INTERHEMISPHERIC CONNECTIONS OF PRESTRIATE CORTEX IN MONKEY

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INTRODUCTION

The prestriate interhemispheric projection system in the monkey is very extensive and complex. To begin to understand it requires a knowledge not only of the topographic organization of the transcallosal prestriate projections themselves, a task which is rendered somewhat difficult by the complexity of the gyral and sulcal pattern in this region, but also of the manner in which this projection system is related to the representation of visual fields in the prestriate cortex. In addition, an explanation of the nature of interhemispheric interaction requires an account of the more intimate anatomy of this system in terms of the laminar distribution of callosal fibers as well as their mode of termination in relation to cell parts and cell types.

Recently, an anatomical account was given of the representation of visual fields in prestriate cortex of monkey. In that study, the interhemispheric connections of a restricted portion of the prestriate cortex were also examined. It appeared that those regions of prestriate cortex to which areas of midline representation (vertical meridian including the fovea) in striate cortex project, also receive a projection from the opposite hemisphere via the splenium of the corpus callosum. However, the use of the single survival time of 9 days in that study, and of relatively long survival times in other studies, has not allowed a study of the shifting patterns of degeneration in regard to characteristics and relative densities, nor of the laminar distribution, of the degenerating callosal fibers at different survival times. In addition, previously only a restricted portion of prestriate cortex was studied after splenial section and, since the sections were taken at millimeter intervals, a careful study of the relationship of the degenerating fields was not possible. This was particularly the case in the region of the annectant gyri of the lunate sulcus and the region at which the lunate and inferior occipital sulci co-exist and the superior temporal sulcus bends increasingly anteriorly. All these omissions are taken account of in the present study which may be regarded as an extension of the previous work.

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MATERIALS AND METHODS

The hemispheres of 6 rhesus monkeys, 5 immature males and 1 mature female*, were studied following splenial section. The operative procedures were as described earlier except that in this series neither urea nor cortisone were used. Gross examination of the brains as well as silver stained sections revealed that in all the animals the splenium had been sectioned to about 8–9 mm from its tip.

The animals were perfused through the aorta with Ringer solution followed by either paraformaldehyde or a mixture of paraformaldehyde and glutaraldehyde following survival periods of 3, 4, 5, 8, 10 and 32 days. The perfusion fluids used were found to give excellent results when the brains were subsequently stained by a slight modification of the Fink–Heimer staining technique involving reduced times in permanganate, uranyl nitrate and the first silver bath. The brains were sectioned horizontally at 30 μm. In some brains sections were saved at every 150 μm whereas in others the interval varied, depending upon the region. In the region of the annectant gyri, for example, every section was saved whereas in the region ventral to that sections were saved at every 300 μm.

RESULTS

The first unequivocal signs of degeneration appear at 4 days. Extremely sparse and dust-like degeneration appears at 3 days, more prominent in some regions than in others (see below). The characteristics of the degeneration vary at different survival times, as will be described later. However, the total topography of the degenerating fields does not appear to vary with survival time. Here the topography of the degeneration as seen in horizontal sections is described level by level, the description being restricted to lateral prestriate cortex.

(A) Dorsal levels of the lunate sulcus

This is the most complicated sulcus of the prestriate region. It is wide superiorly and narrow inferiorly and buried within it lie the annectant gyri, crossing it obliquely from postero-superior to antero-inferior. The complexity of the sulcus is reflected in the pattern of degeneration ensuing after callosal section. The striate prestriate boundary contains degenerated fibers throughout (see Fig. 1, patch 1). This degeneration continues as a narrow band into area 17, extending for about 0.5 mm mainly into layer 4 of the striate area. In the cortex of the anterior bank, an area of degeneration occupying the depth and the medial quarter may be seen (Fig. 1, patch 2). At the level shown in Fig. 1A, two fields of degeneration may be seen, one in the middle annectant (a) and another in the posterior annectant (a) gyri. These two fields of degeneration eventually come together to yield a single field, as the shallow sulcus separating the two annectant gyri disappears. They may therefore be regarded as a

