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THE LAMINAR ORGANIZATION OF THE LATERAL GENICULATE BODY AND
THE STRIATE CORTEX IN THE SQUIRREL MONKEY (SAIMIRI SCIUREUS)

by

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the Department of
Psychology in the Graduate School
of Duke University

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ABSTRACT

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As a result of a number of anatomical and physiological studies, it is now generally agreed that there are two distinct retino-geniculo-cortical pathways relayed through separate layers in the lateral geniculate body of monkeys: the "X"-cell pathway which relays through the parvocellular layers and terminates in the lower tier of layer IV of the striate cortex, and the "Y"-cell pathway which relays through the magnocellular layers and terminates in the upper tier of layer IV.

In other species such as the cat and the prosimian Galago, three distinct retino-geniculo-cortical pathways have been identified. Two of these pathways have characteristics in common with the "X" and "Y" pathways in the monkey, while the additional pathway is remarkably similar in cat and Galago. This third pathway (so-called "W-cell" pathway) is characterized anatomically by small and pale staining cells, fine caliber retinal input, and terminations in the superficial layers of the striate cortex; and physiologically, by its slow conduction velocity and the heterogenous response properties of its cells.

The purpose of the present study was to re-examine the laminar organization of the lateral geniculate body and striate cortex in Saimiri to determine whether a comparable pathway is also present in monkeys. First, the retinal projections to the lateral geniculate body were examined using the anterograde transport of wheat germ agglutinin conjugated to horseradish peroxidase (WGA-HRP). Then the projections to striate cortex were examined by making injections of WGA-HRP into the lateral geniculate body and by making restricted injections of HRP into the superficial layers of striate cortex.

The results of these experiments indicate that in addition to the magnocellular and parvocellular layers, a third type of layer, the intercalated layer, can be identified in the lateral geniculate body of monkeys. The intercalated layers are characterized by small pale-staining cells, fine caliber retinal input, and projections to layers III and I of striate cortex. The projections of the intercalated layers to striate cortex differ from the principal layers, not only in their layer of termination, but in the discontinuous or "patchy" fashion in which they terminate.

The similarities in the organization of these pathways in both carnivores and primates suggests that similar pathways existed in their common ancestor. However, since there are differences in the way in which these pathways are arranged into layers within the lateral geniculate body, these differences must reflect the independent acquisition of lamination in different lines of descent.

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INTRODUCTION

The striate cortex seems to be organized according to a similar plan in distantly related species, the tree shrew (Tupaia), the prosimian Galago, and the cat. In each of these species layer IV is divided into two tiers, each of which receives fibers from a distinct class of lateral geniculate cells; these lateral geniculate cells, in turn, may or may not be segregated into different layers (Ferster and LeVay, 1978; Glendenning et al., 1976; Harting et al., 1973). The cortex above layer IV is also the target of lateral geniculate axons. Following injections of anterograde tracers into the lateral geniculate body, labeled terminals are found in layers I and III of striate cortex in cat (LeVay and Gilbert, 1976), Galago (Casagrande and Skeen, 1980; experiments in progress) and Tupaia (experiments in progress). The significant point for the present purpose is that the cells of origin for those fibers projecting to layers I-III also have several features in common in the three distantly related species. The source of this projection is from those geniculate layers with the smallest cells: layer 3 in tree shrew, layers 4 and 5 in Galago (Carey et al., 1979) and the parvocellular C layers. These layers are characterized by receiving fine caliber retinal fibers, and in cat and Galago, at least, these retinal fibers have been described as arising from a certain type of ganglion cell, the so-called "W" cell class as defined by electrophysiology (Norton and Casagrande, 1982; Wilson, Rowe and Stone, 1976; Wilson and Stone, 1975). These layers are also similar in that

they receive projections from the superficial layers of the superior colliculus (Fitzpatrick, 1980; Graham, 1977; Niimi et al., 1970).

The remarkable similarity in the organization of the striate cortex in these distantly related species suggests that a similar organizational plan should apply to the monkey. Considerable evidence supports the idea that layer IV of the monkey striate cortex is subdivided into two tiers which receive projections from different classes of lateral geniculate neurons (Hendrickson et al., 1978; Hubel and Wiesel, 1972; Lund, 1973). Yet it is not clear whether there are geniculate projections to the more superficial layers of striate cortex in the monkey. Anterograde degeneration experiments have shown degeneration in layer I of striate cortex following lesions of the lateral geniculate nucleus (Hubel and Wiesel, 1972; Lund, 1973), but anterograde transport studies do not support the idea of direct geniculate input to layers I-III (Hendrickson et al., 1978; Rezak and Benevento, 1979).

In the present study, the laminar organization of the projection from the lateral geniculate body to striate cortex in the squirrel monkey has been reexamined using the anterograde transport of wheat germ agglutinin conjugated to HRP. The results to be presented will show that there is a direct projection from the lateral geniculate body to the most superficial layers of striate cortex and that this projection arises from a distinct class of geniculate neurons. Furthermore, these relay neurons share a number of common features with the neurons which project to the superficial layers of the striate cortex in the cat, Galago, and Tupaia.

METHODS

Injections of Tracers

Injections of wheat germ agglutinin conjugated to horseradish peroxidase (WGA-HRP, from Sigma) were made bilaterally into the lateral geniculate bodies of eight squirrel monkeys (Saimiri sciureus). A 5% solution of WGA-HRP was made by dissolving the WGA-HRP in either .1 M trizma buffer containing 2% lysophosphatidylcholine (Sigma type 1) for large injections or .9% saline containing .05-.1% poly-L- -ornithine (Sigma) for small injections. The injections were made by iontophoresis (.5 - 2 uA, 2 pulses/sec, 200-300 msec/pulse, 30-45 min. duration) through glass micropipettes which were pulled and broken to an inner diameter of 5-15 um. Positioning of the injection site within the geniculate was aided by recording (through the injection pipette) the responses of neurons to light flashes in the ipsilateral or contralateral eye.

Restricted iontophoretic injections of HRP were made bilaterally into the striate cortex of four squirrel monkeys. A 10% solution of Miles HRP in .9% saline containing .3% poly-L- -ornithine was used. Micropipette tip size and stimulation parameters were the same as for the WGA-HRP injections. Generally, several HRP injections were placed in an area of 1-2 mm in order to label a sufficient number of cells in the lateral geniculate body. Injections in the most superficial layers (I-IIIB) were made by aligning the filled micropipette tangential to the surface of the cortex and just piercing the pia. Injections into deeper layers were made with vertical penetrations.

Three squirrel monkeys received injections of HRP into the posterior chamber of the eye. Injection volumes ranged from 50-100 ul of a 20% solution of HRP dissolved in .9% saline containing 2% lysophosphatidylcholine.

Tissue Processing

After 48 hours survival, animals were perfused with a solution containing 8% formalin, 2% sucrose in .1M phosphate buffer pH 7.4. Fixation was followed by a 10% sucrose buffer rinse, after which the brain was removed, frozen, and sectioned at 50 u. Tissue was reacted for HRP by the de Olmos method (1977) using benzidine dihydrochloride as the chromagen.

Cell Measurements

In order to measure the area of the cells in the lateral geniculate body, drawings of individual cells were made with the aid of a camera lucida and a 100x oil objective. To insure that fragments of cells were not measured, only somas with well-defined nucleoli were drawn. Cell bodies were drawn in the focal plane of the nucleolus. From these drawings, the areas of the cells were measured using an Apple graphics tablet and computer. Measurements were made on both frozen (tissue which had been processed for HRP) and celloidin material. Since the results are identical, only the results from the celloidin material are presented here.

