

The processing and encoding of information in the visual cortex

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Our knowledge of the response properties of visual cortical neurons has increased steadily since the original studies of Hubel and Wiesel in the 1960s. By comparison, an understanding of the neural mechanisms responsible for these properties has proved more elusive. Models for the mechanisms involved in even the most basic responses, such as the orientation tuning of simple cells in the primary visual cortex of the cat, remain controversial. Recent studies, however, are providing further support for a simple model (first suggested by Hubel and Wiesel), in which it is hypothesized that the response properties of simple cells in layer 4 of the cortex are dominated by the convergence of highly specific thalamic inputs.

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Abbreviations

LGN lateral geniculate nucleus
V1 (primate) primary visual cortex

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Introduction

In recent years, the processing of visual information in the cerebral cortex has been studied at many different levels, from synaptic physiology to functional imaging. At the finest level, new experimental strategies are being used to study the synaptic mechanisms responsible for well known visual response properties of cortical neurons. This new emphasis on synaptic mechanisms is directed at the primary visual cortex of the cat, which will be the main focus of this review.

A thorough description of the anatomy and function (i.e. the receptive fields) of the neurons that form a cortical circuit, as well as of their inputs, is required before an informative examination of the mechanisms involved can be achieved. Both multi-electrode and intracellular recording experiments are providing insight into the precise relations between presynaptic and postsynaptic neurons, as well as the mechanisms by which this input is integrated. The data they provide, in combination with the firm foundation of our understanding of visual response properties in cat lateral geniculate nucleus (LGN) and visual cortex, are making it possible to design realistic models of this cortical circuit.

In the primate, no such detailed models of the workings of its striate cortex exist, primarily because the physiology and anatomy are far more complex. For this reason, the receptive field physiology is less well known than in the cat, and, more importantly, the difficult experiments that are designed to probe the synaptic mechanisms involved, such as whole-cell recording, have not been done. There is, however, a comparatively greater knowledge of extrastriate visual regions in the primate than in the cat, which was made possible by the widespread use of the awake-behaving preparation. Although these experiments are still at a phenomenological level, it is likely that a mechanistic understanding of the extrastriate cortex will first be realized in the primate.

Cat primary visual cortex

It is generally agreed that the cat visual cortex creates oriented responses from unoriented or weakly oriented geniculate inputs [1]. By contrast, there has been little agreement on the mechanisms by which the cortex generates this orientation selectivity. The most contentious issue concerns which pathway—afferent or intracortical, excitatory or inhibitory—plays the dominant role in this circuit.

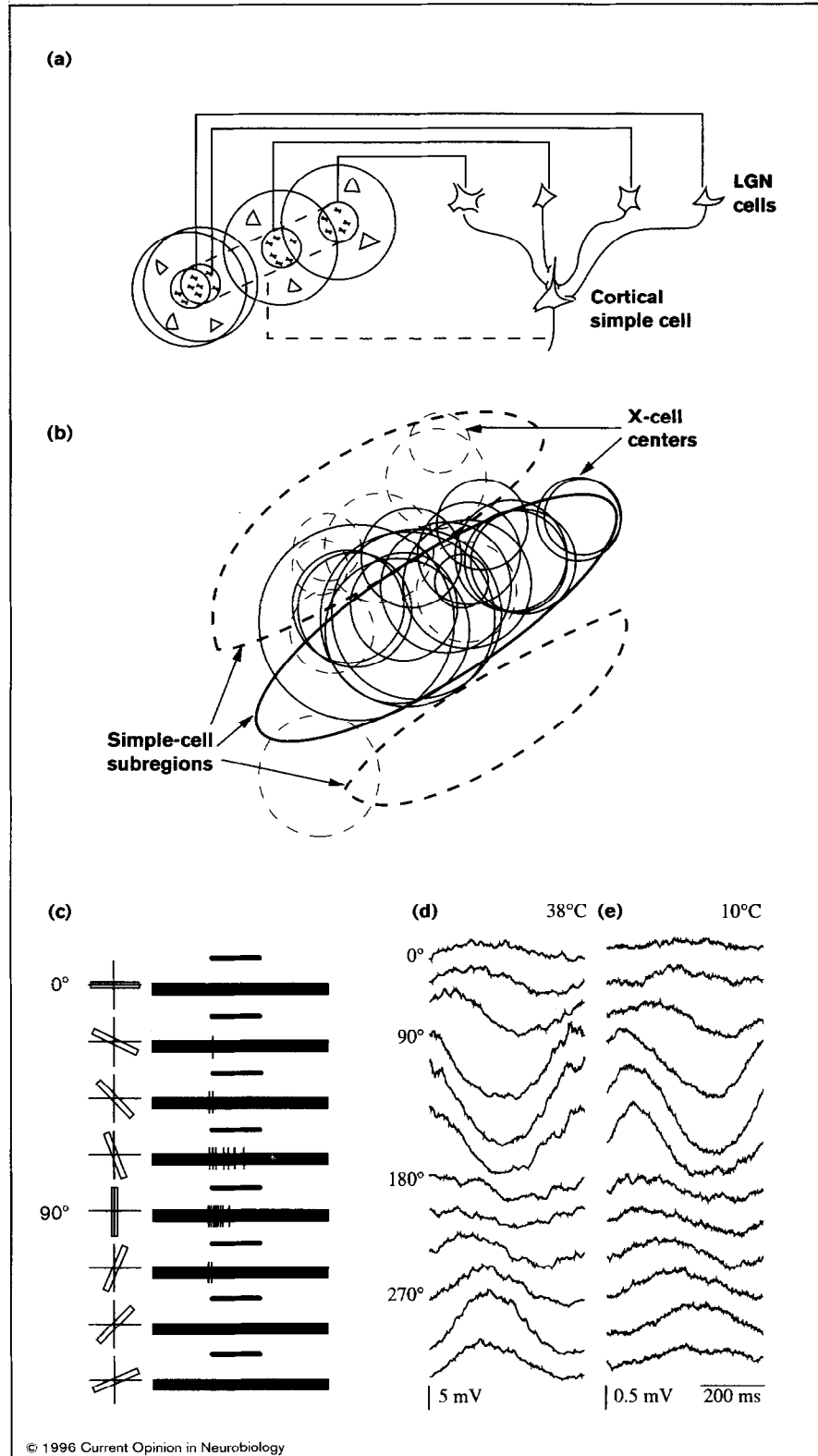
The neural connections in visual cortex can be divided into three main groups: afferent connections from the thalamus, intracortical excitatory connections, and intracortical inhibitory connections. The two types of intracortical connections can be further subdivided into local and long-distance horizontal connections. Over the past thirty years, each of the three main pathways has been elevated to a dominant role in determining cortical response properties.

