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What Are the Local Circuits?

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Abstract. Intrinsic circuitry of the cerebral cortex is rich and varied. Current structure–function correlations depend upon a variety of techniques including: Golgi analysis of the axons of cortical neurons, laminar and cellular distributions of thalamic afferent fibers, intracellular injection of physiologically characterized cells, receptive field analysis, selective blockade of inputs to individual layers, and immunocytochemistry. These studies reveal that neurons in almost every layer are capable of being monosynaptically activated by thalamic inputs, and that thalamic or intrinsic interlaminar connections may predominate in the setting up of the receptive fields of neurons in individual layers or of particular types. A certain degree of controversy prevails regarding the role of gamma aminobutyric acid in cortical function and regarding that of interlaminar connections in the generation of certain kinds of receptive fields. To date, most physiological data acquired regarding internal cortical circuitry derive from studies of the two dendritic spine-bearing varieties of cortical neuron, and conjectures derived therefrom depend primarily upon excitatory actions. The functional properties of the multiple classes of GABAergic intrinsic neurons are only just beginning to be explored.

INTRODUCTION

Not so very long ago, it was possible for the majority of neuroscientists interested in cerebral cortical function to adopt, at least as an operational perspective, the viewpoint that thalamic afferents arrived at layer IV, terminated on a single population of neurons customarily referred to as "stellate neurons", and that activity was relayed from them to the various output, pyramidal neurons with somata situated in other layers. Even at the time of its greatest popularity, there was reason to believe that such a viewpoint of the intrinsic operations of the cortex was an unduly simplistic one. It is now clear that numerous local circuits can be identified in the cortex and that some or all may be operational in determining the manner in which cortical cells respond to a peripheral stimulus.

There are three major areas that will be considered as topics for discussion in this position paper:

(1) the role of direct inputs from the thalamus in defining the response properties and receptive fields of cortical neurons;

(2) the role of excitatory intrinsic interneurons and collaterals of pyramidal cell axons in defining these characteristics and;

(3) the role of intrinsic, GABAergic, inhibitory interneurons in defining these characteristics.

Inevitably, in considering any one of these, discussion of the visual cortex will predominate, since it is from there that most data are available. However, I shall attempt to present this paper in as general a way as possible and introduce data from sensory-motor and auditory cortex where these are available.

THE ROLE OF THALAMIC INPUTS

The Cortical Terminations of Thalamo-cortical Fibers

Laminar segregation and hierarchical processing. There is a lack of uniformity in the laminar terminations of thalamocortical axons from area to area of the cortex. It now seems apparent that a dorsal thalamic nucleus can potentially contain multiple populations of relay neurons, each projecting to different cortical layers in the same or different cortical areas; some may have diffuse and others focal ramifications. An example of this diversity can be seen in the cortical connections of the lateral geniculate nucleus of the cat or monkey (Fig. 1).

Recent structure–function correlations have caused the discarding of the concept dating to Ramón y Cajal, namely that thalamic afferent fibers ending in the middle layers of the cortex contact only local circuit neurons which then serve as the sole relays to the pyramidal neurons. A second concept, dating to the fundamental work of Hubel and Wiesel (1977) of a hierarchical elaboration of neuronal receptive fields in the visual cortex, has also come under fire, and alternative or superimposed parallell processing models have come into vogue. Figure 1 shows the multiplicity of visual cortical layers receiving lateral geniculate input, and illustrates how difficult it is to regard either hierarchical or parallel models, even if correct, as being based upon a single layer of thalamic terminations and a single population of thalamic recipient cells. Of course, it is still possible, by invoking a great deal of specificity in the connections of individual types of thalamocortical axon with different varieties of cortical cells, to conjecture that either one or both models are still appropriate. For example, X-type and Y-type axons ending at different levels (lower and upper) of layer IV in the cat visual cortex might contact separate populations of postsynaptic cells, which then