RESULTS

Laminar Organization of the Lateral Geniculate Body in Saimiri

The photomicrograph in Figure 1 makes it clear that as a first approximation, the lateral geniculate body of Saimiri consists of two main components, the magnocellular and parvocellular layers separated by an interlaminar zone. But the interlaminar zone also contains cells--small and pale staining--and another thin band of small cells lies below layer 1. Even the choice of names, "magnocellular" and "parvocellular", reflects the fact that these truly small cell layers have been overshadowed, if not overlooked. There are some notable exceptions: Le Gros Clark was the first to call attention to the thin bands of small, pale-staining cells on either side of the magnocellular layers in both Aotus and Saimiri. A drawing from his 1942 paper is presented in Figure 2 because it clearly reveals his conception, of three distinct classes of geniculate layers.

Similar zones adjacent to the magnocellular layers of Rhesus have been described by Guillery and Colonnier (1970). These authors emphasized the fact that these small cell zones show many of the characteristics of the magnocellular and parvocellular layers including the presence of relatively cell-free strips on either side of the band of cells. Guillery and Colonnier referred to these bands of cells as "intercalated" layers. This terminology has been adopted for both of the small cell zones in Saimiri since it confers upon them the status of a layer and indicates something about their position, that is to say, they are inserted between the principal layers or between layer 1 and the optic tract.

Figure 1 Lateral geniculate body in Saimiri.

- a) Low power photomicrograph of a Nissl stained section through the lateral geniculate body in Saimiri showing the prominent magnocellular layers (layers 1 and 2), the parvocellular mass (consisting of concealed layers 3-6), and two lightly staining intercalated layers on either side of the magnocellular layers (IL).
- b) Higher power photomicrograph from the same section shown in Figure 1a. The internal (ILi) and external (ILe) intercalated layers consist of small pale staining cells. These zones are different from the interlaminar zone (i) which contains few neurons.

a.

Figure 2 Laminar organization of the lateral geniculate body in Saimiri and Aotus according to Le Gros Clark.

Drawings of Nissl stained sections through the lateral geniculate body in Saimiri (a) and Aotus (b) from the 1942 paper by Le Gros Clark. These drawings show his conception of three distinct classes of layers.

a

b

Judgments about cell size without measurements can sometimes be misleading, so measurements of the cross-sectional area were made for the cells in the magnocellular, parvocellular and intercalated layers. The results, shown in Figure 3, leave little doubt that there are three distinct and significantly different distributions of cell size. The two distributions taken from the two intercalated layers are almost identical.

The intercalated layers, like the principal layers, receive retinal input and this can be shown by injecting the eye with HRP. The results of one experiment are illustrated in Figures 4 and 5. In the intercalated layer between layers 2 and 3 there is a clear zone of labeled terminals from the contralateral eye (Figure 4a), as well as a less dense zone of ipsilateral input (Figure 5a). A close examination suggests that within this layer the projections from the two eyes are segregated, with fiber terminals from the ipsilateral eye lying predominantly adjacent to layer 2 (Figure 4c), and fiber terminals from the contralateral eye lying predominantly next to layer 3 (Figure 5b). The intercalated layer ventral to layer 1 receives fibers almost entirely from the contralateral retina, and this contralateral input is distributed in a distinctly patchy fashion (Figure 4b). An ipsilateral projection to this zone, if present, is very small and limited to several sections.

The anterograde transport of HRP from the eye also gives one the opportunity to compare the caliber of the labeled processes among different layers of the lateral geniculate nucleus (Figure 6). Within the magnocellular layer large bulbous terminals are present; the terminals within the parvocellular layers are slightly smaller. In contrast, very fine caliber processes predominate within the intercalated layers. Of course, these observations do not rule out the possibility that fine caliber

Figure 3 Distribution of cell sizes in the lateral geniculate nucleus of Saimiri. Measurements were made on 150 cells from each of the indicated regions.

Figure 4 Retinal projections to the lateral geniculate body in Saimiri:
Contralateral projections.

- a) Distribution of labeled terminals in the lateral geniculate body following an injection of HRP into the contralateral eye. In addition to dense projections to layers 1, 4, and 6, there is a less dense projection to the internal and external intercalated layers (ILi, ILe).
- b) Higher power photomicrograph from an adjacent section showing discrete "puffs" of terminals in ILe. A thin strip of terminals in ILi is also present.
- c) Photomicrograph from a counterstained section showing the relationship between the retinal terminals in ILi (arrows) and layer 2 and layer 3. The projections from the contralateral eye terminate near layer 3 leaving a blank zone next to layer 2. Note the presence of lightly labeled terminals in ILe and the lack of terminals in the interlaminar zone (i).

C.

a.

Figure 5 Retinal projections to the lateral geniculate body in Saimiri: Ipsilateral projections.

- a) Distribution of labeled terminals in the lateral geniculate body following an injection of HRP into the ipsilateral eye. In addition to dense terminals in layers 2, 3, and 5, there is a less dense projection to ILi (arrow heads).
- b) Higher power photomicrograph showing the relationship between retinal terminal clusters in ILi (arrows) and layers 2 and 3. The terminals are located next to layer 2 leaving a blank zone next to layer 3. Compare with Figure 4c.

Figure 6 Caliber of retinal terminals in the lateral geniculate body.

Camera lucida drawing of HRP labeled terminals in the lateral geniculate nucleus following an injection of HRP into the contralateral eye. Layers 5 and 6 have been omitted. The retinal terminals in the magnocellular layers are the largest, the terminals in the parvocellular layers are intermediate, while the terminals in the intercalated layers are distinctly fine.

processes are also present within the magnocellular and parvocellular layers; or that the fibers projecting to the intercalated layers are collaterals of axons that terminate in the principal layers. But this difference in the size of terminals taken with the other evidence of cell size and staining intensity does suggest that the intercalated layers may be the recipient of a separate class of retinal input.

Up to this point, the similarity between the cells of, and the retinal fibers terminating in, the intercalated zones on either side of the magnocellular layers has been emphasized. However, the cells below layer 1 require a further and more detailed analysis because they actually consist of two separate and distinct regions and it is of crucial importance to the argument that these not be lumped together, as is a common practice, into a single "S" layer or "O" layer.

In addition to the pale staining band of small cells which has been described, at certain levels of the nucleus (and this level appears to vary) a cluster of very large, dark-staining cells appears between layer 1 and the optic tract. This large cell cluster is further distinguished from the small cells of the intercalated layer on the basis of retinal input: the large cell cluster receives large caliber terminals from the ipsilateral eye, while the intercalated layer receives fine caliber terminals from the contralateral eye. The results to be presented next will show that this large cell cluster is actually a displaced portion of layer 2, a point recognized by Casagrande and Joseph (1980) in their studies of the large cell "S" layer in Galago.

Figure 7 shows the transport of HRP from the eye to the ipsilateral and contralateral geniculate bodies. Layers containing HRP-labeled terminals are

Figure 7 Retinal input to the magnocellular layers.

Drawings of frontal sections through the lateral geniculate body in Saimiri showing the retinal input to the magnocellular layers. This figure shows the way in which a portion of layer 2 extends through and below layer 1. Black indicates layers which contain labeled terminals; stipple represents unlabeled layers. The caudal section is #42. The most rostral section is #52. Photomicrographs of section 48 are shown in Figure 8.

shown in black; unlabeled zones are shown as stipple. Section 50 on the side ipsilateral to the eye injection shows two distinct targets of the ipsilateral eye separated by the unlabeled geniculate layer. Undoubtedly, this separate zone of ipsilateral input lying ventral to layer 1 would have been called the "S" layer. However, if this "S" layer and layer 2 are traced caudally in successive sections, it is clear that these two separate regions are actually continuous. It seems that layer 1 becomes divided and that portions of layer 2 pass through the point of division. A very similar picture is apparent on the contralateral side. Photomicrographs of Section 48 on the ipsilateral and contralateral sides are presented in Figure 8.