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Fig. 1. Degeneration seen following splenial section on the lateral surface of the brain (degeneration anterior to patch 6 is not described). The areas of degeneration are numbered to facilitate comparison of the degeneration in this and the following figures. This and the following figures represent horizontal sections, from dorsal to ventral, and may be read continuously as one figure. Note the manner in which the degeneration in the anterior and posterior parts of the annectant gyri come together, giving rise to a single field of degeneration (patch 2). Degeneration patch 4 first appears at C. Notice the manner in which it spreads towards patch 5 and the way in which patches 5 and 6 are joined by a zone of sparser degeneration. 1 = lunate sulcus; st = superior temporal sulcus; a = annectant gyrus; io = inferior occipital sulcus.

single field of degeneration which is split by the sulcus lying between the middle and posterior annectant gyri. This region of degeneration probably falls in the anterior limit of the area 19, as defined earlier. To ascertain this point, a monkey (FN) was prepared with a lesion in area 17, placed superiorly just behind the region of repre-
representation of the vertical meridian\textsuperscript{12} (see Fig. 2). The ensuing degeneration fell in the posterior annectant gyrus. That the middle annectant gyrus was not involved may be explained by the position of the lesion, which was not at the representation of the vertical meridian but posterior to it.

More laterally, the anterior bank of the lunate sulcus shows an uninterrupted field of degeneration occupying the whole of the remainder of the anterior bank and of the visible surface of the prelunate gyrus (Fig. 1A). But although the degeneration is continuous, it shows greater density at two regions which are particularly evident at earlier survival times of 4 and 5 days.

\textit{(B) Crown of prelunate gyrus and upper part of the superior temporal sulcus}

The degeneration on the crown of the prelunate gyrus differs as the sections are examined from dorsal to ventral. In sections dorsal to that shown in Fig. 1A, the crown is covered by a field of degeneration which is continuous with the degeneration in the anterior bank of the lunate sulcus, although there is a localized condensation of degenerating elements. More ventrally (Fig. 1A, patch 5) the degeneration spreads out to cover increasing proportions of the posterior bank of the superior temporal sulcus. As more ventral sections are examined (Fig. 1B), the degeneration in the posterior bank of the superior temporal sulcus breaks off from the degeneration on the crown of the prelunate gyrus (which, itself, recedes more posteriorly) and comes to occupy a more medial position roughly halfway down the posterior bank of the superior temporal sulcus. Although this degeneration becomes localized, it again shows, in some sections, local condensations of degenerating elements. Moreover, in some sections it is practically continuous with the degeneration at the bottom of the superior temporal sulcus. It is this apparent continuity and discontinuity and the increase and decrease in relative density of degeneration from section to section that makes a study of this system so difficult. This change did not appear to be due to

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inconsistencies of staining for some of these sections were stained 3 times and yet the relative increase and decrease in the density of degeneration could still be seen in the adjacent sections.

Beyond the degeneration at the bottom of the superior temporal sulcus, in its anterior bank, there is another field of degeneration (not shown in the figures) which has a somewhat different morphology. This difference consists in its exhibiting a finer dust than the other regions of degeneration at earlier survival times. In some sections, this field appears to be practically continuous with the degeneration at the bottom of the superior temporal sulcus whereas in other sections it is distinct. The

Fig. 3. Degeneration following splenial section at the levels indicated. Note that degeneration patches 2 and 3 change their relative positions. This shift can be more clearly seen in Fig. 4.
connections of this area with striate or prestriate cortex, if any, are not known and this area will not be further considered in this paper.

As the degeneration is traced more ventrally through the horizontal sections, the crown of the prelunate gyrus at first becomes empty of degenerated fibers (Fig. 1B). But in still more ventral sections, a new field of degeneration appears in the anterior part of the prelunate gyrus and increases in density as more ventral sections are examined (Fig. 1, patch 4).

