A Numerical Analysis of the Geniculocortical Input to Striate Cortex in the Monkey

Using data that are available in various publications, a quantitative analysis has been made of the geniculocortical input to layer IVC of the macaque striate cortex. The data suggest that only 1.3–1.9% of the excitatory, or asymmetric synapses in layer IVCα of striate cortex are provided by the neurons of the magnocellular layers of the LGN. This amounts to only 18–40 of the 1000–2100 asymmetric synapses that the average layer IVCα neuron receives. The parvocellular afferents to layer IVCβ, on the other hand, provide 3.7–8.7% of the asymmetric synapses formed by the average layer IVCβ neuron, or 37–191 synapses to each neuron. If it is assumed that the boutons in the geniculocortical axonal plexuses are evenly spread, it can be calculated that the input to an individual layer IVC neuron is provided by some 24 axonal plexuses. This is regardless of whether the neuron lies in layer IVCα or in IVCβ. This calculation suggests that a single axonal plexus provides not more than one or two of the excitatory synapses received by an individual layer IVCα neuron, and between one and eight excitatory synapses for a layer IVCβ neuron. Consequently, it is unlikely that the response properties of a particular cortical neuron are dominated by its input from a single geniculate neuron.

Since the geniculocortical input essentially determines the response properties of neurons in layer IV of macaque striate cortex, it is surprising that this input amounts to such a small number of synapses to an individual neuron, although we obtained a somewhat similar result in our earlier quantitative analysis of the geniculate input to the striate cortex of the cat (Peters and Payne, 1993). But it has to be questioned whether the low values obtained are correct. Interestingly, the geniculocortical input to cortex has been largely neglected in favor of analyses of intracortical circuitry, but in view of the basic importance of this afferent input, it is suggested that more quantitative data about it should be generated, so that a better assessment can be made of its extent.

In a previous article (Peters and Payne, 1993) we gave a numerical analysis of the geniculate input to the primary visual cortex of the cat. This analysis was based upon the data available in diverse publications, and after the analysis had been carried out it was concluded that the data indicated that only about 5% of the total excitatory input to layer IV neurons in cat striate cortex is provided by the geniculocortical afferents. The present article is a comparable analysis of the geniculate input to the primary visual cortex of the macaque monkey.

The striate cortex of the monkey differs from that of the cat in a number of ways. In Nissl-stained preparations, for example, it is obvious that the monkey striate cortex contains about twice the number of neurons per unit volume than the cat (e.g., Peters, 1987), and that in the monkey layer IV is greatly expanded into four sublayers that occupy about a third of the depth of the cortex (e.g., see Brodmann, 1905; Lund, 1973). Of the four sublayers in the macaque (Fig. 1), the outermost one, layer IVA, is quite thin and the neurons are small and closely packed. Beneath layer IVA is layer IVB in which the neurons are more loosely packed. This sublayer can be defined by its content of large neurons, the outer cells of Meynert, and in myelin stained preparations it is apparent that the location of layer IVB coincides with the stria of Gennari, which contains many horizontally aligned myelinated axons. Beneath layer IVB is layer IVC, and this is composed of two sublayers. The sublayer most easily recognized in Nissl-stained preparations is the deepest one, layer IVCa, in which the neurons are closely packed and seem to be aligned in vertical rows. Sublayer IVCb contains mostly spiny stellate cells, as does layer IVCa, in which the neurons are more widely separated (see Lund, 1973; Mates and Lund, 1983; Saint Marie and Peters, 1985).

The layers above and below layer IV contain mostly pyramidal cells, and in preparations stained with an antibody to a microtubule-associated protein, MAP2, many of these pyramidal cells can be seen to be arranged into vertical units that Peters and Sethares (1991a) have called "pyramidal cell modules." These modules are centered upon the apical dendrites of the layer V pyramidal cells, groups of which come together to form clusters. These clustered layer V apical dendrites pass through layer IV unaltered, but as they ascend through layer II/III the apical dendrites of the pyramidal cells in those layers add their apical
dendrites to the clusters. Consequently, the clusters become thicker and less defined, until the apical dendrites reach layer I, where they break up into their terminal tufts.

The apical dendrites of the pyramidal cells in layer VIA do not join the clusters. Instead, they form a separate set of groupings, or fascicles, that are more irregular than the clusters, and most of the dendrites in these fascicles form their terminal tufts in layer IV.

It is suggested that the pyramidal cell modules are the basic units of neuronal organization in the striate cortex (Peters and Sethares, 1991a), and that stimulation of different sets of modules by afferents, including those from the lateral geniculate nucleus (LGN), leads to the production of the ocular dominance and orientation columns that can be displayed in the striate cortex (e.g., Hubel and Wiesel, 1968, 1972, 1974). Since these two sets of columnar systems occupy the same cortical space and appear to be independent of each other, an individual pyramidal cell module could be recruited to form a component of each of these two columnar systems. In addition, a given module would respond to stimulation of a specific part of the visual field, since there is a topographic representation of the visual field on the striate cortex (e.g., see Tootell et al., 1988b).

The input to monkey striate cortex from LGN is by way of geniculo-cortical afferents (see Fig. 1) that enter the cortex from the white matter and give off a few branches to layer VI before ascending obliquely to form their terminal tufts in one of the sublayers of layer IV (Blasdel and Lund, 1983; Freund et al., 1989).

The LGN contains six layers of neurons; the two ventralmost layers are called the magnocellular layers because they contain larger neurons than the four parvocellular, or smaller-celled layers that are dorsal to them. In the LGN, however, the inputs from the retinas of the two eyes are segregated, so that optic nerve fibers from one eye terminate on neurons in two of the parvicular layers and one of the magnocellular layers, while the afferents from the other eye terminate in the remaining three layers of the LGN. But all six layers of each geniculate nucleus project to the striate cortex of the cerebral hemisphere on the same side of the brain. There they form asymmetric synapses mainly with dendritic spines and dendritic shafts (Garey and Powell, 1971; Freund et al., 1989).

Layer IVB receives no direct input from the dLGN, while the parvicular layers of the LGN project to layers IVA and IVCB, and the magnocellular layers terminate in layer IVCa. Of these terminations only those in layers IVCa and IVCB have been examined in any depth (Blasdel and Lund, 1983; Freund et al., 1989). Little is known about the input to layer IVA other than it seems that the axon terminals are not to be taken as circular, terminal-poor regions, with the consequence that viewed from above the pattern formed by the axon terminals resembles the walls of a honeycomb (Hendrickson et al., 1978; Blasdel and Lund, 1983).