A slightly different pattern of association between this ventral large cell cluster and layer 2 is shown in Figure 9. In this case, the cluster of large cells and terminals occurs in the middle of the nucleus (Section 78). At more caudal levels, the cluster breaks up into smaller pieces and these patches appear to pass through layer 1 and become continuous with an evagination of layer 2.

Several pieces of evidence suggest that the S layer, as this term was originally used, designated just this displaced portion of layer 2. First, the S layer was thought to receive just ipsilateral projections (Campos-Ortega and Hayhow, 1970; Giolli and Tigges, 1970). The present results show ipsilateral projections to the cluster of large cells that lies below layer 1, but contralateral projections to the small cells of the intercalated layer. Second, the large cells overshadow the small cells. Indeed, there are accounts of transneuronal degeneration of the S layer following removal of the ipsilateral eye and it is hard to imagine that changes of this sort would have been detected in the small pale staining zones referred to here as intercalated layers (Chacko, 1955; Giolli and Tigges, 1970). Third,

Figure 8 Retinal input to displaced portions of the magnocellular layers.

- a) This photomicrograph is from section 48 (illustrated in Figure 7) and shows a large cluster of terminals (arrow) overlying magnocellular neurons which lie ventral to layer 1. This section shows the retinal input from the ipsilateral eye.
- b) Same section as in (a), but this shows the retinal input to the contralateral lateral geniculate body. Unlabeled layer 2 (arrow) is seen lying between two separate segments of layer 1.

Figure 9 Displacement of magnocellular layer 2: A second pattern.

Closely spaced frontal sections through the lateral geniculate of Saimiri which received an injection of HRP into the ipsilateral eye. A small evagination seems to emerge from the ventral aspect of layer 2 (sections 71, 73). As one moves rostrally, this evagination breaks up into several clusters which pass through layer 1 and eventually coalesce into a large cluster (section 78) ventral to layer 1.

degeneration methods may not have been sensitive enough to detect the fine caliber terminals that characterize the intercalated layer, but they would have shown the large caliber projections to the displaced portion of layer 2.

Displacements of the magnocellular layers have been noted in the lateral geniculate nucleus of man (Hickey and Guillery, 1979) and chimpanzee (Tigges et al., 1977); and the complex branching patterns of the parvocellular layers are well-known (Kaas et al., 1978). The displacement of the magnocellular layers in Saimiri is often associated with the presence of large blood vessels entering the hilus of the lateral geniculate and that could be some clue to the cause (see Figure 8). Whatever the cause, the intercalated layer below layer 1 is clearly a separate entity consisting of small cells that are targets of fine caliber retinal input chiefly from the contralateral eye.

The Striate Cortex in Saimiri

Before presenting the results of experiments designed to trace the projections of geniculate layers to cortex, it is necessary to describe the laminar organization of the striate cortex. Since the names given to some of the layers of the striate cortex in this report differ from those most commonly used, this choice of terms must be defended. Discussions about nomenclature are often apologetic, apparently because what a structure is called seems less significant than what functions it serves or what connections it has. But if terminology reflects an effort to reveal homology and connections, an appropriate name for a structure is one of the goals of the inquiry.

The terminology presented here is based on relating the study of cytoarchitectural features to the laminar organization of the connections of

striate cortex in Saimiri. Using both cytoarchitecture and connections to define the laminar organization of striate cortex poses a problem since in order to define the subdivisions, reference must be made to the results of connectional experiments, and yet to present the results of connectional experiments using prevailing terminology would only confuse the issues. In order to avoid this problem, photomicrographs of several Nissl stained sections through the striate cortex are presented in Figure 10 and the present terminology is described by anticipating the connectional evidence that will be presented in the next section.

The most conspicuous feature in the laminar pattern of the striate cortex of Saimiri is the very dark band of small cells that is characteristic of layer IV in most cortical areas. Immediately superficial to this dense band of dark staining cells is a light zone with fewer pale staining cells. The terminology presented here differs most from previous terminology in the name applied to this light staining band. In the terminology used by Hassler and Wagner (1965) and Tigges et al. (1977) this light staining zone is referred to as a part of IIIC, while those who adhere to the Brodmann terminology (1905), such as Colonnier and Sas (1978), refer to this zone as a subdivision of IVB. While the name applied to this zone differs in these two schools of terminology, the terms IIIC and IVB are similar in the sense that their use implies that these zones correspond to the stripe of Gennari and are not a major target of projections from the lateral geniculate body. However, as will be shown, this light staining zone is the target of axons from the magnocellular layers of the lateral geniculate body. Furthermore, the cells that comprise this layer appear small and spherical in Nissl stained material and are only slightly larger than cells in the subadjacent dark band. This same description could be applied to the upper tier of layer

Figure 10 Cytoarchitecture of striate cortex in Saimiri.

- a) Low power photomicrograph of a section through the striate cortex surrounding the calcarine fissure. The arrowheads point to the borders of area 17 with area 18. This is from a celloidin section stained with cresyl violet.
- b) Higher power photomicrograph from the same section illustrated in Figure 10a. This photomicrograph illustrates a difference in the density of the cells within IV_{β} and the large size of the cells in IIIC.
- c) Frozen section through striate cortex stained with neutral red. This section shows the differences in cell packing density and size which characterize the subdivisions of layer III.

IV in the striate cortex of Rhesus which is also the target of magnocellular axons. Because of these features, the pale staining zone is referred to as IV_{α} .

The dark staining band of cells immediately underneath IV_{α} is simply called layer IV in the Hassler terminology (Hassler and Wagner, 1965) and layer IVC in the Brodmann terminology (1905). The concentration of small cells in this band is not uniform, but greater at the base. Without the benefit of knowing the targets of the magnocellular and parvocellular layers, it might be tempting to assume that the dark band of cells represents the entire target of geniculate terminals and that this slight difference in packing density is related to the termination of axons from the magnocellular and parvocellular layers. However, as the results will show, the entire extent of the dark band is the target of the parvocellular layers and will be referred to here as IV_{β} .

The upper border of IV_{α} is marked by a thin strip of dark staining cells. This strip contains a number of large pyramidal cells in addition to other cell types. The presence of large pyramidal cells marks the dorsal border of layer IV in the striate cortex of other species as well as in other cortical areas, and to be consistent with this scheme, the strip of cells and the light band immediately above it are referred to as IIIC. Layer IIIC is distinguished connectionally by the fact that the cells in this layer project to the middle temporal area (MT) (Spatz, 1977; Tigges et al., 1981), they receive a prominent descending projection from the superficial layers of the striate cortex, and they do not receive a direct projection from the lateral geniculate body.

The layer immediately above IIIC has a distinctly granular appearance which is best seen in Figure 10c. To be sure, granular cells are not the

only cell type found in this layer, but the small size of the cells and the increased density of the population clearly defines this as a separate zone. In the Brodmann terminology, this layer would be called IVA and in the sense that this term reflects the granular quality of the layer, it may be appropriate. But it is inappropriate to call the zone which lies beneath the granular tier IVB since that would obscure the homology between this pyramidal cell layer and the base of layer III in other cortical areas. Furthermore, the term IVB obscures the homology of this zone with similar layers in the striate cortex of other species such as prosimians which have no "IVA" (for example, Galago).

In order to avoid an awkward sequence of layers, the upper granular tier is considered a separate part of layer IIIB ($IIIB_{\beta}$). The base of this zone receives a direct projection from the lateral geniculate body and this layer is also distinguished by a projection from the stellate cells of layer IV. The upper part of IIIB, $IIIB_{\alpha}$, is the primary source of projections to area 18 (Tigges et al., 1981; personal observation) and, as will be shown in the next section, is also the primary target of the intercalated layers of the lateral geniculate body. The upper border of $IIIB_{\alpha}$ is not sharp but following injections of HRP into area 18, few labeled cells are found in this zone. In the Nissl stained section this zone (called IIIA) appears to consist of a smaller class of pyramidal cells than those in $IIIB_{\alpha}$. Finally, layer IIIA is bounded dorsally by a thin band of darkly staining cells which is layer II.