(C) Region of close apposition of inferior occipital and lunate sulci

The picture of degeneration described above gradually undergoes a dramatic change at this region (see Fig. 3). The change is brought about by the fact that all the fields of degeneration that have been described come very close together to form a continuous field of degeneration interrupted only at the shallow beginning of the inferior occipital sulcus. It must not be imagined, however, that this continuity can be seen in every section through this region. Rather, the continuity can be seen in some regions in some sections and in other regions in other sections, as may be verified by reference to Figs. 3 and 4. In addition, a change occurs in the relative positions of the degeneration patch 2 to degeneration patch 3. The manner in which this occurs can be seen clearly in Fig. 4. The obliteration of the lunate sulcus and the commencement of the inferior occipital sulcus produce this change. The patch 3 of degeneration

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disappears in more ventral levels. Before doing so, however, it gets pushed against
the posterior bank of the inferior occipital sulcus (Figs. 3 and 4, patch 3). Fig. 4,
incidentally, also demonstrates the continuity between the degeneration at the bottom
of the lunate sulcus (patch 2, which more dorsally lies in the anterior bank of the
lunate sulcus and corresponds to the representation of the vertical meridian in area 19)
and the degeneration in the bottom of the inferior occipital sulcus (patch 2, which
more ventrally moves to the anterior bank of this sulcus and also corresponds to
the representation of the vertical meridian of area 191,16). It should be stated that these
changes cannot be observed easily except where the brain is sectioned slightly ob-
liquely, with a downward anterior tilt, as shown in Fig. 4.

(D) Inferior occipital sulcus and inferior occipital gyrus

In more ventral sections, once the lunate sulcus has disappeared completely
and the degeneration patch 3 has also disappeared, the picture of degeneration
consists of a patch at the striate prestriate boundary (Fig. 3, patch 1) which, as before,
invades the area 17 as a narrow band restricted mainly to layer 4. Another patch of
degeneration appears in the anterior bank of the inferior occipital sulcus (Figs. 3 and
4, patch 2). More lateral to this there is a gap which is followed by a broad band of
degeneration occupying the surface of the inferior occipital gyrus. Although this band
is continuous, there appear condensations of degenerating elements in it. The posterior
bank, as well as the depth, of the superior temporal sulcus is almost free of degener-
ation at this level at earlier survival times (5 days) although at other survival times
clusters of degeneration may be seen. It is assumed, therefore, that the degeneration
at the bottom of the superior temporal sulcus which can be seen in more dorsal
sections has, at this level and with the increasingly anterior course of the superior
temporal sulcus, shifted to the surface (Fig. 3, patches 4, 5 and 6)*.

This picture of degeneration continues more or less unchanged with the dis-
appearance of the inferior occipital sulcus (Fig. 3). At more ventral levels there is
an area of degeneration continuous with patch 2 more superiorly. On the lateral
surface (the inferior occipital gyrus) the broad band of degeneration is maintained but
with condensations in three regions becoming more distinct (Fig. 3, patches 4, 5 and
6). At times, each area of condensations appears to break up into two sub-regions
in which the degeneration is slightly heavier than in the intermediate region connecting
them. This change is not, however, consistent and it can only be seen in some sections.

More ventrally, the anterior part of this band of degeneration breaks off and
becomes a separate field (Fig. 3, patch 6), discontinuous from the more posterior

* It is possible that the degeneration at the bottom of the superior temporal sulcus (Fig. 3) represents
patch 6; that is, that patch 6 breaks off earlier than envisaged here. This is considered somewhat
unlikely because at earlier survival times (5 days) when patch 6 is clearly visible at more dorsal levels,
it is not so at the bottom of the superior temporal sulcus. Moreover, the degeneration at the bottom
of the superior temporal sulcus (Fig. 3) starts off sparsely, at later survival times, in the region of
close apposition of the inferior occipital and lunate sulci and increases in density as more ventral
levels are examined. Such a change has not been seen for patch 6 at more dorsal levels.

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Fig. 5. Photographs of the degeneration at various cortical levels taken from a monkey with a 5 day survival period following sectioning of the splenium. The cortical region illustrated here is patch 2 (× 400).
band (Fig. 3B, patches 4 and 5). The posterior part, however, although showing the 2 condensations, remains continuous until it disappears. It is important to emphasize this point. In the schema of Fig. 9, the posterior band of degeneration has been considered as though it breaks up into two bands. This, however, is an extrapolation and the material shows no more than a suggestion that discontinuity occurs. The anterior part (Fig. 3, patch 6) comes close in more ventral sections to a region of degeneration at the bottom of the superior temporal sulcus (not numbered) and in the most ventral sections merges with it.