Hubel and Wiesel's [1] original explanation of orientation selectivity was compelling in its simplicity. They proposed that selective connections made by geniculate afferents could account for elongated simple-cell receptive fields, and thus for orientation selectivity (Figure 1a). However, this was certainly not the only possible explanation, nor was it claimed to be. Many alternative models have been suggested over the years, with varying degrees of experimental support.

In 1975, Sillito [2] found that orientation selectivity was strongly reduced when inhibitory connections were blocked in a region of striate cortex. From this and other findings, it was proposed that intracortical inhibition was the main determinant of orientation selectivity. More recently, evidence against such a central role for inhibition has accumulated [3,4], and new models that minimize the role of strong, specific inhibition have emerged [5–7]. These models have been successful in accounting for a

Figure 1

Receptive field mechanisms in simple cells in cat area 17. **(a)** Hubel and Wiesel's [1] original model of afferent connections from LGN cells to a cortical simple cell. LGN cells, whose receptive field centers form an elongated line, project monosynaptically to a simple cell whose receptive field has the same orientation. **(b)** Summary of the data from a recent cross-correlation study by Reid and Alonso [17*] of the monosynaptic connections between LGN cells and simple cells. The elliptical regions are the central (solid lines) and flanking (dashed lines) subregions of an idealized simple cell. Actual simple-cell receptive fields were rotated and stretched to match the idealized cell. The circles represent the receptive field centers of X cells (23 out of the 74 cells studied with overlapping receptive fields) that were connected monosynaptically to a simple cell: solid line, same sign (on or off) as the strongest (central) simple-cell subregion; dashed line, same sign as the weaker, flanking subregions. The same-sign (solid) LGN cells tended to lie along the length of the central subregion, the opposite-sign (dashed) LGN centers tended to be over the more prominent flank. Thus, the wiring from the LGN to cortex is very precise, as in the original model (a). **(c)** An orientation tuning curve of a visual cortical neuron in the cat [60]. This cell responded best to a bar at 90°. **(d,e)** Orientation tuning of the intracellular potential of a simple cell, recorded with a patch electrode in a recent study by Ferster, Chung and Wheat [19**]. Responses were measured over a full 360° so that direction selectivity could be studied as well. This neuron responded best at 120° and slightly less well in the opposite direction, at 300°. **(d)** Baseline responses before cortical cooling. **(e)** Responses after the cortex was cooled to 10° C, at which point the primary drive was presumed to be from geniculate neurons. The responses are qualitatively the same and are in fact more directional in the cooled cortex. Thus, the tuning of this neuron, both for orientation as well as for direction, can be explained solely from its thalamic input.



broad range of phenomena, including Sillito's results [2], by incorporating a strong element of intracortical excitation and only a weak thalamic input [7].