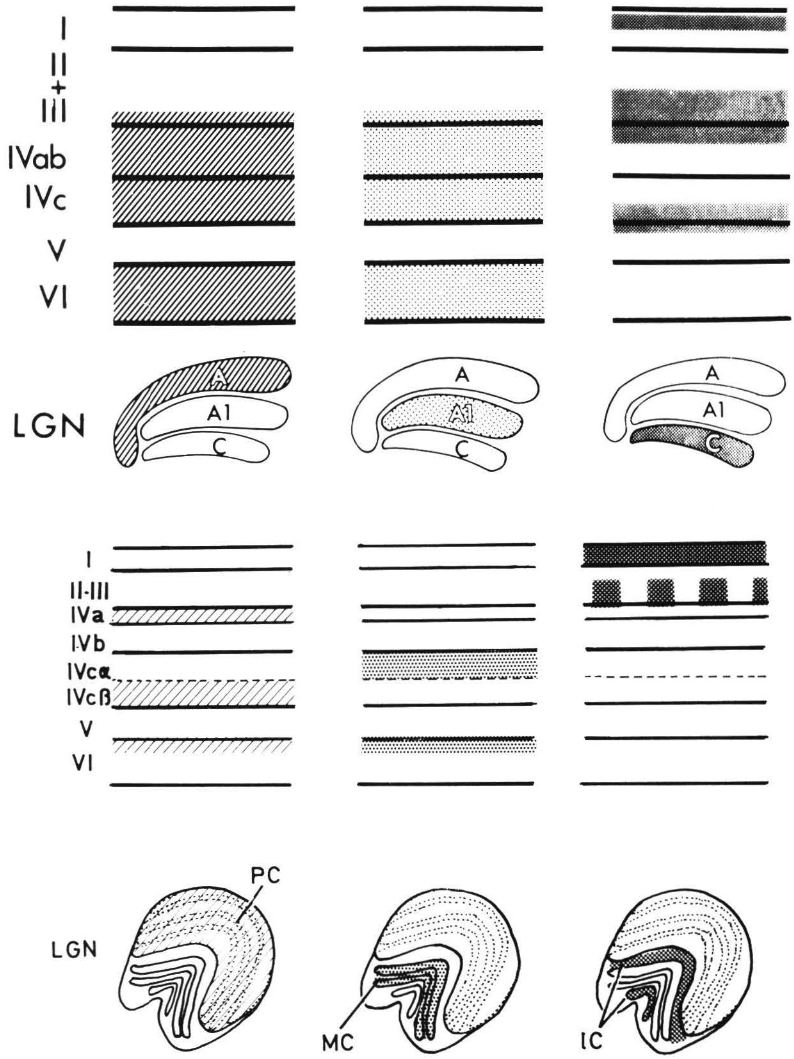

Fig. 1—Laminar patterns of cortical termination of lateral geniculate afferents arising from different layers of the cat (above) and monkey (below) dorsal lateral geniculate nucleus. From Jones (1985), upper figure after S. Le Vay and C.D. Gilbert.

relay their influences independently to other specific cell populations in other layers (although a strict separation of X and Y axon terminations is not as clear as once thought: Humphrey et al. 1985). Most evidence now seems to be against a laminar or sublaminar specificity of connections in hierarchical terms, but interlaminar processing, specificity of neuronal connections, and parallel circuits are still the subject of much debate.

Cells contacted by thalamic synapses. The belief that the small, spiny intrinsic neuron of layer IV (The "spiny-stellate" cell) was the principal thalamic recipient cell in the cortex was never based on firm evidence, and a number of earlier studies had implicated pyramidal cells as additional recipients of thalamic synapses. The fact that all postsynaptic potentials occurring at monosynaptic latencies in cortical neurons following stimulation of extrinsic afferent pathways were excitatory, while disynaptic potentials were mixtures of both EPSPs and IPSPs, should also have implied that thalamic fibers ended directly on at least two kinds of cortical cells: excitatory and inhibitory.

