Morphology and physiology of the geniculocortical synapse in the cat: The question of parallel input to the striate cortex

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Physiological studies of the neural circuitry of the visual cortex have so far analyzed only the initial action of visual afferents to the cortex. These studies have, moreover, been limited to the cat. The present review is correspondingly limited in scope and attempts: (1) to summarize present understanding of the morphology and physiology of the termination in the cat's striate cortex of afferent fibers from the lateral geniculate nucleus (LGN); (2) to summarize recent physiological work which indicates that these afferent fibers comprise several functionally distinct, parallel-running subgroups; and (3) to formulate questions about the terminations of geniculocortical afferents raised by the functional subgrouping of afferents.

I. The morphology and synaptic connections of geniculostriate axons

(1) Morphology of the geniculocortical synapse. O'Leary and Szentagothai have described the morphology, in Golgi-stained material, of the terminal arborizations of thalamic afferents to the cat's striate cortex. Each axon enters the cortex fairly directly, then runs an often oblique course through layers VI and V, beginning to branch in these layers. On entering layer IV the axon branches repeatedly, the branches running tangentially for distances up to 500 µ before ending. Some fine terminal endings extend into the deeper part of layer III but the majority of endings are confined to layer IV. This pattern is closely confirmed by studies of terminal degeneration seen in the striate cortex after lesions in the lateral geniculate nucleus destroyed the cells of origin of the afferents. Colonner and Rossignol and Carey and Powell also observed a small number of degenerating terminals in layer I.

Electron microscopic observations have provided evidence that all synapses made by geniculostriate afferents are of the asymmetrical spheroidal (AS) type. The presynaptic boutons formed by the afferents contain synaptic vesicles which appear spheroidal (actually circular in profile) in aldehyde-fixed material, and the postsynaptic membrane appears markedly thickened. (The presynaptic membrane is not thickened, hence the synapse is asymmetrical). These synapses are distinct from symmetrical, flat (SF) synapses, in which the synaptic vesicles often appear flattened in aldehyde-fixed material, and in which there is no postsynaptic membrane thickening. The most striking description of these two synaptic types in cat visual cortex is that of Colonner, who noted their approximate correspondence with the Type I and Type II synapses described by Gray. There seems to be general agreement that AS synapses are excitatory in action and SF synapses inhibitory and that therefore geniculostriate axons are uniformly excitatory in action.

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excitatory. Physiological observations (discussed below) support this generalization.

Three lines of evidence suggest that SF (inhibitory) synapses are formed only by cortical interneurones (principally stellate cells). First, Szentagothai found axosomatic synapses of this type in normal numbers in chronically isolated slabs of cortex. Conversely, Jones and Powell report that (in somatosensory cortex) degenerating SF synapses were found only after lesions involving the cortex and only in the vicinity of such lesions. Third, Szentagothai, Colonnier, and Garey found that synapses on pyramidal cell bodies are all of the SF type. In Golgi preparations these bodies can be seen to be contacted by pericellular basket terminals derived from a particular type of stellate cell.

The great majority of presynaptic boutons formed by geniculostriate axons synapse onto dendritic spines (83 per cent in the data of Garey and Powell). A minority (17 per cent) synapse onto dendritic shafts or cell somas. In agreement with Colonnier's description of the distribution of AS and SF synapses on pyramidal and stellate cells of cat striate cortex, it was concluded in all three studies that the synapses formed by geniculostriate axons on dendritic shafts and somas were synapses onto stellate cells of layer IV. Garey and Powell could not unequivocally demonstrate that any structures which they observed to be postsynaptic to pericellular basket terminals derived from a particular type of stellate cell.

(2) Physiology of the geniculocortical synapse. Intracellular recordings from cells of cat visual cortex have been reported by Li and associates for area 17, by Toyama and Matsunami for area 18, and by Ohno and associates for area 19. The recordings of Toyama and Matsunami are simplest to interpret. The cells they impaled responded to stimulation of the optic radiation with a short (0.95 msec.) latency excitatory postsynaptic potential (EPSP) which was invariably followed by an inhibitory postsynaptic potential (IPSP) at slightly longer (1.7 msec.) latency. The EPSP latencies are so short that the EPSP's must be generated monosynaptically, by the fastest geniculocortical axons. The latency difference between EPSP and IPSP is also very short (0.75 msec.) and remained constant with different afferent conduction distances. These two observations indicate that the IPSP's were generated not monosynaptically by slower-conducting afferents but disynaptically via a cortical interneuron. However, the occurrence of additional tri- and multisynaptic IPSP's is not ruled out by these observations.