But what is the evidence that the thalamic input is weak? Over the past few years, two papers on the anatomy of the cat primary visual cortex have emphasized that

the geniculocortical projection is sparse: thalamic afferents make up only 5–10% of the excitatory connections found in layer 4 [8,9]. This contradicts an earlier study [10], which estimated that the percentage is closer to 25%. Given the difficulty in interpreting these studies, an answer is not yet in hand. Whatever the final answer will be, it is clear that the number of synapses formed by a pathway need not determine its strength, because diverse mechanisms, such as the large size of thalamic synapses, synchronized input from thalamic neurons [11,12*,13*] or active conductances [14*], could play a role in boosting the efficacy of thalamic inputs.

Orientation selectivity and the thalamic inputs to cortical neurons

Despite the recent emphasis on the sparse anatomical connections from the thalamus to the primary visual cortex, the only available physiological evidence is that thalamic input is in fact quite strong. In the early 1980s, Tanaka [15] calculated the number and the strength of thalamocortical connections in the cat visual cortex using cross-correlation analysis. He found correlations in the firing patterns of single thalamic and cortical neurons that were both strong and quite fast; the cortical neuron would often fire in the range of 1–4 ms following a thalamic spike (indicative of a monosynaptic connection). When such a correlation was found between a thalamic neuron and a simple cell, between 1% and 20% of the spikes fired by the simple cell were preceded by spikes from the thalamic neuron, which was presumably only one afferent among many. Studies of correlations between visual cortical neurons (see e.g. [16]) have found correlations that were roughly ten times weaker. Therefore, the results of Tanaka's [15] study imply that the thalamic inputs may be particularly important in driving cortical neurons.

In Tanaka's [15] study, cell pairs were selected so that *on*-center geniculate receptive fields overlapped with *on* simple-cell subregions, or that *off* overlapped with *off*, according to qualitative hand-plots of receptive fields. In a recent study, we [17*] measured the same sort of correlations between thalamic and cortical neurons, but found that they are far more specific and precisely determined than previously thought. In this study, we considered all combinations of overlapping receptive fields, not just the same-sign overlaps studied by Tanaka [15]. More importantly, we measured receptive fields with a quantitative technique—reverse correlation with white noise visual stimuli—that allowed the thalamic and cortical receptive fields to be mapped simultaneously with great precision. When receptive fields were mapped in this manner, we found that the probability of finding a monosynaptic connection was strongly related to the degree of overlap between the thalamic and cortical receptive fields (Figure 1b). These results led directly to two main conclusions: first, that the thalamic inputs to simple cells are very strong (confirmation of one

of Tanaka's earlier findings [15]); and second, that the thalamic inputs are extremely specific at the level of single neurons.

Chapman, Zahs and Stryker [18] had found previously specific clustering of afferents at the level of single columns within ferret visual cortex. Our results [17*] complement their findings by showing that connections are specific at the level of individual neurons in cat visual cortex. An *on*-center thalamic afferent whose receptive field is perfectly centered over the *on* subregion of a simple cell has a very high probability of being connected to that simple cell. With even greater certainty, it will not be connected to a neighboring simple cell with a superimposed *off* subregion. These results suggest that in the geniculocortical projection, few errors are made, either of omission or of commission.

Even though the above study [17*] has provided strong evidence that the precision inherent in the Hubel and Wiesel model (see [1]) is present, the results cannot be interpreted as proving that the thalamic afferents alone are responsible for the highly tuned responses of simple cells. By the same token that a highly tuned cell can have relatively non-specific connections [5–7], a cell with very specific connections need not be very highly tuned. The results of a study by Ferster, Chung and Wheat [19**], however, provide this complementary piece of information: they found that the tuning of simple cells in the absence of cortical input is almost indistinguishable from its tuning in the intact cortex. Our study [17*] demonstrates that the geniculate inputs of a simple cell are aligned in visual space; Ferster *et al.*'s [19**] study demonstrates that this alignment is sufficient to explain the simple-cell's orientation tuning.

Ferster *et al.*'s [19**] experiment represents a technical *tour de force* in which two difficult techniques were combined. First, a whole-cell intracellular recordings of a simple cell was made, *in vivo*, and its orientation tuning was determined (Figure 1d). Second, the cortex was cooled to the point where no cortical action potentials were recorded (except perhaps in layer 6) (Figure 1e). During the cooling, the sole visual input to the simple cells was assumed to be from the thalamic afferents. Even though the amplitudes of the simple-cell responses were greatly attenuated—presumably both from the direct effects of the cooling and from the removal of intracortical excitation—the orientation tuning was almost unchanged. An intriguing observation was that the direction selectivity was likewise not diminished, and in two cases, became even more pronounced. Direction selectivity has been shown to be largely attributable to differences in the timing of inputs (either cortical or thalamic), which are then added together linearly [20–22]. Ferster *et al.*'s [19**] new results imply that the inputs from the thalamus are sufficient to provide these differences in timing [23].