It should be pointed out that the projections from the retina to the striate cortex via the LGN, are often considered to form two distinct pathways; these are referred to as the M (magnocellular) and P (parvocellular) pathways. To a large degree the signals carried by the two pathways remain segregated and while the neurons in the P pathway that projects to layers IVA and IVCB of striate cortex from the parvicular layers of the dLGN provide for spatial resolution of images and selectivity of color, they have a low contrast sensitivity. On the other hand, the neurons in the M pathway, which involves the magnocellular layers of the dLGN and layer IVCa of striate cortex, are not selective for color, but have high contrast sensitivity and respond well to moving stimuli (e.g., see Livingstone and Hubel, 1984; Merigan and Maunsell, 1993). However, some investigators (Schiller and Logothetis, 1990) consider the two systems as complementary: the M system extends sensitivity in the contrast and dynamic domains, whereas the P system extends sensitivity in the spectral and spatial domains.

The Basic Quantitative Data
The only useful basic quantitative data about the striate cortex and the dorsal lateral geniculate nucleus (dLGN) available in the literature concern the geniculo-cortical inputs from the magnocellular layers of the dLGN to layer IVCa of striate cortex, and from the parvicular layers of the dLGN to layer IVCB of striate cortex. Consequently, these are the only two inputs to striate cortex that will be analyzed quantitatively in this presentation. Obviously, this is only part of the input from the dLGN to striate cortex, since as pointed out, both layer IVA and layer VI also received geniculo-cortical afferents. The extent of the input to layer IVA is not known, but since this layer is so thin, it can be assumed that the number of geniculo-cortical afferents it receives is many fewer than those terminating in layer IVCB. Also, while it is known that both magnocellular and parvicular afferents to striate cortex in the monkey give off minor collateral branches to neurons in layer VI (Hubel and Wiesel, 1972; Blasdel and Lund, 1983; Fitzpatrick et al., 1983; Freund et al., 1989), the extent of this input has not been quantified, and so it cannot be dealt with in the present context.

The Area Occupied by Striate Cortex
There have been a number of calculations of the area occupied by the striate cortex within one cerebral hemisphere (Table 1, A), and the results differ widely. The earliest estimate by LeGros Clark (1941) gives the area occupied by striate cortex as 1445 mm², and this is similar to the estimate of 1320 mm² determined by Daniel and Whitteridge (1961) and that of 1525 mm² obtained by Tootell et al., (1982). The most complete study, however, is that of Van Essen et al. (1984). They examined the brains of 31 Macaca fascicularis and obtained values ranging from 690 to 1560 mm², with a mean value of 1200 mm². A lower mean value was obtained by O’Kusky and Colonnier (1982). They give a mean value of 841 mm² for the area occupied by primary visual cortex in the brains of five macaques.
Figure 1. Micrograph of Nissl-stained section of the striate cortex of *M. mulatta*. The layers are identified on the left, and the inputs from the parvocellular and magnocellular layers of the LGN are shown on the right. The arrows indicate the input from the two populations of LGN axons, and are not meant to imply that all axons have branches that terminate in layers other than IVC.

But it is of special interest for the present purposes that these five brains included three from *Macaca mulatta* and two from *Macaca fascicularis* and that O'Kusky and Colonnier (1982) find no differences between them in the area occupied by striate cortex. With that in mind, for the purposes of subsequent calculations, the mean value of 1200 mm$^2$ obtained by Van Essen et al. (1984) for the largest sample group can probably be used as a reasonable estimate of the area occupied by striate cortex in macaques.

**Lateral Geniculate Nucleus**

**Magnocellular Layers**

There have been at least three estimates of the number of neurons in the LGN of the monkey (Table 1, B1). The first one is that of LeGros Clark (1941), who determined that there are some 209,000 neurons in the magnocellular layers. Utilizing the cell density data obtained by LeGros Clark (1941), but using their own measurements of the thickness and areas occu-
Table 1
Basic data on geniculate and cortical neurons and synapses

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Primary visual cortex surface area</td>
<td>1445 mm²</td>
<td>LeGros Clark, 1941</td>
</tr>
<tr>
<td>1320 mm²</td>
<td>Daniel and Whitteridge, 1961</td>
<td></td>
</tr>
<tr>
<td>1525 mm²</td>
<td>Tootell et al., 1982</td>
<td></td>
</tr>
<tr>
<td>841 mm²</td>
<td>O'Kusky and Colonnier, 1982</td>
<td></td>
</tr>
<tr>
<td>690-1500 mm²</td>
<td>Van Essen et al., 1994</td>
<td></td>
</tr>
<tr>
<td>Mean, 1200 mm²</td>
<td></td>
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</tr>
</tbody>
</table>

B. Magnocellular pathway
1. Number of magnocellular neurons in LGN | 293,000 | LeGros Clark, 1941 |
| 144,000 | Connolly and Van Essen, 1984 |
| 91,000-235,000 | Ahmad and Spear, 1993 |
| Mean, 146,000 | | |

2. Percentage of GABA neurons in LGN | 35% | Montero and Zempel, 1985 |

3. Number of visual relay neurons | 98,200 | line B1 x (100 - line B2) |

4. Area occupied by an axon arbor in layer IVCa of cortex | Two large clumps; mean size, 0.3 mm² | Freund et al., 1989 |

5. Number of boutons per arbor | 3/10 | Blasdel and Lund, 1983 |
| 7.7 x 10⁶/mm² | Blasdel and Lund, 1983 |
| 3200 | Freund et al., 1999 |

6. Number of synapses per bouton | 2.03 and 2.1 | Freund et al., 1989 |

7. Number of neurons in layer IVCa under 1 mm² | 17.3 x 10⁶ | O'Kusky and Colonnier, 1982 |
| 19.2 x 10⁶ | Beaulieu et al., 1992 |

8. Number of synapses in layer IVCa under 1 mm² | a. 37 x 10⁶ | O'Kusky and Colonnier, 1982 |
| b. 55 x 10⁶ | Beaulieu et al., 1992 |

9. Percentage of GABA synapses in layer IV | 25.6% | Beaulieu et al., 1992 |

10. Number of asymmetric synapses in layer IVCa under 1 mm² | a. 27.5 x 10⁶ | line B8 x (100 - line B9) |
| b. 41 x 10⁶ | |