Laminar Organization of Geniculo-Striate Projections

Total pattern of geniculate terminals in striate cortex. In order to see the entire pattern of geniculate terminals, large injections of WGA-HRP

were made into the lateral geniculate nucleus of several animals. The injection site for one of these cases (case 2288L shown in Figure 11) involved all layers of the lateral geniculate nucleus but did not spread into the pulvinar nucleus. Labeled terminals from this experiment were distributed throughout a wide sector of the calcarine fissure, and Figure 12a shows a low power darkfield photomicrograph of these labeled terminals. The broad labeled band of terminals in the middle of the cortex corresponds to layers IV_{α} and IV_{β} . Superficial to this broad band of terminals is a zone--IIIC--that is virtually devoid of terminals. Superficial to layer IIIC is a very thin band of terminals that lies just at the base of $IIIB_{\beta}$. Both the projections to layer IV and to the base of $IIIB_{\beta}$ have been reported by other investigators (Hendrickson et al., 1978; Hubel and Wiesel, 1972; Lund, 1973; Tigges et al., 1977). The surprising part of this picture is the presence of terminals above the strip in $IIIB_{\beta}$. These terminals are distributed in discrete patches the centers of which are separated by roughly 400 μ m. The patches of label within layer III appear to lie predominantly within the zone which has been defined as $IIIB_{\alpha}$; however, they are not confined to this zone and in many sections they appear to start a short distance above the terminal band in $IIIB_{\beta}$ and continue into $IIIB_{\alpha}$ (Figure 12c).

In another experiment, the injection site involved more caudal levels of the geniculate, and this permitted an examination of the distribution of geniculate patches in a more oblique plane. Figure 12b shows the mosaic pattern they form across the cortical surface. Each patch is cylindrical in shape and the distances between adjacent patches are uniform.

In addition to the patchy projection to layer III, a sparse distribution of terminals was noted in the upper portion of layer I. While layer I in Figure 12a appears to have a large number of labeled terminals, the lightness

Figure 11 Injection sites of WGA-HRP into the lateral geniculate body
in Saimiri.

These photomicrographs show the center of the injection site
from each of the cases illustrated in this paper.

2288L

2280R

2226R

2280L

2288R

2378R

Figure 12 Distribution of labeled terminals in striate cortex following a large injection of WGA-HRP into the lateral geniculate body.

- a) Low power darkfield photomicrograph showing the laminar distribution of terminals from the lateral geniculate body. In addition to projections to both subdivisions of layer IV, and to the base of $IIIB_{\beta}$, there is also a patchy projection to layer III. The lightness of layer I in this photomicrograph is largely an edge artifact associated with the low power darkfield condensor. The actual density of terminals in layer I is shown in Figure 12c which is taken from the same section.
- b) Low power darkfield photomicrograph of a section through the caudal part of the calcarine fissure following a large injection of WGA-HRP into the lateral geniculate body. In this section layer III is cut obliquely and the mosaic-like distribution of terminal patches within this layer can be seen.
- c) Higher power photomicrograph from the same section illustrated in Figure 12a. The relationship between the terminals in $IIIB_{\alpha}$ and $IIIB_{\beta}$ is shown in this photo. The patch in $IIIB_{\alpha}$ on the right appears to have continuity with the band of terminals in $IIIB_{\beta}$, while the patch on the left appears separate. A few terminals are present in the outer half of layer I.

of this zone is an edge artifact due to the low power darkfield condensor. The actual density of terminals in layer I is best represented by the higher power photomicrograph in Figure 12c that is taken from the same section.

In addition to labeled terminals in the superficial layers, a large number of labeled cells were found in layer VI. These labeled cells makes it impossible to say whether or not there are also geniculate terminals in this layer.

The precise relation between the axon terminals of lateral geniculate neurons and the boundaries of layers $IIIB_{\beta}$, $IIIC$, and IV , is shown in Figure 13. In Figure 13b the arrows point to two conspicuous large pyramidal cells which lie at the lower border of layer $IIIC$. By comparing the position of these pyramidal cells with the extent of terminals revealed in the darkfield photomicrograph (Figure 13a), it is apparent that geniculate terminals occupy a wide zone which begins at the bottom of the dark granular layer IV and ends just below the base of the pyramidal cells that lie in layer $IIIC$. No geniculate terminals are found within this band of cells or in the cleft which lies dorsal to the strip of cells. A second zone of geniculate terminals does appear just at the base of $IIIB_{\beta}$. Thus, the extent of geniculate terminals supports the proposed definition of layer IV : it is the zone bounded by the pyramidal cell layer above and layer V below. In the darkfield photomicrograph, a difference in the density and caliber of the terminals in the upper and lower portions of layer IV can be seen. The next section will show that this difference reflects the difference between the magnocellular projections to IV_{α} and the parvocellular projections to IV_{β} .

The contributions of the various layers of the lateral geniculate to the total pattern. The contribution of the various layers of the lateral geniculate body to the total pattern was studied in two ways: first, by

Figure 13 Distribution of geniculate terminals in relation to the cytoarchitecture of the striate cortex.

These darkfield (a) and lightfield (b) photomicrographs show the same portion of a section through the striate cortex following a large injection of WGA-HRP into the lateral geniculate body. The arrows point to two prominent pyramidal cells which define the lower boundary of IIIC. Terminals from the lateral geniculate body end just below the base of these pyramidal cells. The difference in the caliber of the input to IV_{α} and IV_{β} reflects the projection of the magnocellular and parvocellular layers, respectively.

restricting WGA-HRP to certain layers of the lateral geniculate body, and second, by restricting HRP to certain layers of the striate cortex.

Case 2226R illustrates the results of an injection of WGA-HRP aimed at the magnocellular layers. Figure 14 shows that the injection site included the intercalated layer below layer 1, but only slightly encroached on the internal intercalated layer between layers 2 and 3, and spared the parvocellular layers. A band of labeled terminals is found in layer IV_{α} , patches of labeled terminals are present in layer III and sparse terminals are present in layer I. A photomicrograph of the injection site and the transport to cortex is shown in Figures 11 and 15, respectively.

The relation between the border of the terminals arising from the magnocellular layers and the border between IV_{α} and IIIC is indicated more precisely in the photomicrographs of Figure 16. The arrow in the lightfield photomicrograph points to a large pyramidal cell which lies within IIIC. The upper border of the labeled terminals lies just at the base of this pyramidal cell. No labeled terminals were found in IV_{β} , while IV_{α} from border to border was densely filled with terminals.

The results of an injection of WGA-HRP into the parvocellular layers are illustrated by experiment 2280R in Figure 17. The injection site involves the most dorsal part of the parvocellular layers but does not involve the magnocellular or intercalated layers. Labeled terminals are found within IV_{β} and in the band at the base of $IIIB_{\beta}$. No labeled terminals were found above $IIIB_{\beta}$.

From these two experiments, the parvocellular layers can be ruled out as a source of the patches in $IIIB_{\alpha}$ and the magnocellular layers and the intercalated layer below layer 1 can be ruled out as the source of the band at the base of $IIIB_{\beta}$. Further, the results support the idea that the

Figure 14 Case 2226R: Results of an injection of WGA-HRP into the ventral layers of the lateral geniculate body. A photomicrograph of the injection site is shown in Figure 11. A photomicrograph of the labeled terminals in striate cortex is shown in Figure 15.