These results have important implications. First they demonstrate that the initial synaptic action of at least the fast geniculocortical axons is excitatory. Second, Toyama and Matsunami concluded, after tracing the tip positions of their electrodes, that the cells they impaled were in layer III of area 18, and presumably were the large pyramidal cells of this layer. Thus their work provides physiological evidence of synaptic contact of geniculocortical afferents onto the basal dendrites of layer III pyramidal cells. Third, the results imply that geniculocortical axons monosynaptically excite some inhibitory cortical cells (presumably basket-type stellate cells) which monosynaptically inhibit layer III
pyramidal cells. Thus their work supports the evidence from morphological studies (discussed above) that geniculocortical afferents terminate on both pyramidal and stellate cells.

Watanabe and colleagues\textsuperscript{17} found similar evidence of monosynaptic EPSP's and disynaptic IPSP's in area 17 cells following stimulation of the optic radiation. Although Li and colleagues\textsuperscript{16} and Watanabe and colleagues\textsuperscript{17} noted cells in which the initial response to stimulation of the optic radiation was hyperpolarizing, the latency of such responses was never short enough to be unambiguously monosynaptic. Watanabe and colleagues\textsuperscript{17} and Toyama and Matsunami\textsuperscript{18} both conclude that unambiguously monosynaptic PSP's are EPSP's and that IPSP's are generally disynaptic in latency. Toyama and Matsunami\textsuperscript{18} point out that because it is disynaptic the inhibition must be of the "feed-forward" rather than the collateral "feed-back" type described in thalamic nuclei. This basic similarity in the cat between area 17 and area 18 is in accord with Garey and Powell's\textsuperscript{9} observation that the patterns of degeneration seen in these two areas, following lesions in the lateral geniculate nucleus, are very similar.

Toyama and Matsunami\textsuperscript{18} observed only short latency EPSP's in the cells they impaled in area 18. By contrast Ohno and colleagues\textsuperscript{19} found only longer latency EPSP's in cells impaled in area 19 and concluded that 19 receives slower conducting afferents than 18. Watanabe and colleagues\textsuperscript{17} found a range of EPSP latencies in area 17 cells and suggested that area 17 receives both fast and slow afferents. In striking parallel, Rossignol and Colonnier\textsuperscript{20} reported that the degenerating axons observed in areas 17, 18, and 19 after lesions in the LGN varied characteristically. In 18 only coarse degenerating axons were apparent, in 19 only fine axons and in 17 both coarse and fine. (Ohno and co-workers\textsuperscript{19} were aware of the possibility that the afferents to 19 whose synaptic action they observed might not originate in the LGN. They noted, however, that many of their cells responded at short latency to stimulation of the optic chiasm, suggesting that the afferents involved are visual in modality and relay directly to the cortex, through the LGN.) These observations of fine and coarse afferents terminating differently in areas 17, 18, and 19 are in good accord with previous accounts\textsuperscript{21, 22} of the different cortical projections of the large and small cell components of the LGN. The presence of fine and coarse fibers projecting to area 17 suggests a duality in the geniculocortical input, an idea taken up in more detail in the following paragraphs.

II. Parallel input to visual cortex

(1) Basic observations establishing parallel input. The studies drawn on for the foregoing descriptions of the morphology and physiology of the geniculostriate synapse have essentially assumed that the geniculostriate axons form a homogeneous functional group. Evidence that these axons might not be functionally homogeneous had been in the literature for some time, but a clear description of their functional sub-grouping has been provided only in the last year or so, and is probably still incomplete.

It has been known for a considerable time that the axons running from the retina to the lateral geniculate nucleus, and from this nucleus to the visual cortex, vary widely in conduction velocity.\textsuperscript{23-25} The retina-LGN axons (in the optic nerve) form two predominant conduction velocity groups, and the geniculocortical axons appear to fall into velocity groups analogous with those of the optic nerve and tract.\textsuperscript{27, 28} Until recently, however, the question of the functional significance of conduction velocity groupings remained unanswered.