C. Parvocellular pathway
1. Number of parvocellular neurons in LGN | 1.59 x 10⁹ | LeGros Clark, 1941 |
| 1.12 x 10⁹ | Connolly and Van Essen, 1984 |
| 0.8-1.7 x 10⁹ | Ahmad and Spear, 1993 |
| Mean, 1.27 x 10⁹ | | |

2. Percentage of GABA neurons in LGN | 25% | Montero and Zempel, 1985 |

3. Number of visual relay neurons | 950,000 | line 1 x (100 - line 2) |

4. Area occupied by an axon arbor in layer IVCb of cortex | 21 examples of 200 µm diameter = 0.03 mm² | Blasdel and Lund, 1983 |
| 2 arbors of 200 µm diameter = 0.08 mm² | Freund et al., 1990 |
| 1 arbor of 150-200 µm diameter = 0.03 mm² | Freund et al., 1999 |

5. Number of boutons per arbor | 7.4 x 10⁶/mm² | Blasdel and Lund, 1983 |
| 1520 and 1380 | Freund et al., 1989 |

6. Number of synapses per bouton | 1.79 and 2.6 | Freund et al., 1989 |

7. Number of neurons in layer IVCb under 1 mm² | 30 x 10⁶ | O'Kusky and Colonnier, 1982 |
| 27.5 x 10⁶ | Beaulieu et al., 1992 |

8. Number of synapses in layer IVCb under 1 mm² | a. 44 x 10⁶ | O'Kusky and Colonnier, 1982 |
| b. 78 x 10⁶ | Beaulieu et al., 1992 |

9. Percentage of GABA synapses in layer IV | 25.6% | Beaulieu et al., 1992 |

10. Number of asymmetric synapses in layer IVCb under 1 mm² | a. 32.7 x 10⁶ | line C8 x (100 - line C9) |
| b. 58.8 x 10⁶ | |

...
tween 91,000 and 235,000 for the total number of neurons in the magnocellular layers. Ahmad and Spear (1993) give a mean value of 148,000 for the total number of neurons in the magnocellular layers, and since this is the most recent and complete estimate of the number of neurons in the magnocellular layers of the LGN of the monkey, and not too different from that obtained by Connolly and Van Essen (1984), this is the value that will be adopted in the calculations that are to follow.

Given that the mean number of neurons in the magnocellular layers of the LGN is 148,000, the next question that arises is, what proportion of them project to the striate cortex? It is known that the LGN contains both projection and local circuit neurons, and since the latter use GABA as their neurotransmitter, a determination of the proportion of local circuit neurons can be obtained by using antibodies to GABA. On this basis Montero and Zempel (1986) estimate that 35% of the neurons in the magnocellular layers of the LGN are local circuit neurons (Table 1, B2). And subsequently, in a study in which neurons in the LGN were labeled with horseradish peroxidase (HRP) retrogradely transported from the striate cortex, Montero (1986) showed that none of the HRP-labeled neurons bind antibodies to GABA. Only neurons not containing transported HRP were GABA immunopositive. From these values we can assume that an average of 96,200 magnocellular neurons relay visual signals to area 17 (Table 1, B3).

It should be pointed out, however, that in an earlier study in which injections of the HRP were made into striate cortex, Norden and Kaas (1978) estimated that between 94% and 99% of the neurons in the LGN of the rhesus and owl monkeys are relay neurons. Thus, they conclude that the primate LGN contains almost no interneurons. This seems unlikely, because Smith et al. (1987), for example, have also shown that the LGN and other thalamic nuclei in the squirrel monkey also contain significant numbers of GABAergic, or inhibitory neurons.

**Parvicellular Layers**

LeGros Clark (1941) estimated that there are some $1.59 \times 10^6$ neurons in the four parvocellular layers of the LGN (Table 1, C1), and in their calculations based on the neuronal density values given by LeGros Clark (1941), Connolly and Van Essen (1984) arrived at an estimate of $1.12 \times 10^6$ neurons. As with the magnocellular layers, the most comprehensive estimate of the number of parvocellular neurons is the one produced recently by Ahmad and Spear (1993). In the five young rhesus monkeys examined they obtained values ranging between 0.9 and $1.7 \times 10^6$ for the total number of neurons in the parvocellular layers, with a mean value of $1.27 \times 10^6$ neurons (Table 1, C1). This is about nine times more neurons than are present in the magnocellular layers. For the reasons given above, this mean value obtained by Ahmad and Spear (1993) is the one that will be used in the subsequent calculations, and on the basis of the study by Montero and Zempel (1986), using antibodies to GABA, it can be surmised that the percentage of neurons in the parvocellular layers of the dLGN that are local circuit neuron containing GABA is 25% (Table 1, C2). From these values we can assume that 950,000 parvocellular neurons relay visual signals to area 17 (Table 1, C3). This is 10 times the number of magnocellular relay neurons.

**Numbers of Boutons and Synapses in Geniculate Axon Arbors in the Striate Cortex**

**Magnocellular Arbors in Layer IVCa**

Blasdel and Lund (1983) revealed the extent of geniculocortical axon arbors by injecting HRP either into single axons or into the white matter beneath the striate cortex. They recovered 38 apparently completely filled axons. Five of them had relatively thick trunks and formed terminal arborizations in layer IVCa. One of the axons had an arborization 0.3 mm wide and 1.2 mm long, so that in the tangential plane it covered a total surface area of 0.4 mm² (Table 1, B4). Blasdel and Lund (1983) determined that this arborization had 3085 boutons, or a density of $7.7 \times 10^3$ boutons beneath each square millimeter of cortical surface (Table 1, B5). In another study (Freund et al., 1989) two magnocellular axons were impaled and filled with HRP. Both of these axons arborized in layer IVCa, where they formed elongated clumps of terminal boutons 300–500 × 600–1200 µm in size, and from the top reconstructed view that Freund et al. (1989) provide of one magnocellular axon (see their Fig. 1D), the arbor extends over an area of about 0.3 mm² (Table 1, B4). In the one arbor in which Freund et al. (1989) counted the number of boutons, they found that it contained 3200 boutons (Table 1, B5), which is very similar to the number of boutons in the arbor examined by Blasdel and Lund (1983).

In addition, Freund et al. (1989) examined two geniculocortical arbors by electron microscopy to determine the number of synapses formed by boutons. They determined that in one arbor individual boutons formed an average of 2.03 synapses, while the boutons in the arbor of the second magnocellular axon produced an average of 2.1 synapses (Table 1, B6).