(E) Laminar distribution of degeneration and the characteristics of the degeneration at different survival periods

As previously mentioned, the characteristics of the degeneration in terms of both morphology and laminar distribution vary at different survival times (Fig. 5). Here these variations are described.

Practically no degeneration is visible after a survival period of 3 days except at the posterior bank and depth of the superior temporal sulcus. Here the degeneration is sparse and dust-like and limited to layers 4, 5 and 6. This degeneration could not be very clearly seen in every section, however. Again, this variability does not appear to be due to the staining method because this brain was stained twice and the same picture appeared in adjacent sections. At this survival period a few dust particles could be seen in the other regions.

The picture changes but slightly at 4 days' survival. The dust-like degeneration becomes more evident. This shows up particularly well at the striate-prestriate boundary and in the superior temporal sulcus (patches 1, 5 and 6). The dust is heaviest in layer 4, but involves all the other layers, with a handsome amount of dust in layers 2 and 3 and some in layer 1. There is practically no fiber degeneration at this survival time. In patches 3 and 4 only a very small amount of dust may be seen.

The picture changes dramatically at 5 days' survival. At this stage, fine dust-like degeneration can be seen in all layers and in all the regions described and the laminar distribution is the same in all the regions. The majority of the degenerated fibers fall in layer 4 but a considerable amount of dust collects in layers 2 and 3 and layer 1 contains the least of all (see Fig. 5). Beaded fibers may be seen at this stage but they are mostly restricted to layers 5 and 6 of degeneration patches 1, 2, 5 and 6. Patches 3 and 4 contain fewer beaded fibers and more dust, proportionally.

At 8 days' survival, the following changes occur. In patches 1, 2, 5 and 6 the majority of the beaded fibers are restricted to layers 4, 5 and 6. Layers 2 and 3 contain sparse amounts of degenerated fibers and there is very little dust-like degeneration in these patches. Fibers coursing horizontally may be seen in layer 1. More such beaded fibers are seen in layer 1 of patch 1 (striate-prestriate boundary) than in the layer 1 of the other patches. Patches 3 and 4 contain proportionally less beaded fibers at this survival time. The degeneration in these patches (3 and 4) is mostly dust-like and involves layers 4, 5 and 6 mainly and layers 2 and 3 to a lesser extent. Some dust particles may also be seen in layer 1. At 10 days' survival the laminar distribution of

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the degeneration is very similar except that practically all of the degeneration consists of beaded fibers.

This picture remains substantially the same at 32 days' survival. At this time, however, the large majority of the fibers are of the coarse type and layers 2 and 3 show practically no signs of degeneration. In addition, patch 4 contains fewer degenerated fibers than observable at earlier survival periods. Previously, degeneration in layer 1 at the striate–prestriate boundary only was reported. It is now found that degeneration occurs in layer 1 in all the regions that receive interhemispheric connections although the amount of degeneration in layer 1 at the striate–prestriate boundary is still found to be heavier than in the other regions.

DISCUSSION

In Fig. 6 is given a schema of the organization of the prestriate interhemispheric projection system, incorporated into which is the earlier schema of the areas 18 and 19. There is much that militates against the presentation of a schema at the present stage. It is more than likely that the actual projection system will turn out to be much more complex than suggested here. This is because in the present schema areas of degeneration which were continuous, irrespective of local densities, were considered as a single field, as for example patch 3. This seems not unreasonable at the present stage.
Fig. 7. A summary diagram of the connections of the various regions described in this, and a previous, study. Only those connections that have been actually determined anatomically have been included. Lesions at the striate-prestriate boundary lead to degeneration in the prelunate gyrus (not shown). Presumably this is also the case with the inferior occipital gyrus but lesions at the ventral striate-prestriate boundary have not yet been reported.