Two kinds of studies helped lead to the realization that thalamic inputs could not be channelled into a single type of intracortical circuit. First was the renewed evidence that pyramidal cell dendrites were often in a position to receive thalamic synapses (see below) and that nonpyramidal cells possess a variety of stereotyped forms, primarily based upon their axonal ramifications. Making use of the then new Golgi-electron microscopic procedure in the rat visual cortex, Peters and his colleagues (1978) were able to show that virtually any cortical neuron with dendrites in a layer of thalamic terminations was capable of being contacted by a thalamic synapse, and this observation has now been confirmed many times with the same method and with other techniques that include labeling of postsynaptic cells by retrograde transport from their target sites or by immunocytochemistry (e.g., Hornung and Garey 1981; Freund et al. 1985a,b; Jones 1986; Kisvardy et al. 1986; Benshalom and White 1986; Somogyi and Soltesz 1986). Morphological evidence now exists for thalamic synapses on spiny intrinsic neurons, on one or more forms of nonspiny, GABAergic intrinsic neuron, and on corticocortical, callosal, corticothalamic, corticostriatal, corticospinal, and possibly other forms of pyramidal neuron.

In dealing with cortical circuitry, it is now essential to consider both direct and indirect pathways of thalamic input. Undoubtedly, many synapses are made by thalamic afferent fibers directly on output cells as just discussed, and thus enable major groupings of interneurons to be, as it were, bypassed. But many additional routes leading through various chains of interneurons may also intervene between input and output.

Most morphological studies of the type used to define thalamic inputs to cortical cells have been of a qualitative nature and, because of the sampling problem, it has been difficult to generate quantitative data regarding the relative numbers of thalamic synapses on cortical cells of different types. Those quantitative data we have come from the mouse somatosensory area (Benshalom and White 1986). Working among the major region of thalamic terminals in layer IV and the adjacent part of layer III, White and his colleagues find that 10.4% to 22.9% of asymmetrical synapses on the small spiny, putatively excitatory, intrinsic neurons are thalamic in origin. This is greater than the number on nonspiny, presumably GABAergic interneurons, on which about 10% of the asymmetric synapses are thalamic; it is much greater than on certain classes of pyramidal neurons with dendrites in the layer. Thalamic synapses form only 0.3% to 0.9% of the asymmetric population on corticostriatal neurons, 1.5% to 6.8% of that on corticocortical neurons projecting to the motor cortex, and 6.7% to 20% of that on corticothalamic neurons. Still, only a relatively small number of cells have been examined in these studies, so that the relevance of these findings, especially to other cortical areas, may need to be treated cautiously. They do, however, suggest differential thalamic inputs to individual classes of cortical neuron. It has not yet been possible to count the numbers of synapses made by individual classes of thalamic axon on cortical cells.

Input latencies. Measurements of the latency of response of neurons situated in particular layers of the cat visual cortex following lateral geniculate nucleus, optic radiation, and/or optic tract stimulation, indicate that many neurons well outside layer IV can respond monosynaptically to thalamic input (Bullier and Henry 1979; Martin 1984). It seems that all layers except layers I and II can contain neurons activated at monosynaptic latencies. Neurons with somata in these layers presumably receive direct thalamic synapses as certain of their dendrites pass through a layer of thalamic terminations.

Correlative studies involving antidromic activation of identified cells and recovery of intracellularly labeled cells (Gilbert 1983; Martin 1984), indicate that there is a significant proportion of pyramidal neurons among the monosynaptically excited cells. The other major group of monosynaptic cells is formed by the spiny intrinsic neurons of layer IV. Smaller numbers of various forms of nonspiny intrinsic neuron have also been recovered; sample populations may contain fewer of the latter because of the generally small size of most of them. Large basket cells are an exception.

The following types of output/pyramidal cells have been demonstrated with these methods to receive monosynaptic inputs in visual cortex: corticothalamic cells with somata in layer VI, and corticocortical and callosal neurons with somata in layers III and V. There is disagreement over whether corticotectal cells of layer V do. No comparable physiological studies on other cortical areas have yet been published. In the motor cortex of the cat, however, stimulation of the dentate and interposed nuclei or brachium conjunctivum of the cerebellum can elicit large EPSPs at disynaptic latencies in neurons projecting to the red nucleus or to the pontine nuclei (Shinoda et al. 1983). In the cat somatosensory cortex, antidromically identified corticocortical and corticothalamic neurons (known to be pyramidal cells) can also be driven by peripheral stimulation at short latencies, indicative of probable monosynaptic thalamic inputs (Landry et al. 1984).