**Parvocellular Arbors in Layer IVCB**

Both Blasdel and Lund (1983) and Freund et al. (1989) also filled parvocellular geniculocortical axons with terminal fields in layer IVCB of striate cortex. Blasdel and Lund (1983) record that they recovered 21 axons with terminal arbors in layer IVCB and that in each arbor the terminals spread no farther than 200 µm laterally, so that relative to the cortical surface they would typically cover an area of 0.03 mm² (Table 1, C4), or 1/10 of the area occupied by a single magnocellular axon. They further state that in terminal clusters the density of boutons is $7.4 \times 10^3$ boutons/mm² (Table 1, C5). Freund et al. (1989) give data about two parvocellular axons terminating in layer IVCB, one of which arborized to form two clumps of boutons, each clump being 200 µm in diameter, while the other one formed a single clump of boutons 150–
Although Beaulieu et al. (1992) do not give a value for the synapse-to-neuron ratio of 2879. Consequently, it can be determined that according to their data the number of synapses beneath 1 mm² of cortical surface is 55 x 10⁶ (Table 1, B8). These values are much higher than those obtained by O’Kusky and Colonnier (1982), and Beaulieu et al. (1992) suggest, quite reasonably, that the differences can probably be attributed to the use of different formulas to make the calculations. In any event, when we subtract the number of GABAergic, symmetric, synapses from these numbers, we determine that between 27.5 x 10⁶ and 41 x 10⁶ asymmetric synapses are present in layer IVCa beneath each square millimeter of cortical surface (Table 1, B10).

**Layer IVCa**

As stated above, in layer IVCa the numbers of boutons and synapses in layer IVCa beneath each square millimeter of cortical surface are 1.79 and 2.6 for the two arborizations (Table 1, C6).

Since the axon terminals of the geniculocortical input to layer IVCa form asymmetric, or excitatory synapses (e.g., see Winfield et al., 1982; Freund et al., 1989), it is useful to know what proportion of the total number of synapses in layer IVCa are of this type. No direct counts of asymmetric synapses appear to have been made, but the proportion of GABAergic synapses that are symmetric in morphology and inhibitory in function has been determined by Beaulieu et al. (1992), by labeling axon terminals with antibodies to GABA. They have calculated that 25.6% of the synapses in layer IVCa as a whole are GABAergic (Table 1, B9 and C9). Consequently, it can be concluded that 74.4% are asymmetric ones.

**The Magnocellular Input**

The Number of Geniculocortical Axon Terminals in Layer IVCa of Striate Cortex Derived from the Magnocellular Layers of the LGN

As stated above, in layer IVCa the numbers of boutons have been counted in two axonal arbors. In one axonal arbor, Blasdel and Lund (1983) counted 3085

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Source</th>
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</thead>
<tbody>
<tr>
<td>1. Number of boutons per arbor</td>
<td>3085-3200</td>
<td>Table 1, B4</td>
</tr>
<tr>
<td>2. Number of synapses per arbor</td>
<td>626/6720</td>
<td>line A1 + Table 1, B8</td>
</tr>
<tr>
<td>3. Number of geniculocortical axons</td>
<td>96,200</td>
<td>Table 1, B3</td>
</tr>
<tr>
<td>4. Total number of magnocellular synapses</td>
<td>602-946 x 10⁶</td>
<td>line A2 + line A3</td>
</tr>
<tr>
<td>5. Number of magnocellular synapses beneath 1 mm² of cortical surface</td>
<td>0.5-0.54 x 10⁶</td>
<td>line A4 + line A1</td>
</tr>
<tr>
<td>6. Total number of asymmetric synapses beneath 1 mm² of cortical surface</td>
<td>27.5-41 x 10⁶</td>
<td>Table 1, B10</td>
</tr>
<tr>
<td>7. Percentage of magnocellular synapses in layer IVCa</td>
<td>1.3-1.9%</td>
<td>line A5 + line A6</td>
</tr>
<tr>
<td>8. Number of geniculocortical synapses per layer IVCa neuron</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Total number of synapses per neuron</td>
<td>1.9 x 10⁶</td>
<td>O’Kusky and Colonnier, 1982</td>
</tr>
<tr>
<td>2. Percentage of non-GABAergic synapses</td>
<td>74.4%</td>
<td>Beaulieu et al., 1992</td>
</tr>
<tr>
<td>3. Number of asymmetric synapses per neuron</td>
<td>1.4-2.1 x 10⁶</td>
<td>line B1 × line B2</td>
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<tr>
<td>4. Number of geniculocortical synapses per neuron</td>
<td>18-40</td>
<td>line B3 × line A7</td>
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Table 3.
Calculations and estimates about the parvocellular input to layer IVCa of striate cortex

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Number of boutons per arbor</td>
<td>a. 1520 and 1380 b. 222</td>
</tr>
<tr>
<td>2. Number of synapses per arbor</td>
<td>2720-3588</td>
</tr>
<tr>
<td>3. Number of geniculocortical axons</td>
<td>950,000</td>
</tr>
<tr>
<td>4. Total number of geniculocortical synapses</td>
<td>2580-3409 x 10^6</td>
</tr>
<tr>
<td>5. Number of parvocellular synapses beneath 1 mm^2 of cortical surface</td>
<td>2.15-2.84 x 10^6</td>
</tr>
<tr>
<td>6. Total number of asymmetric synapses beneath 1 mm^2 of cortical surface</td>
<td>32.7-58.8 x 10^6</td>
</tr>
<tr>
<td>7. Percentage of parvocellular synapses in layer IVCa</td>
<td>3.7-8.1%</td>
</tr>
<tr>
<td>B. Number of geniculocortical synapses per layer IVCa neuron</td>
<td></td>
</tr>
<tr>
<td>1. Total number of synapses per neuron</td>
<td>1.4 x 10^6</td>
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<tr>
<td>2. Percentage of non-GABAergic synapses</td>
<td>74.4%</td>
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<tr>
<td>3. Number of asymmetric synapses per neuron</td>
<td>1.8-2.2 x 10^6</td>
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<tr>
<td>4. Number of geniculocortical synapses per neuron</td>
<td>37-191</td>
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</tbody>
</table>

The Parvocellular Input

The Number of Geniculocortical Axon Terminals in Layer IVCa of Striate Cortex Derived from the Parvocellular Layers of the LGN

The only two counts of the numbers of boutons in geniculocortical axonal arbor terminating in layer IVCa of striate cortex are those made by Freund et al. (1989). They found one arbor to have 1520 boutons (axon PA1) and the other to have 1380 boutons (axon PA2) (Table 1, C5; Table 3, A1). In their study, Blasdel and Lund (1983) examined 21 axonal arbors in layer IVCa, but they give no individual counts of the numbers of boutons in these arbors. However, they state that an arbor occupies an area of 0.03 mm^2 and in regions where there are tight clusters of boutons the concentration of boutons is 7.4 x 10^6 boutons/mm^2. From these values given by Blasdel and Lund (1983) it can be estimated that each axonal arbor would contain only 222 boutons (Table 3, A1). This number is extraordinarily small in comparison with the counts made by Freund et al. (1989) and its use would lead to an extremely low value for the percentage of synapses in layer IVCa that are derived from the LGN. With this in mind, the calculations concerning the geniculate input to layer IVCa will be made using the counts given by Freund et al. (1989).