2226R

Figure 15 Distribution of labeled terminals in the striate cortex after injections in the ventral layers of the lateral geniculate body.

- a) From case 2226R. This case shows a patchy distribution of terminals in IIIB_α , light terminals in layer I, and a dense projection to IV_α . Few labeled terminals were found at the base of IIIB_β .
- b) From case 2288R. This case shows patches in IIIB_α , a prominent band in IIIB_β and IV_α .

Figure 16 Distribution of terminals from the magnocellular layers of the lateral geniculate body in relation to the cytoarchitecture of the striate cortex.

Darkfield (a) and lightfield (b) photomicrographs from the striate cortex of case 2226R. The arrow points to a prominent pyramidal cell which defines the border of IIIC. Terminals from the lateral geniculate body end just below the base of this cell. Asterisks indicate the same blood vessel in both photomicrographs.

Figure 17 Case 2280R: Results of an injection of WGA-HRP into the parvocellular layers of the lateral geniculate body. A photomicrograph of the injection site is shown in Figure 11.

2280R

magnocellular layers project to IV_{α} and the parvocellular layers project to IV_{β} and to $IIIB_{\beta}$.

Two additional experiments, 2288R and 2280L, provide more information on the source of the projections to $IIIB_{\alpha}$ and $IIIB_{\beta}$ (Figures 18 and 19). In these experiments the internal intercalated layer was included in the injection site but the parvocellular layers were spared. In both cases no labeled terminals were found in IV_{β} (as one would expect), yet labeled terminals were found both at the base of $IIIB_{\beta}$ and in the patches of $IIIB_{\alpha}$. This finding suggests that the labeled terminals at the base of $IIIB_{\beta}$ following large injections of the geniculate are not solely the result of the involvement of the parvocellular layers and that the internal intercalated layer may also contribute to the axon terminals at the base of $IIIB_{\beta}$. One final anterograde experiment (2378R) (see Figure 20) also supports the idea that the internal intercalated layer sends a projection to $IIIB_{\beta}$ as well as $IIIB_{\alpha}$. In this experiment, the injection site is centered in the internal intercalated layer with a slight involvement of layer 2 and 3 on either side. Labeled terminals were found in both subdivisions of layer IV as well as in the base of $IIIB_{\beta}$ and in the patches of $IIIB_{\alpha}$. However, two aspects of the labeling in this case support the idea that the label in the superficial layers is due to the involvement of the internal intercalated layer.

First, the labeled terminals in $IIIB_{\alpha}$ and $IIIB_{\beta}$ extended over a wider area of the cortex than the label in layer IV. Second, except for the center of the region which contained labeled terminals, the projection to the superficial layers was more dense than the projection to layer IV. This is particularly clear in the photomicrograph shown in Figure 21a. In the central region, the projection to layer IV was about equal in density to the projection to the more superficial layers (Figure 21b). In the case of large

Figure 18 Case 2288R: Results of an injection of WGA-HRP into the ventral layers of the lateral geniculate body. A photomicrograph of the injection site is shown in Figure 11 and a photomicrograph of the transport to striate cortex is shown in Figure 15b.

2288R

Figure 19 Case 2280L: Results of an injection which includes the magnocellular layers and the internal intercalated layer. A photomicrograph of the injection site from this case is shown in Figure 11.

2280L

Figure 20 Case 2378R: Results of an injection centered in the internal intercalated layer.

The injection site encroaches upon parvocellular layer 3 and magnocellular layer 2. A photomicrograph of the injection site is shown in Figure 11, and a photomicrograph of the anterograde transport to striate cortex is shown in Figure 21.

2378R

Figure 21 The distribution of terminals in the striate cortex following an injection of WGA-HRP centered in the internal intercalated layer.

- a) Distribution of terminals in the area surrounding the central zone of labeled terminals in case 2378R. There are a large number of terminals in IIIB_α and IIIB_β , but only a few in IV_α and IV_β .
- b) Distribution of terminals in the central zone of labeled terminals in case 2378R. Patches of labeled terminals are present in IIIB_α and IIIB_β . In addition sparse terminals are present in IV_α and three well defined patches of label are present in IV_β .

injections of WGA-HRP which include all layers of the geniculate, the projection to layer IV appears more dense than the projection to layer III (see, for example, Figure 12a).

There is one additional feature of this case that is worth noting. In the center of the zone which contained labeled terminals (Figure 21b), the labeled terminals in IV_{β} were clearly arranged in patches separated by terminal-free zones. This arrangement is reminiscent of ocular dominance patches which are found in other species and may be related to the involvement of ipsilateral parvocellular layer 3 in the injection site without the involvement of layer 4. While transneuronal transport studies have failed to demonstrate ocular dominance columns in Saimiri, Hubel and Weisel (1978) have presented physiological evidence for a less well-defined ocular dominance system in this species.

Next, an attempt was made to confirm the results of these anterograde experiments by restricting HRP to the superficial layers of the striate cortex. In using this approach, a compromise between two conflicting problems must be reached. The injection must be limited in the vertical dimension (for example, restricted to only a few layers), but must cover a large enough surface area to produce a significant number of labeled cells in the lateral geniculate nucleus. To achieve this, the strategy of placing two or more injections of HRP (see METHODS) within a space of 1-2 mm was adopted.

When HRP was restricted to the area dorsal to the zone of geniculate input in $IIIB_{\beta}$, labeled cells were found predominantly in the intercalated layers of the lateral geniculate body. Figure 22 shows an example of one such experiment. A photomicrograph of the injection site from this case is shown in Figure 23. From the superficial injection site, labeled fibers can be seen running through IVB and into IIIC where large numbers of terminals

Figure 22 Case 2263: Results of superficial injections of HRP into the striate cortex.

Two separate injections were made on the dorsal surface of the striate cortex. The injection sites included IIIB_α , IIIA , II , and I , but did not encroach upon the base of IIIB_β . Two prominent bands of labeled terminals were located in IIIC and in layer V . The open triangles in these layers indicate the presence of labeled cell bodies as well.

Labeled cells in the lateral geniculate body as a result of these injections are indicated as dots. Each dot represents one labeled cell. The cells from adjacent sections were superimposed on the same drawing.

2263

INJECTION A

INJECTION B

Figure 23 Injection sites of HRP into the striate cortex of Saimiri.

- a) This is injection site A from case 2263. Labeled fibers can be seen leaving the injection site and two bands of labeled terminals are present in IIIC and V.
- b) Injection sites in case 2320: The dark spots in layer IV and layer V are due to the presence of labeled cells and terminals (see Figure 24).

a.

b.

are found. Additional fibers course through layer IV into layer V where a second conspicuous zone of terminals is found. Due to the large numbers of terminals, it is difficult to determine whether labeled cells are present within these terminal regions. Some layer V pyramidal cells are clearly labeled. Layer IV is conspicuously free of labeled cells or terminals.

Following this injection, 49 cells were labeled in the lateral geniculate body. Of these cells, 43% were in the internal intercalated layers, 51% were in the external intercalated layers, and 6% were in the parvocellular layers. This result suggests that the labeled terminals found in the superficial layers of the lateral geniculate body can be largely attributed to the intercalated layers.

This interpretation is, of course, based on an accurate assessment of our injection site. In order to test the interpretation of the ventral extent of the injection site and to verify the source of the terminals within the ventral portion of IIIB_β , an attempt was made to produce an injection of HRP which included the base of IIIB_β . Figure 24 shows an example of such an experiment. In this experiment, the two injections were centered in IIIB_β and included its base, without much involvement of IIIC . The injection site itself is instructive because it shows a different pattern of intracortical connections than that found in the more superficial injections. Labeled fibers can be seen leaving the injection site and coursing through IIIC and IV into layer V where a cluster of terminals are found. In contrast to the superficial injection, few labeled terminals were found within IIIC , while a good number labeled cell bodies were found within layer IV. This suggests that cells in layer IV project predominantly to layer IIIB_β and not to the more superficial layers.

