found throughout all cortical layers. Retrograde labeled cell bodies were only found in supragranular layers 4B and 3 according to the lamination scheme of Brodmann. Fine dust-like HRP reaction product, typical of axonal terminals, were found on either side of a region that is relatively free of HRP reaction product. These two regions of label in V1 come together at the V1/V2 border giving a typical U-shape. The region between the two arms of the ‘U’ is traversed by occasional axons which course away from the V1/V2 border towards the white matter. When an HRP-processed section is compared to the adjacent section processed for cytochrome oxidase, it is possible to allocate the callosal terminals to specific cortical layers. The upper band of callosal terminals falls in layer 4B and the lower band in layer 5, thereby avoiding zones of high cytochrome oxidase activity. There were some sparse axonal terminals in layers 2 and 3. In cortex subserving the fovea, labeling in supragranular layers 2 and 3 was slightly denser and was arranged in patches or columns as was the labeling in layer 4B.

Callosal connections of area V2

In area V2, callosal projecting neurons were concentrated at the V1/V2 border and stretched 3–8 mm down the posterior bank of the lunate sulcus. The numbers of retrograde labeled neurons in V2 were much higher than in V1, which accounted for only 1–3% of the total. Callosal connections in V2 were also found to be influenced by eccentricity. In V2 subserving the fovea, callosal neurons stretched out for 8 mm, whilst in peripheral cortex the maximum extent of callosal connections in V2 was about 3 mm. Callosal connections were not found evenly distributed in V2, but instead were found in very obvious clusters (Fig. 2). Clustering of callosal...
Fig. 1. Horizontal section through V1/V2 border, showing the callosal connections of area V1. In V1, callosal terminals are found in two bands which form a characteristic U-shape. The upper arm of the 'U' is in layer 4B and the lower arm in layer 5. The apex of the 'U' on the right-hand side of the photo (asterix) marks the anterior limit of area V1. Callosal connections in V1 are reciprocal, as occasional retrogradely labeled cell bodies are found. Labeled cells are only found in supragranular layers, 2 can be seen in this microphotograph, one in layer 4B and one in layer 3 (arrows). Scale 1 cm = 185 μm.
activity which receive direct thalamic input\textsuperscript{25}. Retrograde labeled neurons were only found in supragranular layers, where they were found in the bottom of layer 3. Callosal terminals had a more widespread distribution, and although they were more numerous in layer 3, they also occupied layers 4 and 2.

**Heterotopic connections**

Injections of HRP or WGA–HRP which were limited to areas V1 and V2 gave rise to extensive labeling of the contralateral hemisphere (Fig. 3). This extensive labeling of the contralateral hemisphere raises the question of heterotopicity of callosal connections, that is to say the existence of projections linking the V1/V2 border to regions other than its contralateral homologue. Our results showed that the V1/V2 border receives and projects heterotopically to two sites, one in the fundus of the lunate sulcus and the other in the posterior bank of the superior temporal sulcus. Nissl and Myelin counterstaining showed that the heterotopic site in the temporal sulcus corresponded to Zeki’s movement area V5\textsuperscript{64}, alternatively known as MT\textsuperscript{58}. Zeki has shown that areas V3 and V3A, which are located in the anterior bank of the lunate sulcus, adjoin on a representation of the vertical meridian which is callosally connected\textsuperscript{65}. Therefore, the heterotopic site in the anterior bank of the lunate sulcus almost certainly corresponds to the V3/V3A border.

Both heterotopic sites showed similar laminar locations of callosal connections. In both regions retrograde labeled neurons were almost exclusively located in layer 3, and axonal terminals were sharply focused in layer 4. In MT sparse axonal terminals were found in layer 6.

**Fluorescent dye experiments**

Injection of fluorescent dyes in area V1 leads to extensive labeling of the ipsilateral cortex, and retrograde labeled cells are found in at least 6 known visual areas including V2, V3, V3A, V4 and MT\textsuperscript{20,38}. The extent of labeling in infragranular layers is much greater than in supragranular layers. In the present experiment, we wished to examine the correspondence between the location of cortical neurons which project to the contra-

connections in V2 could be as clearly seen in cortex subserving the peripheral visual field as in cortex subserving the fovea. Examination of the material in darkfield using crossed polarized filters made the periodic distribution of callosal connections much more apparent, suggesting that clustering of axonal terminals is more pronounced than clustering of cell bodies.