Since axon PA1 formed an average of 1.79 synapses per bouton, and axon PA2 averaged 2.6 synapses per bouton (Table 1, C6), axon PA1 formed 2720 synapses and axon PA2 formed 3588 synapses (Table 3, A2). Assuming that all 950,000 parvocellular relay neurons project to layer IVCa (Table 3, A3), the total number of geniculocortical synapses in that layer throughout the cortex would be 2580-3409 x 10^6 (Table 3, A4), and if the surface area of the striate cortex is taken to average 1200 mm^2, then there are 2.15-2.84 x 10^6 geniculate synapses beneath 1 mm^2 of cortical surface (Ta-
These synapses comprise 3.7–8.7% of the 32.7–58.8 x 10^6 asymmetric synapses beneath 1 mm^2 of cortical surface (Table 3, A6 and A7). In absolute numbers and in percentages, this is three to four times greater than the number of asymmetric synapses contributed to layer IVCa by axons from the magnocellular layers of the LGN.

The Number of Geniculocortical Synapses per Neuron in Layer IVCβ
O'Kusky and Colonnier (1982) calculate that the synapse-to-neuron ratio in layer IVCβ is 1.4 x 10^4, while Beaulieu et al. (1992) give a general value of 2.9 x 10^5 synapses per neuron for all neurons in layer IVC. Using these two values, if 74.4% of the synapses in layer IVC are non-GABAergic and asymmetric in type, then each neuron would have 1.0–2.2 x 10^5 asymmetric synapses (Table 3, B3). This range of values is similar to the number of asymmetric synapses formed by layer IVCa neurons (Table 2, B3). Since it has been calculated in the previous section that 3.7–8.7% of all asymmetric synapses in layer IVCβ are derived from neurons in the parvicellular layers of the LGN (Table 3, A7), then each neuron in layer IVCβ would form 37–191 synapses with geniculate axons. Again, this wide range is due to the differences in the values for the numbers of neurons and synapses given by O'Kusky and Colonnier (1982) and by Beaulieu et al. (1992).

Geniculocortical Afferents and Pyramidal Cell Modules
As stated at the beginning of this article, Peters and Sethares (1991a) have postulated that the striate cortex is composed of repeating modules of pyramidal cells, and that these represent the basic units of neuronal organization. It is proposed that these modules are centered on the clustered apical dendrites of the layer V pyramidal cells, and since these clusters of dendrites have a center-to-center spacing of 30 μm, it is proposed that this is the mean diameter of a module. If the modules approximate the forms of cylinders, then each one has a cross-sectional area of about 700 μm^2 (Table 4, A2), and if the area occupied by striate cortex is taken to be 1200 mm^2, then one hemisphere contains some 1.7 x 10^6 pyramidal cell modules (Table 4, A3).

Blasdel and Lund (1983) have measured the sizes of 21 parvocellular axonal arbors in layer IVCβ and found the arbors to all have a similar appearance and to spread no farther than 200 μm laterally. Since the terminal fields of the axonal arbors are essentially circular, this means that a typical parvocellular axon arbor covers an area of some 0.03 mm^2 (Table 1, C4). The axonal arbors examined by Freund et al. (1989) have a similar size (Table 1, C4), and so it can be calculated that a typical parvocellular axonal arbor extends over an area of 0.03 mm^2 in layer IVCβ (Table 4, B1) and encompasses 40 pyramidal cell modules (Table 4, B2). In contrast, the spread of the magnocellular arbors in layer IVCa is 10 or more times greater (Table 1, B4), and they each encompass some 400–570 pyramidal cell modules (Table 4, C2).

Another aspect of the innervation of the striate cortex to consider is the convergence of the geniculocortical afferents on to pyramidal cell modules and their neurons. As shown earlier, the number of parvocellular axons projecting on to striate cortex is 950,000 (Table 4, B3), and if each axon produces an arbor that covers an area of 0.03 mm^2, then collectively the arbors of all of the parvocellular axons would spread over an area of 28,500 mm^2. But instead, these arbors are confined to the area occupied by the striate cortex, which is 1200 mm^2, so that the number of axonal arbors that overlap, or converge on the neurons of a single pyramidal cell module within layer IVCβ, is 24 (Table 4, B4). For the magnocellular input, if there are 96,200 projection neurons in the magnocellular layers of the LGN (Table 4, C3) and the spread of an average axonal arbor in layer IVCa is 0.3–0.4 mm^2 (Table 4, C1), then 24–32 magnocellular axonal arbors in layer IVCa converge upon each pyramidal cell module (Table 4, C4).
Discussion

There is obviously a wide range in the results of the numerical analyses based on the data available about the geniculocortical input to striate cortex and, in the calculations that have been presented here, this is largely a consequence of the differences in the data generated by O'Kusky and Colonnier (1982) and Beaulieu et al. (1992) about the numbers of neurons and synapses in the striate cortex. However, the range in the results would have been even wider if instead of using the mean values for the area occupied by the striate cortex (Table 1, A) and the numbers of neurons in the LGN (Table 1, B and C), account had been taken of the differences among animals as recorded by various authors. If these differences are real, and presumably they are because the same authors have recorded differences among animals, it would be useful to know whether there is a constant relationship between such factors as the number of neurons in the LGN and the area occupied by the striate cortex. For example, do those monkeys with the fewest neurons in the LGN have the smallest striate cortices and the monkeys with the greatest numbers of neurons in the LGN have the largest striate cortices, or is there no such correlation? If there is a constant relationship, it might be predicted that the proportion of synapses that layer IV neurons receive from the LGN is also relatively constant.