Figure 24 Case 2320: Results of injections of HRP into layer IIIB $_{\beta}$ of the striate cortex.

Two separate injections were made on the dorsal surface of the striate cortex. The injection sites were centered in IIIB $_{\beta}$ and encroached slightly into IIIB $_{\alpha}$ and IIIC. The open circles in IV $_{\alpha}$ and IV $_{\beta}$ below the injection site indicate the presence of labeled cell bodies. Labeled cell bodies and terminals were also present in layer V.

Labeled cells in the lateral geniculate body as a result of these injections are indicated by dots. Each dot represents one labeled cell. The cells from adjacent sections were superimposed on the same drawing.

2320

Following this injection, 69% of the cells were located within the parvocellular layers and 31% of the cells were located in the intercalated layer between layers 2 and 3. This, along with the anterograde evidence, supports the idea that the band of geniculate terminals in IIIB_β can be attributed both to cells within the parvocellular layers and to cells within the interlaminar zones.

Relation of Geniculate Terminal Patches to Metabolic Markers

Recently, there have been several reports demonstrating a patchy distribution of metabolic markers (cytochrome C, deoxyglucose) within the superficial layers of the striate cortex in Saimiri (Humphrey and Hendrickson, 1980) and Rhesus (Horton and Hubel, 1981). Also, the distribution of GAD immunoreactivity indicative of the presence of the neurotransmitter GABA has been shown to occur in patchy fashion (Hendrickson et al., 1981). The interpatch distance reported for these patches is similar to what was found for the anterogradely labeled patches in the striate cortex, so the obvious question is whether these patchy patterns are coincident or interdigitating. Figure 25 shows the basic pattern of cytochrome oxidase staining in the striate cortex as reported by Humphrey and Hendrickson (1980) and Horton and Hubel (1981). The similarity with the whole pattern of geniculate inputs (Figure 12) is compelling. The heaviest levels of cytochrome oxidase staining occur in the zones which receive geniculate input: layer IV_α and β , the base of IIIB_β , and the patchy zone largely in IIIB_α .

In the experiment illustrated in Figure 25 WGA-HRP was injected into the lateral geniculate body (involving all layers) and adjacent sections were processed for cytochrome oxidase staining and for peroxidase. The asterisk

Figure 25 The distribution of cytochrome oxidase staining in the striate cortex and relation to the projections from the lateral geniculate body.

The lateral geniculate body was injected with WGA-HRP and adjacent sections of striate cortex were reacted for a) cytochrome oxidase and b) the presence of HRP. The asterisk denotes the same blood vessel in both figures. The patches of cytochrome activity coincide with the patches of geniculate terminals in IIIB_α.

a.

b.

denotes a blood vessel which can be seen running through the cortex in both figures. This experiment shows that the cytochrome patches coincide precisely with the patches of terminals from the lateral geniculate body.

DISCUSSION

The main significance of these results is that they provide evidence for a third visual pathway relaying in the lateral geniculate nucleus of monkeys. Earlier anatomical studies by Hubel and Wiesel (1972), Lund (1973), and Hendrickson et al. (1978) had demonstrated two pathways, one relayed by the parvocellular layers to cortical layer IV_{β} and the second relayed by the magnocellular layers to cortical layer IV_{α} , and the present results confirm these findings. The present study also confirms the existence of a projection from the parvocellular layers to IVA, or in the new terminology, $IIIB_{\beta}$. In addition to these pathways from the magnocellular and parvocellular layers, a third pathway can be defined in Saimiri by the following characteristics and connections: First, the size of the lateral geniculate relay cells is distinct--they are easily distinguished by size alone from those cells that are the hallmark of the magnocellular and parvocellular layers. Second, the caliber of retinal terminals in the intercalated layers is finer than the terminals in the parvocellular and magnocellular layers. Third, the intercalated layers are the main geniculate target of projections from the superficial layers of the superior colliculus (Harting et al., 1978). Finally, these layers project to the most superficial layers of striate cortex and do so in a discontinuous "patchy" fashion. These features taken together point to a separate and distinct pathway from retina to striate cortex.

The fine caliber of the retinal terminals in the intercalated layer has been taken as evidence that these zones receive input from a separate class of retinal ganglion cells. Support for this interpretation comes from the fact that the parvocellular C layers in the cat lateral geniculate body and layers 4 and 5 of the Galago lateral geniculate body are also distinguished by the fine caliber of their retinal input (Fitzparick et al., 1980; Guillery, 1970; Guillery and Oberdorfer, 1977; Mason and Robson, 1979), and both retrograde tracing experiments and physiological studies have shown that these layers receive input from a distinct class of retinal ganglion cells (Itoh et al., 1981; Norton and Casagrande, 1982; Wilson and Stone, 1975; Wilson et al., 1976). Unfortunately, there is as yet no physiological evidence that the intercalated layers of monkeys are the targets of a distinct type of retinal input. But this failure may simply be related to the problems of recording from small cells, only further compounded by the small area that these cells occupy in comparison to the magnocellular and parvocellular layers. The size of the intercalated layers and their relation to the principal layers would also make it very difficult to produce a small injection of HRP confined only to an intercalated layer in order to determine the type of ganglion cells which project to it (see Leventhal et al., 1981). While the evidence presented here supports the idea that the intercalated layers receive input from a distinct class of retinal ganglion cells, clearly this hypothesis will require confirmation from an analysis of the laminar distribution of individual retino-geniculate axons.

Laminar Organization of Striate Cortex and Relation to the Distribution of Terminals from the Lateral Geniculate Body

The results of the present study indicate that the projection of the lateral geniculate body to the striate cortex in the monkey is more extensive

than previously thought and includes a patchy projection to layer III and a sparse projection to the outer portion of layer I. A number of anterograde degeneration studies in Rhesus show that the lateral geniculate body projects to IV_{α} and IV_{β} and the base of $IIIB_{\beta}$ (present terminology) as well as layer I (Hubel and Wiesel, 1972; Lund, 1973). But most anterograde transport studies did not provide confirmation of the projection to layer I (Hendrickson et al., 1978; Rezak and Benevento, 1979) and the interpretation of the degeneration experiments showing this projection became complicated by the discovery that the pulvinar nucleus projects to this layer (Benevento and Rezak, 1975; Ogren and Hendrickson, 1977). In the experiments presented here, labeled terminals were found in layer I only after large injections which involved the magnocellular and surrounding intercalated layers. The labeled terminals in layer I were precisely in register with the terminals in deeper layers and this fact would seem to rule out fibers of passage from the pulvinar as the source. It remains to be determined whether the same cells in the intercalated layers send axons to layer III and to layer I.

The patchy distribution of geniculate terminals in layer III was foreshadowed by reports of a patchy distribution of autoradiographic grains in layer III of Saimiri following the injection of a transneuronal tracer into the eye (Hendrickson et al., 1978; Hubel and Wiesel, 1978). But Hendrickson et al. interpreted this distribution of grains as representing "trans-transneuronal transport" (i.e., it was thought to be due to the transfer of tracer from the axons of lateral geniculate neurons to layer IV granule cells and then to their terminals). It is unlikely that the patchy distribution of terminals in layer III is the result of transneuronal transport since: 1) $IIIB_{\alpha}$ is not a direct target of layer IV granule cells (see following

paragraph), and 2) the results of HRP injections into layer III show a direct projection from the lateral geniculate body to this layer.