When HRP-reacted sections were compared to adjacent sections processed for cytochrome oxidase activity it became immediately apparent that callosal connections in V2 differ markedly from those in V1 in one important respect: whereas in V1 callosal connections are excluded from regions of high cytochrome oxidase activity, just the reverse is true in area V2. In V2, many of the clusters of callosal connections corresponded to the patches of high cytochrome oxidase activity which receive direct thalamic input\textsuperscript{25}. Retrograde labeled neurons were only found in supragranular layers, where they were found in the bottom of layer 3. Callosal terminals had a more widespread distribution, and although they were more numerous in layer 3, they also occupied layers 4 and 2.

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Fig. 3. Areas V1 and V2 are connected across the callosum to the contralateral homologue as well as several other cortical regions. These are known as heterotopic connections (see text). In this figure the contralateral hemisphere has been sectioned parasagittally to reveal the two principal heterotopic sites: one at the fundus of the lunate sulcus, which could correspond to V3, and one in the posterior bank of the superior temporal sulcus, which corresponds, at least in part, to MT.

lateral V1/V2 border and those which project to the equivalent part of ipsilateral area V1 (see Materials and Methods). As callosal projecting neurons are almost exclusively located in upper cortical layers, it is perfectly valid to make the comparison in the spatial location of ipsi- and contralateral projecting neurons within this layer. This comparison is provided by Fig. 4. This figure shows that the tangential extent of neurons projecting to the contralateral V1/V2 and supragranular layer neurons projecting back to the ipsilateral area V1 are very similar. Furthermore, those regions of cortex which give rise to callosal projections also project to ipsilateral area V1. After counterstaining it was possible to allocate callosal and V1 projecting neurons to precise cortical laminae. Although both sets of neurons were found in upper cortical layers the two populations were vertically separated in the depth of the cortex. Neurons projecting to ipsilateral area V1 were located more superficially in the cortex (upper part of layer 3) than were those neurons projecting to the contralateral hemisphere (lower part of layer 3). There was in some instances a slight overlap of the two populations and when this occurred, occasional double-labeled neurons were observed (represented by stars). These neurons, which have a DY-positive nucleus and a FB-positive soma, project by means of bifurcating axons to both hemispheres. Such double-labeled neurons were very rare and were only encountered in V2.

**DISCUSSION**

Callosal connections of areas V1 and V2 show a number of distinctive features. Firstly, they are organized in a columnar fashion; secondly, the parent cell body and the axonal terminals have a laminar distribution which is characteristic for a given area; and thirdly, the extent of callosal connections in both areas is influenced by eccentricity in the visual field. Before proceeding to discuss the functional significance of these
Fig. 4. Localization of neurons projecting to ipsilateral and contralateral V1 and V2. Callosal projecting neurons were labeled by injections of Fast blue in Area V1 and V2 of the contralateral hemisphere (big dots). The corresponding region of V1 was injected ipsilaterally with Diamidino yellow. Diamidino yellow-positive neurons are represented by small dots. Stars represent double-labeled cells. This experiment shows that cortical regions which project heterotopically to areas V1 and V2 coincide with regions projecting ipsilaterally.

anatomic features, we shall first of all compare our findings to those obtained from other mammals including New World and prosimian primates.

Comparison of callosal connectivity in macaque with that in other species
The present results show that callosal connections in area V1 are reciprocal since labeled
neurons were found throughout the 2-mm extent of labeled terminals. Callosal projecting neurons in area 17 are a consistent feature of the mammalian visual system and have been reported in rats, mice, hamsters, rabbits, tree shrews and cats, as well as in New World simians and Old World prosimians. The present results, showing callosal projecting neurons in area V1, demonstrate that callosal connectivity in Old World monkeys conforms to a general mammalian pattern.