Another problem that has to be considered is whether there are significant differences among species of monkeys. It seems to be generally assumed that there are not, but it should be borne in mind, for example, that the extensive data that Van Essen et al. (1984) have generated about the area occupied by striate cortex was obtained using Macaca fascicularis, while the most complete data for the numbers of neurons in the dLGN has been generated by Ahmad and Spear (1993) in their analysis of the geniculo-cortical afferents to striate cortex, for they used Macaca nemestrina, and Blasdel and Lund (1983) used both Macaca nemestrina and Macaca fascicularis. The basic point is that at present there are no sets of numerical data available that have been derived from only one species of monkey.

Relationship between Geniculate Axon Arbors and the Columnar Systems

It is generally accepted that in addition to a retinotopic representation, there are three systems of columns in the primate striate cortex. These are the ocular dominance and orientation columns, which take the form of vertical bands spanning the cortical depth (e.g., Hubel and Wiesel, 1968, 1974; LeVay et al., 1975, 1985), and the system of high-density cytochrome oxidase (CO) blobs that occur in layers II and III and contain cells that respond selectively to colors. The circuitry underlying these systems is not yet known, but it is generally assumed that the eye preference columns, at least, depend directly upon the thalamic input for their manifestation, and that thalamic axons carrying signals from each eye via the segregated layers of the LGN are lined up within layer IV in alternate rows that extend throughout the binocular representation in striate cortex (LeVay et al., 1985). When viewed from the surface in preparations in which the eye preference columns, or stripes, have been revealed through the use of degeneration techniques (e.g., Hubel and Wiesel, 1972), transport of radioactive amino acids (e.g., Wiesel et al., 1974; LeVay et al., 1985), a reduced silver method (LeVay et al., 1975; Hubel and Freeman, 1977), the use of 2-deoxyglucose (Tootell et al., 1988a), or diminished activity of chemical markers following unilateral enucleation (Horton, 1984), it is found that the stripes have a relatively constant width, although the width varies with the species of monkey examined (see Tootell et al., 1988a), and the technique used. But in general the stripes vary in width only between 0.3 and 0.4 mm, regardless of whether these widths are measured in layer IV or in IVB. The width matches the diameter of magnocellular afferents, which have been shown to terminate within labeled stripes following injections of radioactive tracers into an eye that has been activated (Blasdel and Lund, 1983). So presumably magnocellular axons are aligned in an orderly way along the ocular dominance stripes in layer IV.

Since the diameters of the parvocellular axon arbors are only a fraction of the width of the ocular dominance stripes in layer IV, parvocellular axons must be aligned both along and across the ocular dominance stripes. Even so, parvocellular axons relaying signals from one eye are in register with the magnocellular axons that relay signals from the same eye and from the same parts of the visual field (Hubel and Wiesel, 1977; Blasdel and Fitzpatrick, 1984), and one can only be impressed by the sharpness of coincidence of the boundaries of the stripes in layers IV and IVB.

While the match between LGN afferent terminations and the physiologically defined ocular dominance columns is now well established, much less is known about the role of the geniculo-cortical afferents in the generation of orientation preference columns (Blasdel, 1992a,b). The signals necessary for generating orientation selectivity must be carried by the geniculo-cortical afferents. But how the signals are combined to produce the orientation columns is not known, although a number of circuits have been proposed (e.g., see Martin, 1988).

At the beginning of this article it was pointed out that some of the geniculo-cortical afferents from the parvicular layers of the cortex terminate in layer IVA, where the arbors produce a thin sheet of terminals that surround spaces (Blasdel and Lund, 1983). Consequently, when viewed in tangential sections the pattern of termination resembles the CO lattice pattern that is evident in layer IVA (Hendrickson et al., 1978; Horton, 1984; Fitzpatrick et al., 1985; Peters and Sethares, 1991b). How many of the parvicular afferents contribute to the geniculo-cortical input to layer IVA is not known, nor is the function of the input. However, a number of authors have found that the neurons in layer IVA respond to color (e.g., Michael,
differences observed were independent of eccentricity over layer IVCa. In the second part of their study, on average, 1.9 times greater over layer IVCa than over layer IVCb. Counts of autoradiographically generated silver grains in the two layers produced numbers that were, on average, 1.9 times greater over layer IVCb than over layer IVCa. In the second part of their study, Livingstone and Hubel injected HRP into area 17 and found, on average, 5.4 times more neurons labeled in the parvocellular layers of the LGN than in the magnocellular layers. In both parts of the study, the differences observed were independent of eccentricity in the visual field map in area 17. These values are important because they establish the generality of the differences in the magnocellular and parvocellular innervation density across the striate cortex, and because they bracket the values that we have calculated.

Irrespective of the differences between innervation densities in layers IVCa and IVCb, the absolute numbers and proportions of geniculate synapses in striate cortex are very small. Even though some estimates suggest that afferents to area 17 from non-LGN sources outnumber those from the LGN (Doyt, 1983), the contribution the nongeniculate sources make to the input to layers IVCa and IVCb appears minor (Benevento et al., 1975; Oogren and Hendrickson, 1976; Rockland and Pandya, 1981; Felleman and Van Essen, 1991). Consequently, we conclude that although the LGN is the dominant source of extrinsic signals to layer IVC, the vast majority of synapses formed by layer IVC neurons are with axons intrinsic to area 17, and most likely from pyramidal cells.

The very small size of the LGN innervation of layers IVCa and IVCb is surprising and it can be reasonably assumed that these separate inputs do not overlap or converge to any great extent onto individual neurons, since the axonal arbors are basically confined to their respective sublayers, and the spiny stellate cells of layer IVC, which are presumably the main recipients of the geniculo cortical inputs, have rather confined dendritic trees (Lund, 1973, 1987; Valverde, 1985; Saint Marie and Peters, 1985). Although the percentages of asymmetric synapses that are calculated to be derived from the geniculo cortical input in the monkey are low, the values are not too different from the 5–10% of axonal terminals that Garey and Powell (1971) found to be degenerating in layer IV of the monkey visual cortex after making large lesions in the LGN. However, the percentage is much lower than that recorded in layer IV of the squirrel monkey by Tigges and Tiggles (1979). They found that 3 days after making a lesion in the LGN 16.2% of the terminals in layer IV showed signs of degeneration, and this number rose to 19.3% in animals examined 5 days postlesion.