time since to subdivide these regions on the basis of density of degeneration would be unwarranted. The local condensations which appear in patch 3 and in patch 4 and on the surface of the inferior occipital gyrus may signify some functional difference of which we are unaware. The question will be decided by future anatomical and electrophysiological work. In addition, as mentioned earlier, there are small isolated regions of sparse degeneration which appear inconsistently (e.g. in the superior temporal sulcus) and which it is difficult to fit into any pattern. Indeed, the degeneration in the anterior bank of the superior temporal sulcus, which has been only briefly described in this paper, may bear an important relationship to the other fields of degeneration. But at the present time its status is not clear. The overriding reason, however, for giving a schema is that it makes the complex web of prestriate interhemispheric connections much more intelligible. The schema can be modified, or even changed, should future results so warrant. Fig. 7 gives the anatomically determined connections to the various regions. To date, no connection from the area 17 to patch 6 at the bottom of the superior temporal sulcus has been observed. It is possible that this band receives projections from areas 18 and 19.

The interhemispheric projections described in this work are similar, though much more extensive, to the ones already described\(^4,16\). There are, however, some minor differences. The degeneration observed in this study, although respecting the foci previously described, is more extensive than suggested earlier. Also, degeneration has been seen in all layers at the appropriate survival times. The use of a larger range of survival times and an improved staining technique have probably both contributed to giving a more complete picture in the present study.

It is somewhat difficult to compare these results directly to those given by Myers\(^9\). This is partly because Myers has used coronal sections which are not easy to compare with the horizontal sections and partly because the account given by him varies somewhat, as has been discussed at length elsewhere\(^15\).
It is not clear what the functions of these projections are. This much seems certain, that a large part connects areas of midline representation in prestriate cortex. The patches 1, 2 and 5 are coincident with regions that receive fibers from the region of vertical meridian representation in area 17 and patches 3 and 4 receive fibers from the region of representation of the fovea in striate cortex (part of patch 5 also receives fibers from the region of representation of the fovea in striate cortex). Whether the only function of these connections is to connect areas of midline representation across the hemispheres is, however, another matter. It is not known whether the midline is represented in patch 6 and it is known that both the vertical and horizontal meridians are represented in patch 5. Indeed, the reasons for having so many interhemispheric projection fields are interesting and merit more discussion than given here. It is proposed, however, to withhold this discussion until a future date when more is known of the anatomy of this region.

The organization of the callosal fibers in terms of the laminar distribution of its constituent fibers has been a matter of some controversy. One of the reasons undoubtedly lies in the fact that different authors have used different species and techniques. In the monkey, three previous studies have concluded, essentially, that the overwhelming majority of fibers terminate in layers 4, 5 and 6 except at the striate–prestriate boundary where fibers were found to terminate in the other layers as well. It is now found, however, that degenerated fibers appear predominantly in layers 4, 5 and 6 with a handsome number appearing in layer 1. Layers 2 and 3 show the dust effect only at earlier survival times. Thus, there is a distinctive laminar difference in the reception of callosal fibers, as first suggested by Villaverde. What the significance of this in functional terms may be is not clear at present.

Finally, it is clear that the splenium carries many fibers to part, at least, of the inferior temporal areas. Unfortunately, however, it is not possible to say which part of this region is connected to the opposite hemisphere via the splenium. The degeneration would appear to fall partly in the area TE of von Bonin and Bailey and in the areas 20 and 21 of Brodmann. But the inferior temporal area has been localized by behavioral techniques in the main, and not anatomical ones, and is vaguely defined as lying in the posterior part of the temporal lobe. Until its anatomical limits are more accurately known it is idle to speculate on the parts of it that receive splenial fibers.

SUMMARY

1. The interhemispheric connections of the prestriate area have been studied following section of the splenium in 6 monkeys.
2. At least 6 patches of degeneration following splenial section are seen in the prestriate cortex. These are separate superiorly and inferiorly and come together at the middle.
3. All the regions of degeneration, save one, are known to receive fibers from the striate cortex.
4. The laminar distribution of the degeneration varies at different survival times. At 4 days, it involves all layers though mainly 4, 5 and 6. At later survival

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times of 10 and 32 days layers 2 and 3 are minimally involved and the degeneration in layer 1 is less than in layers 4, 5 and 6. Additionally, some regions of connection with the opposite hemisphere show degeneration earlier than other.

5. The findings in this work are discussed in relation to previous studies.

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REFERENCES


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