Interlaminar and other local cortical connections. Older, Golgi-based studies and a number of degeneration- or axoplasmic transport-based studies demonstrated the presence of organized interlaminar and intralaminar connections in the cortex. Pronounced vertical, interlaminar projections from superficial to deep layers (particularly from layers II and III to layer V) have been known for some time. Quite extensive lateral, intralaminar connections (see Lund 1981; Jones 1984), mainly in layers III and V, were also demonstrated early. Axoplasmic transport-based methods further showed that intra-areal connections are patchy, i.e., commonly in the form of multiple column-like foci with intervening unconnected regions (See Gilbert 1983; Jones 1986).

More recent studies of intracortical connectivity have been predominantly involved with demonstrating the axonal ramifications of single neurons. Studies of physiologically characterized and intracellularly stained neurons have dealt almost exclusively with the dendritic spine-bearing neurons, i.e., pyramidal cells and the small, spiny intrinsic neuron of layer IV; two recent reviews on the cat visual cortex have been published (Gilbert 1983; Martin 1984). A summary of the principal intracortical connections inferred from the axonal distributions of these cells is shown in Fig. 2.

The following patterns seem to have emerged: (a) spiny nonpyramidal cells of layer IV, monosynaptically driven from the thalamus, have their predominant axonal ramifications ascending into layers II and III; (b) monosynaptically–driven pyramidal cells with somata in deep layer III have axons projecting to other cortical areas and give off substantial collaterals in both layers III and V; (c) di- and polysynaptically-driven pyramidal cells with somata in layers II and III also have efferent axons, but with substantial ascending collaterals into layers II and I; (d) pyramidal cells with somata in layer V can be driven mono-, di- and polysynaptically from the thalamus, and all project outside the cortex. However, a number of types are present; some have substantial axon collaterals to layer VI extending laterally over long distances and others have few; (e) modified pyramidal cells of layer VI, driven monosynaptically from the thalamus, send axons out of the cortex, but these have collaterals that ascend and terminate densely in layer IV; this connection is reflected in the late, slow depolarization occurring in layer IV subsequent to the more rapid monosynaptic excitation ocurring in layer VI following thalamic stimulation. Each of the patterns of interlaminar connectivity demonstrated in these studies of pyramidal and spiny, nonpyramidal cells have at one time or another been thought to underlie sequential elaborative hierarchies in the visual cortex. The widely extended collateral projection from layer V to layer VI has been implicated, for example, in the formation of the extremely large receptive fields of layer VI visual cortical neurons (Gilbert 1983). Others are mentioned later in this discussion. Layer III, corticocortical neurons projecting from somatic sensory to motor