Assuming that the numerical analyses presented here are correct, and that 1.3–1.9% of the synapses in layer IVCa and 3.7–8.7% of the synapses in layer IVCb of monkey striate cortex are derived from the LGN, this would mean that the geniculo cortical input amounts to 18–40 synapses per neuron in layer IVCa (Table 2, B4), and 37–188 synapses per neuron in layer IVCb (Table 3, B4). But it should be pointed out that these numbers represent upper limits; they do not take into account that layer IV contains neuronal elements other than the spiny stellate cells that reside within it. Some of the geniculo cortical afferents to layer IVC terminate on such neuronal elements as the ascending dendrites of layer V and layer VIA pyramidal cells (e.g., Peters et al., 1979; Freund et al., 1989; White, 1989), but the proportion of the geniculo cortical axon terminals that synapse with these other neuronal elements is not known.

Another question concerns the types of postsynaptic elements with which the geniculo cortical afferents synapse. In their degeneration study Garey and Powell (1971) examined several hundred degenerating axon terminals and found 84% of them to syn-
apse with dendritic spines, 14% with dendritic shafts and 2% with cell bodies, while Winfield and Powell (1983) and Winfield et al. (1982) found about 90% of the degenerating terminals to synapse with dendritic spines. These are quite different values from that obtained by Freund et al. (1989) when they examined the filled axonal arbors of two parvcellular axons and of two magnocellular axons. They found the labeled magnocellular and parvcellular axons to synapse with similar proportions of postsynaptic elements; 52–68% of the axon terminals synapsed with dendritic spines, 33–47% with dendritic shafts and 0–3% with neuronal cell bodies. This is another discrepancy in the data that needs to be resolved.

Convergence of Geniculate Axons onto Cortical Modules and Layer IVC Neurons

Based upon the number of projection neurons in the parvcellular layers of the LGN and the sizes of their axonal arbors, it has been calculated that 24 axonal arbors overlap at any one point in layer IVC\beta of striate cortex (Table 4, B4). If the boutons in their arbors are spread evenly, then any axonal arbor would provide between two and eight of the total number of 37–188 synapses that a layer IVC\beta spiny stellate cell has been calculated to receive. This is only a small fraction of the 100 active synapses that Douglas and Martin (1991) have calculated to be necessary to generate an output discharge from spiny neurons. What this means is that for a spiny stellate cell in layer IVC\beta to generate an action potential, it would require virtually all of the geniculocortical synapses it receives to be active within a few milliseconds of each other.

Interestingly, the convergence of magnocellular axonal arbors onto individual cortical neurons is similar to that of the parvcellular axons, since it is calculated that 24–32 magnocellular axons converge onto an individual neuron in layer IVC\alpha. This comes about because although there are about 10 times more parvcellular neurons in the LGN than magnocellular neurons, the spread of the axonal plexuses of the parvcellular axons is about 1/10 of that of the magnocellular axons. In the case of the magnocellular axons, however, if the spread of the magnocellular axons is even, then any particular arbor would only contribute one or two of the total number of 18–40 geniculocortical synapses that a neuron in layer IVC\alpha is calculated to receive. And even if all of these geniculocortical synapses upon a particular layer IVC\alpha neuron are active at the same time, on the basis of the calculations of Douglas and Martin (1991) they would be insufficient to evoke an action potential.

However, it should be borne in mind that monkey striate cortical neurons are much smaller than cat neurons, which formed the basis for Douglas and Martin's (1991) calculations. Based on information given by Henneman and Mendell (1981), Wilson (1989) suggests that smaller neurons have a higher overall membrane resistance than larger neurons and that smaller neurons require fewer active synapses to achieve the necessary current density for activation. If this argument pertains to monkey striate neurons, then 18–40 geniculocortical synapses may be sufficient to activate layer IVC\alpha neurons.

The difference in innervation density of layer IVC\alpha and IVC\beta is not reflected in current source density analyses of neuronal circuits. The current source density method analyzes the depth profiles of extracellular field potentials, generated by the synchronous stimulation of afferent fibers, to reveal the locations and latencies of excitatory activity of populations of neurons. In well-laminated systems, such as striate cortex, and well-defined fiber populations, such as those from the LGN, it is possible to reveal the mono-, di- and trisynaptic circuits provided that the circuits are stereotyped. Mitzdorf and Singer (1979) have carried out a current source density analysis of LGN input to area 17 in the macaque and have shown, as expected from the known faster-conducting input from the magnocellular layers, that layer IVC\alpha is activated prior to layer IVC\beta. Moreover, they find that the current densities evoked in layers IVC\alpha and IVC\beta are substantial and of similar magnitudes. These observations are surprising given the low density of innervation of layer IVC as a whole, and they illustrate that visual signals are particularly efficacious at activating layer IVC\alpha neurons, which receive less LGN input than IVC\beta neurons. Possible bases for the greater efficacy of the magnocellular pathway include release of greater amounts of transmitter at magnocellular fiber synapses, compared to parvcellular fiber synapses, or differences in the layer IVC\alpha neuron membrane properties that permit greater inward current flow compared to layer IVC\beta neurons. In addition, Mitzdorf and Singer's (1979) study reveals substantial di- and trisynaptic circuits, which emerge from both layers IVC\alpha and IVC\beta and reach neurons located in the superficial and deep layers of cortex. But more importantly, at least from the point of view of this article, they demonstrate the existence of substantial di- and trisynaptic circuits within layers IVC\alpha and IVC\beta.

Anatomical tracing studies also show pathways arising from layers IVC\alpha and IVC\beta, but provide little evidence for pathways within the two IVC sublayers. For example, Fitzpatrick et al. (1985) injected small amounts of HRP to expose axon terminals and neurons in very limited regions (100–200 \mu m) within each cortical layer. In agreement with the data of Mitzdorf and Singer (1979), Fitzpatrick et al. (1985) were readily able to demonstrate substantial projections emanating from layer IVC to reach superficial and deep layers, but they obtained little evidence for substantial circuits within layer IVC. This latter result of Fitzpatrick et al. (1985) is surprising since the data of Kisvarday et al. (1989), who used tritiated aspartate to examine excitatory connections, show substantial local connections. Aspartate is an excitatory transmitter and it is taken up by axon terminals and retrogradely transported to neuronal cell bodies. This experiment showed rich connections within layer IVC, but even more restricted and localized projections within layer IVC\beta. Following small deposits of
The local circuits may be more important in layer IVCa and they may have additional functions. It is generally recognized that neurons in layer IVCa, as well as those in layer IVCβ, have small monocular receptive fields and that they can be activated by line stimuli of any orientation, just as can their afferent neurons in the LGN (Hubel and Wiesel, 1977). However, evidence is accumulating (Schiller et al., 1976; Bullier and Henry, 1980; Blasdel and Fitzpatrick, 1984) that distinct subpopulations in layer IVCa, if not the majority of layer IVCa neurons, show selectivity for line stimulus orientation. Sensitivity to stimulus orientation is a sophisticated and emergent property of cortical neurons, and it requires complex and fundamentally different circuitry from that used by the non-orientation-selective cells, which essentially mime the properties of their afferent neurons in LGN.