The experimental results of the past year and their impact on models of orientation selectivity can be seen as the return of the pendulum to its starting point: from focusing on the contribution of the thalamic inputs, to intracortical inhibition, to intracortical excitation and back again. If the pendulum continues to swing, it is now the turn of inhibitory circuits to receive renewed interest. Clearly, none of the pathways can be the sole source of cortical orientation selectivity.

Horizontal connections

Long-range horizontal connections are a second aspect of visual cortical organization that has recently been incorporated into mechanistic schemes. The axons of single neurons in cat area 17 can extend over several millimeters of cortex [24,25], connecting neurons with rather different retinotopy. Over the past few years, several reports have described possible functional roles for these long-range connections. First, rapid changes in receptive field size ([26]; cf. [27,28]) have recently been related to changes in the strength of horizontal connections [29]. Second, de-afferentation of a cortical region by retinal lesions has been shown to produce long-term changes in the representation of visual space on the cortical surface: that is, cortical regions deprived of input reorganize so that they represent points outside the retinal lesion [30,31]. Recently, these changes have been shown to reproduce the orientation map found prior to the retinal lesion [32•]. Axonal sprouting, which has been found to accompany the long-term changes in visual receptive fields observed in de-afferented cortical regions [33•], represents a possible anatomical substrate for these topographic reorganizations.

Horizontal connections could also be responsible for visual response properties from outside the classical receptive fields [34,35]. At least some of these influences might be mediated by excitatory and inhibitory subthreshold responses [36] that are evoked by nearby cortical columns with similar orientations [37]. On a more speculative level, horizontal connections have been postulated to play a central role in the binding of features along spatially extended objects [38]. The plasticity of these connections may thus be associated with the need to form different processing groups dynamically [39].

Macaque striate cortex

Knowledge of the cat visual cortex has reached a sufficiently sophisticated level that realistic models of cat visual physiology are now feasible. However, because of the inherently more complex organization of the primate primary visual cortex (V1), detailed models of this system are still not possible. In recent work, even the fundamental response properties are turning out to be more complicated than originally envisioned.

Originally, different visual functions in V1 were thought to be strictly segregated. Hubel and Wiesel [40] found

that the parvocellular and magnocellular pathways are segregated into distinct sublaminae within layer 4C. Later, it was reported that layers 2+3 are divided into cytochrome-oxidase-rich blobs (where receptive fields were originally reported to be unoriented and sensitive to color) and interblobs (where oriented receptive fields with little selectivity for color were found) [41,42]. Some recent studies, however, have reported that the functional segregation of pathways is less strict than originally thought, both in layer 4 ([43]; see also [44] for earlier data consistent with this view) and in layers 2+3 [45–47]. To further complicate the picture, a third visual pathway—the koniocellular channel [48], which projects directly to the blobs in layers 2+3 [49]—has been receiving renewed attention. Although the koniocellular neurons are located in the seemingly sparse intercalated layers of the LGN, new staining techniques have demonstrated that they are as numerous as the magnocellular neurons [50]. What is clear is that we are far away from having a mechanistic scheme to explain the receptive field properties in primate striate cortex (although restricted models, based on those used in the cat, have been attempted [51]).

Although beyond the scope of this review, there is a much greater understanding of the physiology of extrastriate visual regions in the primate. Research over the past year has included extensive studies, notably of the middle temporal region [52–54], other higher motion areas [55], and, most recently, inferotemporal cortex [56–59]. From studies such as these, it seems likely that a mechanistic understanding of higher-order visual areas will be realized first in the primate, but this goal is still far from being achieved.

Conclusions

In studies of the visual cortex, the lag between phenomenological and mechanistic descriptions has been very long. The physiology of cat visual cortex has been well understood (with relatively little controversy) for a number of years, but it is only recently that the mechanisms behind these responses are being explored in detail. Although the study of the mechanisms involved is certainly not without controversy, the responses of simple cells in layer 4 are increasingly being found to be determined precisely by their thalamic inputs [17•,19•]. It is important to emphasize, however, that this recent work does not answer many of the old questions concerning the role of intracortical pathways, either excitatory or inhibitory. Future studies should provide more specific information about the precise connections made in these pathways and, most importantly, of their relative importance in the generation of cortical receptive fields.

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