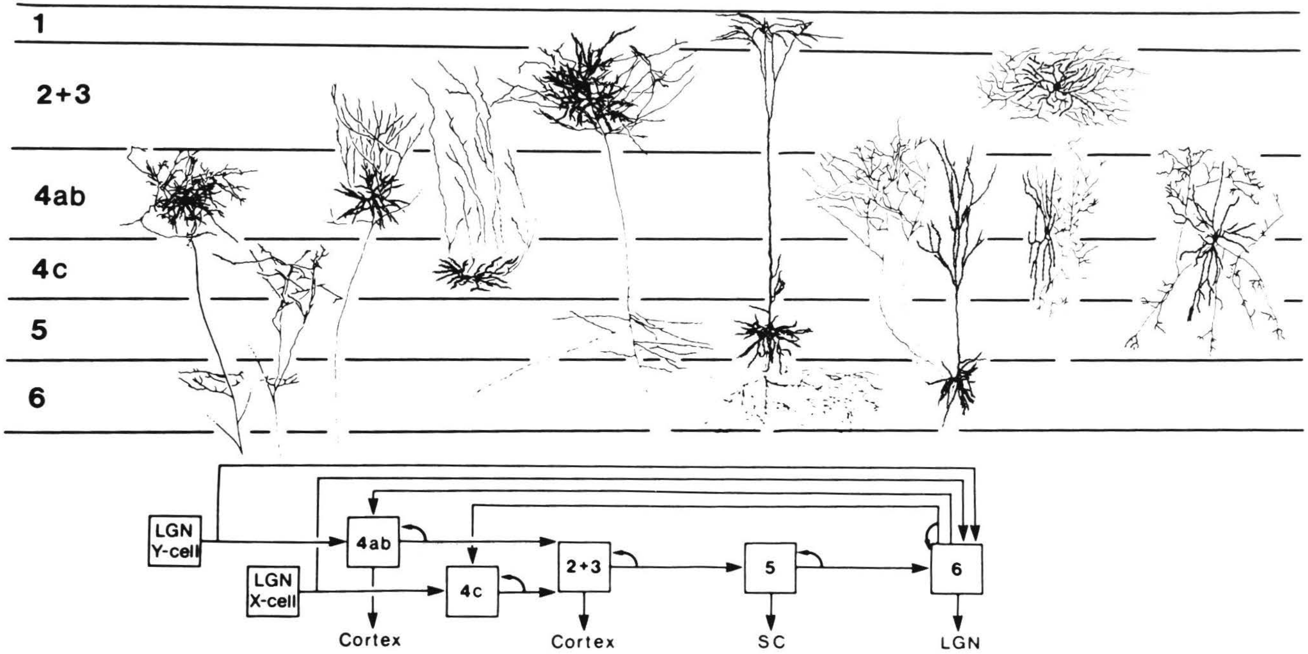

Fig. 2—Patterns of axonal ramification of Y- and X-type geniculate afferents (left) and of spiny and nonspiny neurons in cat visual cortex (From Gilbert 1983). Lower part of figure indicates patterns of interlaminar connection established by above cell types.

cortex in the monkey, are pyramidals and have very long collaterals in layers III and V; these form terminal condensations at widely spaced intervals, mainly through the thickness of layer III in areas 3a, 3b, 1 and 2 (DeFelipe et al. 1986b). Since thalamic inputs to each of these areas are place- and modality-specific, it is thought that these horizontal collaterals could account for the units showing place- and modality-convergence in certain of these areas in unanesthetized monkeys (Iwamura et al. 1983). It is presumably the axons of similar types of cells in area 18 of the cat visual cortex that serve to link selectively patches of cortex containing orientation columns with orientations that are orthogonal to one another (Matsubara et al. 1985), although cross–correlation analyses in area 17 suggest connections between neurons with like orientation selectivities (Ts'o et al. 1986).

The intracortical connectivity of nonspiny intrinsic neurons, virtually all of which may be GABAergic (Houser et al. 1985; Jones and Hendry 1986), have been less well-studied in intracellular injection experiments, mainly because of small samples. There is, however, a large body of data from studies based on Golgi, horseradish peroxidase, and immunocytochemical methods (Lund 1981; Gilbert 1983; Martin 1984; Jones 1984). It is possible to identify certain types among these cells that have very local axonal ramifications, a number of types with long, vertical (interlaminar) axonal ramifications, and one type (the basket cell) with long, lateral ("intralaminar") axonal ramifications (Fig. 3). Many of these types receive direct thalamic axon synapses and at least some have their own axon terminations focused on particular parts of pyramidal cells. Chandelier cells, for example, terminate only on the axon initial segments (Somogyi et al. 1982; DeFelipe et al. 1985), and basket cells mainly on the cell somata and proximal dendrites (Somogyi et al. 1983; DeFelipe et al. 1986a). The individual functions of these inhibitory interneurons are still poorly understood. Although their spiking patterns appear to be different from those of the two major forms of spiny cortical neuron (Connors et al. 1982), their receptive fields, so far as they have been studied, appear little different from those of the spiny cells.