The greater complexity of the orientation-selective generating circuits might lead one to expect that compared to the slavish, non-orientation-selective layer IVCβ cells, a greater proportion of the synapses received by layer IVCa neurons originate from intracortical axons. If this is the case, the net effect would be to reduce the fraction of synapses formed by LGN afferents with layer IVCa neurons compared to layer IVCβ neurons.

**Comparison of the retino-geniculo-striate pathway in cat and monkey**

It has recently been proposed that the basic layout, pattern of connections, and functional components of the cortical visual system in cats and monkeys are similar (Payne, 1993). How does the pathway from the retina to area 17 in the two animals compare? In both animals there is a similar and substantial amplification in the number of communication channels between the retina and the geniculocortical recipient neurons in striate cortex. As can be seen from the numbers that follow, the process of amplification occurs in two stages in the cat, whereas in the monkey it occurs in a single stage. In the cat there are 160,000 retinal ganglion cells (Williams et al., 1986), of which some 60%, or 90,000 form the origin of the pathway to striate cortex (Illing and Wassle, 1981; Leventhal et al., 1985). In the cat LGN there are some 360,000 relay neurons in layers A and A1 (Williams et al., 1993) and these terminate on about 1 x 10⁷ neurons in area 17 (Peters and Payne, 1993). Thus, there is a progressive amplification, which is modest at the retinogeniculate connection (4 x) and substantial at the geniculocortical linkage (25 x), but which results in a total amplification of 100 x. In contrast, in the monkey there are 10 times more ganglion cells giving rise to the retinogeniculate pathway (about 1 x 10⁸; Sanchez et al., 1986; Morrison et al., 1989) than there are in the cat, but in the monkey these ganglion cells synapse with a similar number of LGN neurons (about 1 x 10⁷; Ahmad and Spear, 1993). However, in turn the LGN neurons synapse with some 56 x 10⁷ neurons in layer IV of striate cortex (O’Kusky and Colonnier, 1982; Beaulieu et al., 1992). Thus, in the monkey pathway there is no amplification at the retinogeniculate stage (1 x), but a massive amplification (56 x) at the geniculocortical linkage. Beyond this latter linkage, the amplification within monkey striate cortex probably catches up, or even surpasses, any additional amplification in the cat striate cortex, because there are twice as many neurons per unit volume in the striate cortex of the monkey than there are in the cat (Peters, 1987).

In both cat and monkey there are marked discrepancies in values that have been obtained experimentally for the percentage of axon terminals and synapses derived from geniculocortical afferents. As indicated earlier, based on experimental degeneration studies, the experimental values in monkey vary between 5% and 19.3% and the calculated values from data in the literature fall between 1.3% and 8.3%. In the numerical analysis that we made previously of the geniculocortical afferents to area 17 of the cat (Peters and Payne, 1993), it was calculated that 5% of the total number of asymmetric synapses in layer IV are derived from the X- and Y-cells of the dLGN. This is about the same percentage of terminals that have been found to degenerate after large lesions are made in the dLGN (e.g., Garey and Powell, 1971; Hornung and Garey, 1981), but much lower than the 22% (Einstein et al., 1987) or 28% (LeVay and Gilbert, 1976) of terminals found to be labeled following injections of tritiated proline into dLGN.

At present there seems to be no way to reconcile these two sets of disparate data that exist for the geniculocortical input to both the cat and monkey visual cortices, and it is usual to suggest that the differences are due to problems inherent in the experimental approaches. For example, there are always doubts expressed about whether all of the terminals of lesioned neurons are degenerating simultaneously, and whether small radioactively labeled molecules diffuse from one terminal to another. But, at least, the approach of injecting individual axons with tracers is not subject to such errors, although the cost of animals and time is high, and the available sample is very small (Blasdel and Lund, 1983; Freund et al., 1989). Nevertheless, the size of the geniculocortical axon sample needs to be increased considerably, so that we can be confident that the numbers of boutons stated to be formed by individually labeled axons are an accurate reflection of the population as a whole. This needs to be done because information about the numbers of geniculocortical afferents each layer IVC neu-
ron receives is fundamental to understanding the circuitry that underlies the response properties of layer IVC neurons. Indeed, it is surprising that, with all the attention that is paid to the fundamental response properties of cortical neurons, and the continued shift in research emphasis to extrastriate cortex, this basic piece of information on the entryway to visual cortex is missing.

In any event, it is interesting to note that there are substantial other similarities in geniculostriate connections in monkey and cat. For example, 24–32 magnocellular axons and a similar number of 24 parvocellular axons converge or overlap beneath one point on the surface of monkey visual cortex and similar numbers of 360–540 X-axons and 300–540 Y-axons converge in primary visual cortex of the cat (Peters and Payne, 1993). Moreover, the average numbers of synapses formed by individual axons with single layer IV neurons are within the same range in both animals, one to eight in monkey and one to four in cat. Thus, in both animals there is an extensive convergence of geniculocortical afferents onto any one neuron, with the probability that an individual axonal arbor provides one or only a few synapses to a given neuron. Consequently, it seems very unlikely that any one geniculocortical afferent in either the cat or the monkey could dominate the activity of a particular cortical neuron.

Despite the problems posed by the reasonings presented above, there is no doubt that signals conveyed by the geniculocortical afferents are potent. These signals are the ones principally responsible for the functional characteristics of striate neurons and the large number of neurons throughout the cortical visual system. But from the low numbers of geniculocortical synapses received by layer IVC neurons, it seems unlikely that the LGN input is sufficient by itself. It may be that selected signals are multiplied by positive feedback circuits within area 17, circuits that lead to an explosive amplification in neural activity. Indeed, as suggested by Douglas et al. (1989) in the consideration of their canonical model for neocortex, it seems to be the intrinsic, or intracortical connections between neurons that provide most of the excitation received by cortical neurons. If this is so, the role of the geniculate signals may be to provide only the initial fuse, which sets the local circuits into activity. But we are left with a major question: how do so few geniculocortical synapses get the process started?

Notes
This work was supported by Grant NS 07016 to A.P. and Grant NS 32137 to B.R.P from the National Institute of Neurological Disease and Stroke of the National Institutes of Health.
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