In 1966 Enroth-Cugell and Robson\textsuperscript{29} reported that the receptive fields of cat retinal ganglion cells (first described by Kuffler\textsuperscript{30}) can be classified by certain tests into two types, which they called X- and Y-types (ON- and OFF-center fields fell into both categories). They generated a contrast border on an oscilloscope screen by symmetrically darkening one half of the screen.
and brightening the other half, so that the mean luminance of the screen remained constant. When this contrast border was located in the receptive field of an X-cell, and was turned on and off, the cell's response was often strong but fell to zero when the border passed through the geometrical center of the field (bisecting the field). No corresponding “null" position of the border could be found for Y-cells; the cell responded to the border at any position. On the basis of this and other observations Enroth-Cugell and Robson argued that X-cells sum linearly the influences of center and surround portions of their receptive fields, and that Y-cells sum these influences nonlinearly. They noted that Y-fields are generally larger than X-fields, but were unable to suggest a functional significance for the difference. Their suggestion of a linear/nonlinear grouping of receptive fields has been substantially confirmed, however.28, 31-33

These two sets of findings (conduction velocity groups and the X/Y classification) were brought together, quite independently, by Fukada32 and Cleland and associates.28 Fukada noted that X- and Y-cells could be differentiated by their response to a stationary flashing spot centered in their receptive field. Specifically, X-cells respond tonically to this stimulus and Y-cells respond phasically. Importantly, Fukada showed that Y-cells have generally faster axons than do X-cells. Cleland and associates noted the same tonic/phasic difference (which they termed “sustained/transient”) and devised other distinguishing tests utilizing gratings and black and white targets. By measuring axonal conduction times of X- and Y-cells over a much longer distance than Fukada they established a sharp, non-overlapping grouping: Y-cell axons conduct consistently faster than X-cell axons. Moreover, these two studies indicate that Y-cell axons form the prominent fast-conducting field potential (30 to 40 m/s) of the optic nerve and that X-cell axons form the prominent slower conducting potential (17 to 20 m/s).28

Stone and Hoffmann27 presented evidence that fast- and slow-conducting axons do not converge on the relay cells of the lateral geniculate nucleus. Fast and slow axons activate different relay cells, and relay cells which receive fast axons from the retina have fast axons projecting to the visual cortex, while relay cells receiving slow axons have slow axons. Both fast- and slow-axon relay cells could be activated antidromically by electrical stimulation of visual cortex. Cleland and associates28 reached the same conclusions independently, and added the valuable observation (since confirmed33) that the relay cells of the lateral geniculate nucleus can also be classified as either Y-cells (fast axon) or X-cells (slow axon). Thus the activity of X- and Y-cells of the retina is relayed by different LGN cells to the visual cortex, through functionally separate, parallel neuronal channels, one (the Y-channel) fast-conducting, the other (the X-channel) slow-conducting.

(2) Evidence of the functional significance of X/Y differences.

Retinal distribution of X- and Y-cells. There is considerable evidence that X- and Y-cells are distributed very differently in the retina. First, Hoffmann, Stone, and Sherman33 showed with physiological techniques that the majority of cells at the area centralis (67 per cent in their data) are X-cells. Y-cells increase in relative frequency with eccentricity to a majority (75 per cent in their data) at eccentricities greater than 45°. There is a sharp decrease in the absolute frequency of retinal ganglion cells between the area centralis and the periphery.34 If Y-cells are a minority of the densely packed area centralis cells, and a majority of the scattering of cells in the retinal periphery, it follows that they have a relatively flat distribution across the retina. X-cells, by contrast, would be expected to have a distribution sharply peaked at the area centralis. In support of this idea it can be argued that Y-cells are probably bigger than X-cells. They have larger receptive fields and faster, presumably bigger,
Moreover, there is a close correlation between mean ganglion cell size (calculated from the data of Stone34) and the relative frequency of Y-cells. Both are minimal at the area centralis and increase with eccentricity. Stone's Fig. 5 has shown that large and small ganglion cells are very differently distributed in the retina. Small cells (< 16 µ in diameter) have a very peaked distribution, their numbers falling off very sharply from the area centralis. Large cells have a much flatter distribution, being present in approximately equal numbers throughout the retina, except at the area centralis where the absolute frequency of the largest cells declines to near zero. This is probably a fair guide to the distributions of X- and Y-cells (small and large cells, respectively), and suggests that the X-cells are predominantly concerned with central, detailed vision and Y-cells with peripheral vision.