It would seem therefore that Old World monkeys do not constitute an exception to the rule that area V1 in mammals can exchange information across the callosum with the contralateral hemisphere. However the laminar distribution of callosal connections shows some outstanding differences from those reported in lower primates and in the tree shrew. Callosal connections in area V1 in the macaque, like those in the New World monkey, originate uniquely from supragranular layers. The Old World prosimian, Galago, resembles tree shrews and other non-primates in that callosal connections in area V1 originate from both supra- and infragranular layers. Although tree shrews are closely related to ancestral primates, they share a number of features with non-primates, including an absence of columnar organization and a more extensive callosal connectivity in area V1. It would seem therefore that the columnar organization of callosal terminals in V1 is characteristic of primates and that the more restricted callosal connections within V1 is a feature that distinguishes simians from prosimians and not Old and New World monkeys.

The similarity between Old and New World monkeys in the laminar origin of callosal projections is also found for the distribution of terminals outside of area V1. Within area V1 there is a major difference in the site of termination of callosal terminals in infragranular layers. Whereas in the Old World monkey the axon terminals are in layer 5, in the New World monkey they are in layer 6. The termination of callosal fibers in the cortical layer projecting to the lateral geniculate in the New World monkey, and in the cortical layer projecting to the superior colliculus in the Old World monkey, constitutes a fundamental difference in the cortical wiring of these two primate groups.

Functional significance

The laminar location of the cell bodies and the terminals of ipsilateral cortical connections is characteristic according to whether they constitute a feedforward or a feedback type projection. Feedforward type projections are thought to link ascending levels and feedback descending levels in a hierarchy of processing stages. The basis of this division into feedforward and feedback connections stems from the fact that rostral directed connections (i.e. away from area V1) originate in supragranular layers and terminate in layer 4, whereas caudally directed connections (i.e. towards V1) arise mainly from infragranular layers and terminate outside layer 4. The principal argument in favor of rostral-directed connections underlying a feedforward mechanism and caudal-directed connections a feedback mechanism, is in fact highly speculative and largely depends on analogy with the geniculostriate pathway. Clearly the lateral geniculate is on a lower hierarchical level than area V1, and the main projection from the lateral geniculate terminates in layer 4 (i.e. feedforward) whilst the projection from area V1 to the lateral geniculate originates exclusively from layer 6 (i.e. feedback). The distinction between feedback and feedforward connections has permitted a tentative ranking of visual areas according to hierarchical prominence.

When we apply the feedback and feedforward definition to callosal connections it is immediately apparent that they do not comply with this schema (see Figs. 5, 6). The terminals of callosal afferents in area V1 avoid layer 4 and are therefore typical of a feedback projection. If the callosal projection to area V1 is to comply with a feedback pathway, as it is defined for ipsilateral connections, it should originate from infragranular neurons. Since callosal-projecting neurons are almost exclusively supragranular, then this connection fails to conform to the basic schema. In V2, callosal terminals terminate mainly in cortical layers other than 4 and originate.
Fig. 5. Comparison of the location of ipsilateral and contralateral projections of V2. Contralateral projections to the heterotopic sites (black arrows) give rise to a remarkably dense label in layer 4 of MT and V3. This laminar location of terminals is typical of feedforward projection and overlaps with the output of the ipsilateral V1/V2 (open arrows). This convergence of ipsi- and contralateral pathways is also found in the projections to V1. The projection of V2 to both ipsi- and contralateral V1 terminate in layers 4B and 5. This type of projection pattern, which avoids layer 4, is typical of feedback projections.

from supragranular layers. This pattern is similar to that found between V4 and MT and corresponds to lateral connections between cortical areas on a similar hierarchical level (see Fig. 6C,F). The projection of extrastriate cortex to the contralateral V1/V2 border is almost exclusively from supragranular layers and therefore typical of forward type projections. The reciprocal projection from the V1/V2 border to these regions terminate in layer 4 and are therefore also of the forward type. Clearly, connections of the V1/V2 border with the contralateral heterotopic sites are reciprocal but are not complementary, being forward-type projections in both directions.