The injections of HRP into the superficial layers of the striate cortex, in addition to demonstrating the source of the patchy terminal distribution in layer III, also provide new insights into the intrinsic circuitry of the striate cortex. Injections of HRP into the superficial layers above IIIB_β did not result in labeled cell bodies in layer IV, while injections which included IIIB_β did. Thus, IIIB_β is the primary target for the relay of information from layer IV, while more superficial layers are less directly related to layer IV. This result is consistent with the observation made by Lund (1973) and Lund and Boothe (1975) that granule cells in layer IV have a dense terminal plexus at the base of IIIB (this would correspond to IIIB_β). The study by Lund also suggests that IV_β sends axons into IIIB_β while IV_α does not. In the present study a large number of labeled cells were labeled in IV_β , but fewer were labeled in IV_α . It is possible that the cells labeled in layer IV_α are the result of a slight involvement of the superficial aspect of IIIC which Lund (1973) suggests is a major target of layer IV_α .

Of interest here is the fact that injections of HRP above IIIB_β labeled cells in the intercalated layers of the lateral geniculate body, but did not label cells in layer IV. Thus, the cells in IIIB_β which receive input from the intercalated layers could be monosynaptically related to geniculate input, while those not receiving direct inputs from the intercalated layers, receive geniculate input only after it has passed through at least two additional synapses. (This assumes that the patchy zones represent "isolated geniculate receptive zones" with limited interaction with surrounding patches.) If this is true, then it is reasonable to predict that the cells in these geniculate recipient zones would have physiological characteristics distinct from the

non-geniculate recipient zones, and perhaps similar to other cells in direct contact with geniculate afferents.

Recent studies by Hubel and Livingstone (1981) in Rhesus support this idea. When electrode penetrations were made parallel to the cortical surface in layer III of striate cortex, regions were encountered in which the cells had poor orientation tuning. In the center of these regions, the cells were often completely unoriented, had center-surround receptive fields, and often responded to diffuse light. These regions were found to correspond precisely with the patches of cytochrome oxidase activity which are, in turn, the terminal zones of cells in the intercalated layers.

Another aspect of the intrinsic organization of striate cortex revealed by restricted injections of HRP into the superficial layers is the presence of two prominent bands of terminals in layer IIIC and layer V. A projection from the superficial layers to layer V has been demonstrated before in the striate cortex of primates (Carey et al., 1979; Fisker et al., 1973; Lund and Boothe, 1975; Spatz et al., 1970) and this appears to be a general feature of cortical organization since it is also found in auditory and somatic cortex (Nauta et al., 1973; personal observations). This projection probably arises at least in part from pyramidal cells within layers III and II since Golgi studies in Rhesus have shown that collaterals arise from these neurons as they pass through layer V (Lund and Boothe, 1975).

The presence of a dense collection of terminals in IIIC after the injection of HRP into the more superficial layers suggests that cells within layers II-IIIB also send collaterals to this zone. The band of labeled terminals extended from the base of the pyramidal cells which characterize IIIC to the bottom of IIIB _{β} and, therefore, did not overlap with the terminal zones of geniculate axons. A similar pattern of labeled terminals in IIIC is

found following injections of anterograde tracers into area 18 and the middle temporal area (Tigges et al., 1981; personal observation). The fact that axons from area 18 terminate in both IIIC and IIIB $_{\alpha}$ (as well as layer I) raises the possibility that the band of terminals in IIIC is the result of labeling collaterals of axons which also project more superficially. Likewise, it is also possible that the labeled terminals in IIIC could represent local axon terminals of cells which reside in IIIC and send collaterals to more superficial layers. At present, neither of these possibilities can be ruled out.

Whatever the source of the terminals in IIIC, the restricted horizontal extent of the terminals in both IIIC and V, as well as the restricted labeling of cell bodies in layer IV following superficial injections, emphasizes the precise vertical organization of the striate cortex. Cells within layer IV project to a restricted zone of cortex within IIIB $_{\beta}$. Cells within the superficial layers send projections to layer V and possibly to layer IIIC within a restricted vertical column. These features of cortical organization are undoubtedly responsible for the similarities in receptive field position and orientation selectivity which characterize the cells found during the vertical penetration of an electrode through the striate cortex (Hubel and Wiesel, 1977).

The Patchy Organization of Geniculate Projections to Layer III

The projection from the intercalated layers of the lateral geniculate body to layer IIIB $_{\alpha}$ terminates in distinct patches averaging 200 μ m in diameter with a center to center distance of 500 μ m. It is difficult to understand the significance of this patchy organization without more information on the properties of the cells within and outside these patches and

the differences in the projections of the geniculate recipient and nongeniculate recipient zones. But, hopefully, the reader will bear with the author while he indulges in a little healthy speculation.

The patchy organization of the projections from the lateral geniculate body to the striate cortex does not imply that the small cell pathway is in any sense a discontinuous representation of the visual field. Perhaps the best way to illustrate this point is to consider the amount of the striate cortex that would be activated by stimulation of a single point on the retina (in other words, the amount of cortex occupied by cells whose receptive fields overlap that point). In Rhesus this would involve a square of cortex approximately 1-2 mm on a side (Hubel and Wiesel, 1977). If an area half that size serves the same function in Saimiri, then cells which lie within at least 4 patches of geniculate terminals in IIIB_α could be activated by stimulation of a single point on the retina.

Thus, within IIIB_α there may be multiple complete representations of the visual field, one of which will be influenced by direct projections from the intercalated layers, and others which will not. The patchy distribution of terminals in this layer may reflect a segregation of these representations which is maintained to some degree, in the efferent projections of this layer to area 18 (Tigges et al., 1981; personal observation).

If the significance of the patchy organization in IIIB_α is to segregate geniculate and nongeniculate recipient zones, an obvious question becomes, why is this pattern of segregation different from the pattern of segregation of inputs from the two eyes? Ocular dominance columns, although they appear as patches or columns in a single section, are actually slabs which run in an alternating fashion across the cortex (Hubel and Wiesel, 1977). Perhaps the difference between these two types of organization is simply the number of

elements being segregated. If the important aspects of the segregation which occur within a layer of cortex are, 1) to group like with like, and 2) to provide common borders between each of the segregated elements, then a slab-like arrangement would be the optimal arrangement for two elements whereas a patch-like arrangement would be optimal for three or more elements (see Figure 26). This implies that more than two elements are being segregated within IIIB_α . Recent reports of periodic intrinsic connections within this layer (K. Rockland, personal communication) suggest that they are similar in size but do not overlap with the patches of cytochrome oxidase staining. These intrinsic zones could constitute at least one additional segregated element within IIIB_α .

Finally, it is important to consider the patchy nature of the retinal input to the intercalated layers and how this might be related to the patchy projection to striate cortex. Since complete lesions of striate cortex do not produce a patchy pattern of degenerated cells within the intercalated layers, then both retinal recipient and nonretinal recipient zones must project to the striate cortex. The projection from the superior colliculus to these zones terminates in patches (Harting et al., 1978), and it may be that the patches from the superior colliculus are complementary to the retinal terminal patches. If they are, then perhaps the retinal and tectal zones contribute to different terminal patches within IIIB_α . Clearly, some form of double label experiment would be needed to test these ideas.

Comparison With Other Species

The lateral geniculate body in both prosimians and simians is characterized by readily identifiable magnocellular and parvocellular layers. The similarities in cell size, and connections of these layers in different

Figure 26 Patterns of segregation within the striate cortex.

- a) Pattern of segregation of the pathways from the two eyes.
This diagram is a surface view of a portion of striate cortex showing the strip or slab-type organization for ocular dominance.
- b) Pattern of segregation shown by the projection of the intercalated layers to striate cortex. Dark circles represent patches of geniculate terminals within $IIIB_{\alpha}$. Other labeled circles represent additional hypothetical columns which may account for the pattern of geniculate terminals.

a

Ocular Dominance Pattern

b

Intercalated Layer Pattern

species, along with the constant spatial relationships which these layers have to each other and to the optic tract, support the idea that they are homologous in all primates (Kaas et al., 1978). In the present report an additional class of geniculate layers has been identified in Saimiri and this class is also distinguished on the basis of cell size and connections. The issues to be addressed here are whether similar intercalated layers can be identified in other primates and whether the similarities in these layers are attributable to a common ancestor.