Receptive field properties. The above suggestion is supported by the receptive field properties of X- and Y-cells. In particular X-cells have smaller receptive field centers than Y-cells, and the smallest receptive fields of the retina are fields of area centralis X-cells.33

(3) Target cortical cells of X- and Y-afferents. Hoffmann and Stone35 presented evidence that some complex cells of visual cortex (described by Hubel and Wiesel30) are driven monosynaptically by fast-conducting geniculostriate axons and that some simple and hypercomplex fields (described by Hubel & Wiesel36, 37) are driven monosynaptically by the slow afferents. This implies33 that complex cells receive direct input from Y-cells, and simple and hypercomplex cells from X-cells. The receptive field properties of the various cell types are consistent with this implication. Y-cells have larger receptive fields than X-cells, and complex fields have larger excitatory zones than do simple fields.36, 38 Simple cells are selective for slow speeds of stimulus movement,39 while complex cells respond to a much greater range of speeds.35, 38 Correspondingly, speed-selectivity is seen in X-cells but not in Y-cells.28, 33 Thus some (and presumably the functionally important) X/Y differences appear to be maintained past the initial geniculostriate synapse. However, many details of the picture are certainly still lacking. For example, it is not clear whether all or only some complex cells receive monosynaptic input. It is of prime interest, too, to sort out the destinations of the axons of simple and complex cells, for if these neurons are processing qualitatively different types of retinal activity in parallel their axons might be expected to project to quite different locations.

III. Questions raised by parallel input

In the present consideration of the geniculocortical synapse the presence of functionally distinct subgroupings among the geniculocortical afferents seems to raise at least three basic questions:

1. Do fast- and slow-conducting cortical afferents converge onto the same cortical cells or do they terminate on different subgroups of cells? There is little evidence on this point, but one recent report35 suggests that, at least to some extent, fast and slow afferents terminate on different subgroups of cells.

2. Is there any tendency for fast and slow axons to terminate on different types of cells? There seems to be little evidence that they do. None of the Golgi, degeneration, or electron microscopic studies suggest that geniculocortical afferent arborizations can be differentiated into two types by any criteria. It seems possible that fast and slow afferents to the visual cortex synapse onto different subgroups of the same morphological cell type (or types) rather than onto different types of cell. This suggestion is consistent with the model neural circuitry proposed by Bishop and associates30 for the cortical simple cell but goes against the suggestion that complex cells are pyramidal cells and simple cells are stellate cells.40 The data that prompted this latter suggestion are considerable, however, and the question remains open.
(3) A third question is whether the different cells of the visual cortex (simple, complex, and hypercomplex) are processing afferent input serially, as Hubel and Wiesel have suggested, or in parallel, a possibility suggested by Hoffmann and Stone. Many of the observations discussed above support the idea of parallel processing and in particular the idea that simple and complex cells receive qualitatively different visual input and process it independently. These observations are still incomplete, however, and the descriptions of Szentagothai make clear that many layer IV stellate cells appear to form potentially powerful excitatory synapses onto neighboring pyramidal cells. In other words, there is a clear morphological basis for excitatory relay of activity within visual cortex, and therefore for serial relay of activity from one cell type to another, within the cortex. There thus seem to be substantial grounds for assuming that both parallel and serial mechanisms operate in the visual cortex.

REFERENCES

29. Hoffmann, K.-P., Stone, J., and Sherman, S.: The relay of receptive field properties from the upper and lower layers, where complex and hypercomplex cells occur. The second of these points of course agrees with what no neuroanatomist would deny, that the overwhelm-
The geniculate in the cat projects strongly to layer IV. The evidence on this seems overwhelming. So the problem seems to be directly analogous to that of 18 and the tectum. If there are two inputs to complex and hypercomplex cells, it becomes a matter of determining their relative importance.

Two points mentioned by Jonathan Stone deserve some comment. To correlate field size (or field-center size) of X cells with field size of complex cells seems to me rather misleading. What one should look for in a complex cell, to correlate with field sizes of afferents, is not over-all field size, but the size of the optimal stimulus, e.g., the optimal slit or black bar width. One can have complex cells with fields many degrees across, which respond best to slits a few tens of minutes wide. This would imply that such cells are fed ultimately by geniculate and finally retinal fibers whose field centers are only a few tens of minutes in diameter or less, the centers being scattered over a number of degrees of retinal surface.