The present results show that projections from extrastriate cortex to area V1 and V2 originate from identical cortical regions, irrespective of whether they are directed towards the ipsilateral or contralateral hemisphere. However they do not originate from the same sets of neurons. The projection to the ipsilateral V1/V2 border is predominantly from infragranular layers, whilst the projection to the contralateral V1/V2 border is exclusively from supragranular layers. Contrasting with these different origins of projections to ipsi- and contralateral V1/V2 border, is the convergence of the forward pathways. Both the ipsilateral and contralateral projections of V1 and V2 terminate in layer 4 (Figs. 5,6), thereby permitting an interaction of the interhemispheric and association pathways.
If callosal projections were to comply with a strict visual topography, then they would be restricted to representations of the vertical meridian. When the full extent of callosal projections throughout the whole of the visual cortices are revealed, they are found to be extremely extensive. Van Essen and Zeki\textsuperscript{57} showed that callosal connections are found in about 70\% of extrastriate cortex, similar if not higher values are found in other primates\textsuperscript{8}. As it would not seem that the representation of the vertical meridian has such an exaggerated representation in extrastriate cortex, it would appear that some callosal connections concern cortical regions coding the periphery of the visual field. Cortical connections that respect a topography that is not strictly related to the visual field could provide integrative mechanisms which lie at the base of higher cortical functions\textsuperscript{2}. Connections between cortical regions subserving different visual hemifields could be responsible for the phenomena observed by Rizzolatti and Camarda\textsuperscript{41}. These authors noted that the receptive fields of neurons in the Clare Bishop area of the cat could be influenced by simultaneous presentation of a second stimulus in the ipsilateral visual hemifield. It is difficult to conceive that callosal connections that impinge on cortex subserving the peripheral visual field contribute to the visual response in a straightforward additive fashion. Activity in the corpus callosum could serve to gate feedforward activity from more posterior cortex. The notion that the information processing of the V1 and V2 input to at least two different sites in extrastriate cortex is modulated by activity in the contralateral V1/V2 border is supported by recent clinical data. Lassonde\textsuperscript{24} has shown that deficits in visual perception following section or congenital absence of the corpus callosum are found in both intra- and interhemispheric processing, suggesting that the intact corpus callosum exerts a facilitatory influence on ipsilateral pathways.

For many years, area V1 in primates was considered to be devoid of callosal connections\textsuperscript{3,6,33,34}. The advent of more sensitive techniques has shown that at least part of area V1 in primates, as in all mammals so far studied, is reciprocally connected to the contralateral hemisphere. It could be that this basic mammalian plan fulfills a fundamental requirement concerning intrinsic connectivity of the cortex. Callosal connections could serve to complete intrinsic connectivity by extending the range of lateral connections of neurons situated near area boundaries. There is increasing evidence that long-range intrinsic cortical connections may play an important role in the elaboration of a number of receptive field properties including orientation selectivity, direction selectivity, receptive field size, inhibitory and excitatory influences outside of the classically defined receptive field, and the fact that certain striate cortical neurons respond to random dot stereograms requiring a global calculation of disparity over a large area\textsuperscript{1,30,35,39,48,49,55} (see ref. 13 for a review). Within area V1 long range intrinsic connections span up to 4 mm\textsuperscript{11,27,42} and are restricted to layers on either side of layer 4C, i.e. those layers which are contacted by callosal fibers. A neuron situated on the virtual border of area V1 will only be able to form long-range intrinsic connections over an angle of 180°. Callosal connections with the contralateral area V1 will permit such a neuron to complete its horizontal connectivity over the full complement of 360°. Should the callosal connectivity of V1 serve to complete the intrinsic connectivity rather than a specific psychophysical function, then the extent of visual field represented in the callosally connected part of V1 would be expected to vary between species according to the cortical magnification factor. Consistent with this hypothesis is the fact that callosal connections in V1 extend up to 2 mm for species as diverse as cat\textsuperscript{44,45,47}, tree shrew\textsuperscript{46} and macaque.

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