Layers 4 and 5 of the lateral geniculate body in the prosimian Galago have many features in common with the intercalated layers of Saimiri. First, these layers consist of small pale staining cells and project to layers III and I of striate cortex (Carey et al., 1979; experiments in progress). Second, they are the targets of a distinctly fine caliber retinal input which originates from small retinal ganglion cells (Fitzpatrick et al., 1980; Itoh et al., 1982). Finally, layers 4 and 5 receive a projection from the superficial layers of the superior colliculus (Fitzpatrick et al., 1980).

Similar small-celled intercalated layers are also present in the lateral geniculate body of Aotus. These layers lie on either side of the magnocellular layers as well as between them. Like their counterparts in Saimiri and Galago, these zones receive fine caliber retinal input and project to layers III and I of striate cortex (experiments in progress).

While there is less evidence about the presence of intercalated layers in other primate species, a review of the literature supports the idea that small-celled intercalated layers are a general characteristic of the primate lateral geniculate body. The original description of small pale staining intercalated layers in Rhesus (Guillery and Colonnier, 1970) has already been mentioned and similar zones have been described in the human lateral

geniculate body (Hickey and Guillery, 1979). Patchy or clustered retinal projections to small-celled interlaminar zones surrounding the magnocellular layers have been shown in Rhesus (Hubel et al., 1977; Kaas et al., 1978) and in Callithrix (Spatz, 1978) and there is a "hint" of patchy retinal terminals in these zones in the Chimpanzee (Tigges et al., 1977). The patchy distribution of retinal terminals in these species is similar to the patchy distribution of retinal projections to the intercalated layers in Saimiri.

The similarities in cell size, staining intensity, caliber of retinal terminals, tectal inputs and the laminar organization of projections to striate cortex could be taken as support for the idea that the intercalated layers in all primates are homologous. But, if these layers are homologous, then the position of these layers within the lateral geniculate body should be similar in different primate species, particularly in the light of the constancy in the positions of the magnocellular and parvocellular layers. In fact, the position of the intercalated layers varies. In most prosimians they lie between the parvocellular layers. This is true not only for the lorisiforms (for example, Galago), but also for the lemuriforms, such as the mouse lemur, Microcebus (Cooper et al., 1979). By contrast, in Tarsiers and both new world and old world monkeys the intercalated layers occupy a more ventral position, on either side of the magnocellular layers. Even between monkey species there appears to be some variability in the position of these small cell layers. For example, in Saimiri they are located on either side of the magnocellular layers, while in Rhesus and Aotus they lie between, as well as on either side of, the magnocellular layers. In addition to variability in position, there are also species differences in the organization and spatial relations of contralateral and ipsilateral retinal projections to these zones. For example, the external intercalated layer in

Saimiri and Callithrix (Kaas et al., 1978) appears to receive input almost entirely from the contralateral retina while this area in Aotus (Kaas et al., 1978; personal observation) is the target of both contralateral and ipsilateral retinal projections.

How does one reconcile the remarkable similarities in the characteristics of the cells which comprise the intercalated layers with the variation in position of the layers within the geniculate? A likely explanation is that the similarities in the characteristics of the cells are a reflection of homology, while the differences, most notably the laminar arrangement of the cells, are independent acquisitions of the prosimian and simian lines of descent. In this view, the common ancestor of the prosimian and simian line possessed both magnocellular and parvocellular layers and in addition, a class of cells with features characteristic of the cells in the intercalated layers. This class of cells evolved independently in different lines of descent resulting in differences in its location, ipsilateral vs. contralateral ocular input and probably other features. If this is true, then the well-developed layers 4 and 5 of prosimians are specializations of an ancestral cell type which also gave rise to the less well-developed intercalated layers of primates.

An alternative explanation for the similarities in the cells which comprise the intercalated layers in these species, is that these similarities are the result of convergence. In other words, it is possible that the common ancestor of simians and prosimians did not possess a cell type like that found in the intercalated layers and that the cell type, as well as the laminar pattern, evolved independently in both lines of descent. This hypothesis cannot be tested without examining the common ancestor and several predecessors along the simian and prosimian lineages.

But the idea that the common features of the cells in the intercalated layers of primates are reflections of common ancestry is supported by the fact that cells with similar features can be identified in far more distantly related species such as Tupaia and cat which have evolved under different ecological situations. The cells of layer 3 in Tupaia share a number of features in common with the cells of the intercalated layers of primates. These cells are distinctly small and pale staining (Casagrande et al., 1978; Glickstein, 1967) and they receive fine caliber fibers from the retina (Casagrande et al., 1978). The cells in this layer are also the target of input from the tectum (Fitzpatrick et al., 1980) and the source of projections to the superficial layers of the striate cortex (Carey et al., '79; Conley et al., 1982). These same characteristics could be used to describe the cells in the parvocellular C layers of the cat lateral geniculate body (Graham, 1977; Guillery, 1970; LeVay and Gilbert, 1976; Leventhal, 1979; Niimi et al., 1970; Mason and Robson, 1979). While it is possible that the similarities in cells which comprise the intercalated layer as well as the segregation of this cell type into layers may have occurred independently in all these groups, a more parsimonious explanation is that a common cell type has undergone segregation independently in different lines of descent.

The point being made here is that the cells which reside in the intercalated layers of primates, the parvocellular C layers of the cat, or layers 4 and 5 of Galago share a number of common features, not that they are identical. To be sure, there are differences in the exact laminar organization of the projections to striate cortex as well as in the way the retina and the superior colliculus terminate within these zones. There are also likely to be some differences in the dendritic morphology of these cells

depending upon their laminar arrangement, their relation to adjacent layers, and the organization of their inputs. Also, it is reasonable to expect differences in the receptive field properties of these cells in different species. But these differences may simply reflect the way in which a basic scheme has been modified or refined in response to distinct selective pressures in different lines of descent.

In the examples presented here, the small cell population has been segregated from the rest of the geniculate, but if the basic characteristics of these cells are attributable to a common ancestor while laminar segregation is not, then there should be some species in which the cells with these features are located throughout the lateral geniculate body. There is no evidence for laminar segregation according to cell size in the lateral geniculate body of the rat. Yet, on the basis of conduction velocity, at least three distinct classes of retinal afferents have been identified (Fukuda, 1977; Hale et al., 1979). Furthermore, there seems to be a matching of these different inputs with cell types in the lateral geniculate body so that fast conducting fibers activate fast conducting relay cells while slowly conducting fibers activate slowly conducting relay cells (Fukuda, 1977; Hale et al., 1979). It only remains to be determined whether the slowly conducting relay cells project to the superficial layers of the cortex. The lateral geniculate body in the rat projects to layer VI, IV, III and layer I (Ribak and Peters, 1975) of the striate cortex. A recent study by Parnauelas et al. (1981) has shown that cells can be labeled in the lateral geniculate body of the rat after an injection of HRP into layer I of the striate cortex. But these investigators concluded that the cells labeled after these injections were not "a specific cell group" since they appeared to have different shapes and sizes and were located throughout the nucleus.

Unfortunately, no cell measurements were made of the labeled vs. unlabeled neurons and the amount of HRP filling from small injections to the striate cortex would make the comparison of dendritic morphology impossible. Perhaps a quantitative analysis of the cells which project to the superficial layers of the cortex in the rat may reveal similarities in this cell population that were not revealed by visual inspection alone.

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