A second point concerns latency. If I understood the paper, the finding was that for complex cells the geniculate afferents making direct contact are of relatively large diameter as reflected by the short latencies; in contrast the simple cells are fed mostly by a smaller fiber system. This would have serious consequences for our hierarchy idea if the cells responded, in normal life, to electrical stimuli or even to brief flashes. But in these cells the most powerful responses, and often the only responses, occur to lines swept rather slowly across the retina. Here the complex cell must be continually bombarded from all of its afferent pathways; it would be hard to imagine that the most direct path, or the one with the largest fibers, would necessarily have more potency. Surely the relative densities of two pathways should be more important than conduction times.

In summary, we would stress that what hierarchy there is, is surely not a rigid one. But we also feel that the concept as a whole, with its ability to explain the properties of complex and hypercomplex cells, is not seriously threatened by the findings just presented. I do not doubt the findings, only the interpretation!

STONE: My main emphasis is not on the inability of the “hierarchy hypothesis” to explain the data at hand, and I sought toward the end of my talk to point out that the concepts of parallel and serial processing are not mutually exclusive. What I have tried to emphasize is that there is very substantial evidence of functional subgrouping of the afferents to the visual cortex and that this is a parameter which has to be considered in interpreting cortical receptive-field types. Clearly, some of the differences between cortical receptive-field types may be determined by what sort of input the different cells receive from the geniculate, rather than by any hierarchical arrangement of the cells. We need to sort out what contributions these two different modes of organization in fact make in the determination of cortical field types.

PETTICREW: Could you tell us what proportion of cells, simple and complex, you can drive electrically? I tried this and gave up because I could drive so few cells.

STONE: About 40 per cent (13/30) of the complex cells we identified were activated post-synaptically at short latencies. Simple and hypercomplex cells were more difficult. Twenty-two of 75 responded at latencies which could have been monosynaptic.

BURKE: I take it that you can drive some cells polysynaptically? How are these cells classified?
STONE: Yes indeed. Many cells responded with very long, obviously polysynaptic latencies. These included cells with all receptive-field types. It is important to remember here that the optic radiation is a diffuse structure in which we placed only two stimulating electrode tips. It is likely that we often failed to excite the afferents going to the cell from which we were recording. It is, of course, also highly likely that many cortical cells do not receive direct input from the geniculate.

WURTZ: Wouldn’t your results imply that there should be proportionately more complex cells in the periphery than in the area centralis?

STONE: They certainly would, but I do not know of any published figures on this point.

HUBEL: We have no hint at all that there are differences in the relative numbers of simple and complex cells in the center and periphery of the visual field representations. This holds for both cat and monkey.

WICKELGREN: I wonder if there were any distinguishing features to the complex cells you could not drive monosynaptically?

STONE: We didn’t make any quantitative tests. There were no obvious qualitative differences, such as one group being consistently direction selective and the other not.

COOPER: How do your results compare with those of Baumgartner et al.?

STONE: Denney, Baumgartner, and Adorjani tested the response latencies of simple and complex cells some years before our work. We repeated their experiment and came to the opposite conclusion. It is probably fair to point out that Denney et al.’s sample of complex cells (which suggested that complex cells responded at longer latencies than simple cells) was small. Only three of their sample of 11 complex cells responded at latencies which were possibly monosynaptic. I think if they had looked further they would have found short-latency complex cells.

Striate neurons: Receptive field concepts

P. O. Bishop and C. H. Henry

In this article we want to bring into clear focus a number of ideas about the nature of the receptive fields of cortical neurons.

Definition of a receptive field

It is generally assumed that everyone knows what a receptive field is, but investigators are rarely explicit about their particular definition. Unfortunately, even if a definition is given, more often than not, no notice is taken of it. Perhaps more important than an explicit definition, however, are the unformulated assumptions or ideas that one may have about a receptive field.

In Hartline’s original use of the term “receptive field” he was referring to a single optic nerve fiber in the frog and his definition was simply “the region of the retina which must be illuminated to obtain a response” from that fiber. The definition that is now fairly generally accepted includes the whole region of the retina (or visual field) over which one can influence the firing of the cell, or, in other words, all those retinal areas that are functionally connected to that cell. Unfortunately, as we shall see, this too is a definition that is more honored in the breach than in the observance. In practice, receptive fields have nearly always been mapped, in accordance with Hartline’s original concept, as regions from which a discharge can be obtained. Since regions for discharge generally lie toward the center of the receptive field and inhibitory regions are farther out, the peripheral regions have nearly always been neglected. We shall take this matter up again later on.

Definition in terms of the visual field

For reasons that are by no means trivial, and certainly as far as cortical neurons are concerned, we believe that the definition of a receptive field should be phrased in terms