Receptive field analyses. The receptive field structure of neurons has been examined in far greater detail in the visual cortex than in other areas. The number of neurons in the visual cortex reported to have center-surround receptive fields comparable to those of dorsal lateral geniculate cells has been extremely small in cats, but quite large (ca. 20%) in layer IVC of monkeys. The discrepancy in the cat has sometimes been attributed to the small size of such cells, making it difficult to record from them. If this were so, center-surround cortical cells would probably have to belong to one of the classes of aspiny, GABA neurons since sufficient spiny intrinsic neurons and pyramidal neurons have been identified to make them unlikely candidates. Probably, therefore, the most common, "lower order" receptive

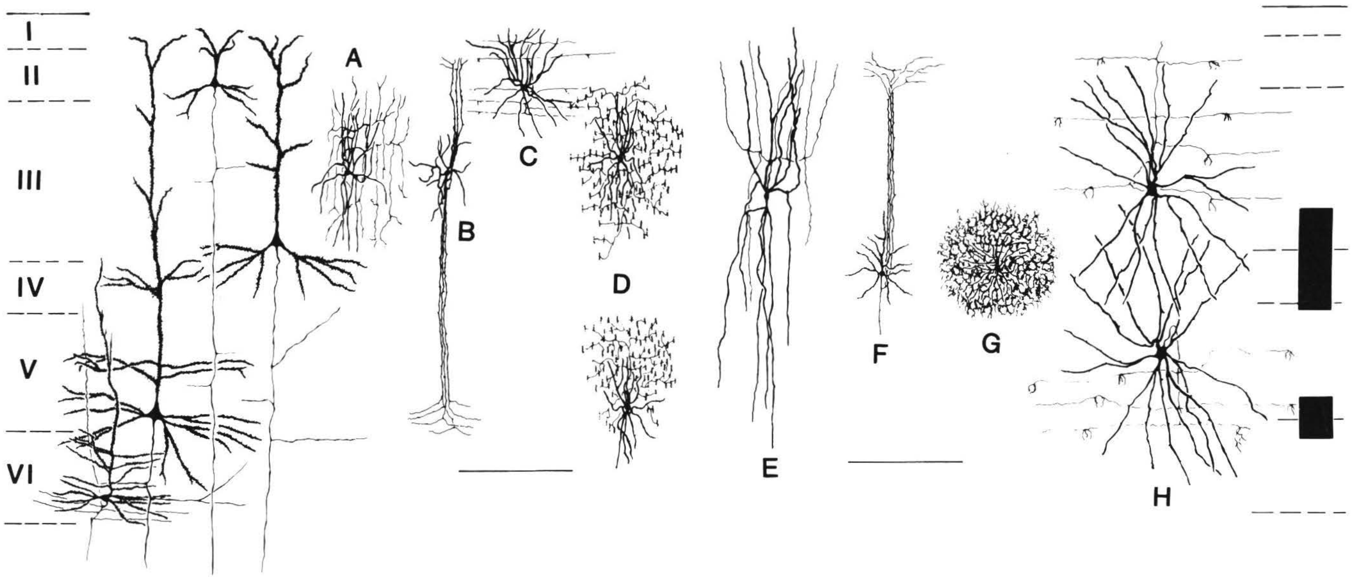

Fig. 3—A general scheme of cortical cell types, based primarily upon Golgi and immunocytochemical studies, of the monkey sensory-motor cortex. Left: putatively glutamergic pyramidal cells. A = nonspiny intrinsic neuron with axonal arcades; E = bitufted cell in which neuropeptides are colocalized with classical transmitters; F = spiny, putatively excitory neuron with ascending axon; G = neurogliaform cell; H = large basket cells. Bar 100 ££m.

field in the cat visual cortex is the classic simple type (Hubel and Wiesel 1977). This should probably be the result of convergence of more than one thalamic axon (each with center-surround receptive fields) on individual cortical cells. Visual cortical neurons with simple receptive fields have usually been reported to form the largest population of neurons recorded in layers IV and VI among the major layers of thalamic terminations in cats (e.g. Gilbert 1977). Neurons with complex receptive fields are more common in other layers. The implication has been that these complex receptive fields result from the outflow of layers IV and VI into other cortical layers via interlaminar connections.

Recently, the dependence of all aspects of receptive field structure in the visual cortex on interlaminar connections has been subject to reinterpretation. Some authors have now suggested that, at least for layers II and III, the relative proportions of neurons with simple and complex receptive fields are similar to those in layer IV (Bullier and Henry 1979; Orban and Kennedy 1981), despite their receiving a substantial input from layer IV. Similarly, layer IV cells are reported not to have an unusually high proportion of complex receptive fields in comparison with layer VI, despite the heavy projection from layer VI to layer IV. It seems to be only in layer V that the proportion of complex cells heavily outnumbers that of simple cells. Other studies, outlined in the next section, indicate that many complex receptive fields can survive the deactivation of thalamic or interlaminar connections. This leads us to ask: what are the relative contributions of thalamic inputs and interlaminar connections to neuronal receptive field structure in the cortex?

Inactivation studies. Malpeli and his coworkers (Malpeli et al. 1986; Schwark et al. 1986; Weyand et al. 1986) have recently studied the effects of blocking either the supragranular cortical layers or lamina A, the C laminae, or the medial interlaminar nucleus of the dorsal lateral geniculate complex on neuronal excitability, orientation selectivity, and direction selectivity in the cat visual cortex.

Inactivation of lamina A of the dorsal lateral geniculate complex, although abolishing neuronal activity in layers IV and VI, scarcely changes the excitability or stimulus selectivity of cells in layers II and III. Therefore, interlaminar connections from layer IV to the supragranular layers may not be major determinants of receptive field structure in layers II and III. Presumably, direct inputs to layer III from the C laminae are just as important. It was also found that the supragranular layers are substantially normal in the absence of C laminae input but cannot tolerate deactivation of both lamina A and the C laminae (Malpeli et al. 1986). The supragranular layers of cortex thus appear to integrate thalamic inputs from two sources in setting up their major neuronal response patterns. The role of the projection to them from layer IV now appears unclear. In contrast to the supragranular layers, layers IV and VI are highly dependent on the input from the A laminae of the geniculate; the strong interlaminar projections to layer IV from layer VI and from layer V to layer VI are reported to support no receptive field properties in those layers in the absence of a geniculate input.

Deactivation of the supragranular layers had little or no effect on the excitability or on the receptive field properties of neurons in layers IV and VI, but had a selective effect on neurons in layer V (Schwark et al. 1986; Weyand et al. 1986). Neurons identified both as corticotectal neurons and as having standard complex or special complex properties (based upon their preference for long or short stimuli) were differentially affected. Following cooling of the supragranular layers, no standard complex cells could be recorded but special complex cells remained. The standard complex properties may therefore depend on interlaminar connections from layers II and III; by contrast, the special complex property may depend on other inputs. Finally, because the length characteristics of receptive fields of layer VI cells do not change under conditions that deactivate standard complex cells in layer V, a conclusion of these studies was that the unusually long receptive fields of normal layer VI cells should not depend solely on the collateral input that layer V standard complex cells have been shown to give to layer VI (Gilbert 1983).

Relative contributions of thalamic inputs and intrinsic GABA neurons. Close to 30% of the neuronal population in any cortical area of monkeys is GABAergic (Hendry et al. 1987). Morphological studies of known GABAergic neurons and studies of the uptake and transport of [^{3}H] GABA in the visual and sensory-motor areas have demonstrated a number of stereotyped patterns of connectivity of known or putative GABA neurons. Some form very local connections, others have long horizontal axons, and others form vertical, bidirectional connections between certain layers (e.g., Somogyi et al. 1981, 1986; DeFelipe and Jones 1985; DeFelipe et al. 1985, 1986a). In the visual cortex, Sillito and his colleagues (Sillito et al. 1981) found that iontophoresis of the GABA antagonist, bicuculline, led to the loss of direction and orientation selectivity in a relatively high percentage of neurons, to the loss of the discrete on and off subregions of the receptive fields of simple cells; and 50% of cortical cells showing marked eye preference showed a shift in ocular dominance to the other eye. Both complex and simple cells could be affected and the implication was that GABA-mediated inhibition in the cortex is cell specific, rather than a tonic regulator of cortical neuronal excitability. In comparable studies on the cat somatic sensory cortex, Dykes et al. (1984) found that iontophoretic application of bicuculline led to a considerable enlargement of the receptive fields of neurons responding with slowly-adapting discharges to peripheral stimuli, but neurons with rapidly-adapting discharges showed no change. This, too, appears to indicate specificity of action of GABA.

Other investigators doubt that GABA plays a preeminent role in shaping receptive fields in the visual cortex. Ferster (1986), recording intracellularly from neurons in the cat, reported that EPSPs and IPSPs induced by visual stimuli are both tuned to orientation and show the same orientation preference in any one cell. The absence of a systematic difference in tuning between the IPSPs and the EPSPs suggests that orientation tuning would not be produced or sharpened by inhibition coming from neurons with different orientation preferences. If orientation preference is not directly provided to cortical neurons by the thalamic input, these findings would imply that orientation selectivity is set up among groups of cortical neurons with a certain commonality of intracortical connections, rather than between groups of neurons with dissimilar connections. However, if thalamic inputs may have some degree of orientation selectivity (Vidyasagar and Heide 1984), and if the inhibitory input is more broadly tuned than the excitatory input in the cortex, then inhibition still present in the least optimal orientation may suffice to cancel a smaller excitation in a nonoptimal orientation (Creutzfeldt et al. 1974). As orientation selective cells are arranged in columns through the thickness of the cortex, any common connections are presumably intracolumnar, and therefore interlaminar. The strong, putatively GABAergic, vertical connections demonstrated by [^{3}H] GABA transport studies might subserve such a role. These interpretations would tend to exclude the long horizontal (transcolumnar) axons of the GABAergic basket cells from the connectivity responsible for setting up orientation selectivity.

Presumed excitatory interlaminar connections have been implicated in shaping inhibitory components of one kind of receptive field in visual cortical neurons. Bolz and Gilbert (1986) showed that inhibition of layer VI cells by injection of GABA led to the loss of endstop inhibition in cells of layer IV. The recurrent axon collaterals that layer VI cells send to layer IV end in asymmetrical synapses to a large extent on the distal dendrites of nonspiny intrinsic cells (McGuire et al. 1984), which are probably GABAergic and inhibitory. Hence, layer VI cells, via such an intermediary inhibitory neuron, may be responsible for end-stopping. The possibility of an additional, direct projection from layer VI GABAergic neurons to layer IV should, however, also be considered.

It seems obvious that certain transformations, such as orientation selectivity (with the reservations expressed above), direction selectivity and binocularity are imposed by the visual cortex over and above its thalamic input. However, the mechanisms and the relevant circuitry are little understood, and few parallels can be drawn between this and other cortical areas. Similarly, any relationships between parallel and independent channels of information flow into and out of a cortical area and any hierarchical processing occurring within an area are not clear. Intracortical and intercortical circuitry are, however, becoming clearer and as more correlative, structure-function studies are done and as the role of GABA-mediated cortical inhibition is gradually revealed, current obscurities may be clarified.

Targets of nonspecific inputs to cortex. The known and potential functional roles of nonspecific thalamocortical connections and of diffuse connections from basal forebrain, brainstem, and other sites have been explored from several functional points of view, but there is very little that one can say about the nature of their synaptic relationships in the cortex although they may be more specific in terms of cells contacted than the name "nonspecific" suggests. Those afferent systems ending in layer I are usually presumed to terminate on the apical tufts of dendrites of pyramidal cells with somata in all underlying layers. Such contacts would be in a position to regulate excitability of the underlying neurons. Some of these connections are probably excitatory in nature but others are uncertain, though none appear to be GABAergic. The actual synapses made by the nonspecific axons have never been satisfactorily demonstrated. Among targets other than pyramidal neurons they could contact in layer I would be the intrinsic neuronal population, which is 100% GABAergic (Hendry et al. 1987), the dendrites of nonpyramidal (also GABAergic) cells with somata in layer II, and neurons that contain both GABA and neuropeptides located at these levels (Jones and Hendry 1986). All of these cells would be capable of extending nonspecific influences beyond the apical tufts of pyramidal cells. Similar comments would apply to synapses of any of these nonspecific systems situated at deeper levels in the cortex.

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