21 Mechanisms of Image Processing in the Visual Cortex

C. ELIZABETH BOUDREAU AND DAVID FERSTER

ABSTRACT Orientation selectivity in primary visual cortex represents a crucial step in the transformation of patterns of light incident on the retina into features that define recognizable objects in the visual world. Orientation-selective responses in cortical cells can be explained well by the pattern of inputs onto the cells, indicating that the design of the network, rather than highly specialized computational abilities of individual cells, may be responsible for creating and refining their very varied and precise response properties. In addition, most properties of cells in primary visual cortex can be accounted for by a model that is largely linear and processes information primarily in one direction. These findings also indicate that the elaboration of complex feature selectivity in the visual cortex results from the careful organization of simple mathematical units.

The visual cortex dramatically transforms the neuronal representation of the visual image. The neurons of the retina and lateral geniculate nucleus (LGN) encode the contrast of the image at each point, more or less independently of the type of the image elements that give rise to local contrast. Yet the neurons of the primary visual cortex (V1), which receive the bulk of their information about the visual image directly from the LGN, encode information about the size, orientation, direction of motion, and depth of image features that fall within their receptive fields. None of this information is contained explicitly in the activity of single geniculate cells, so the cortical neurons are clearly integrating information they receive, either directly or indirectly, from a large number of geniculate inputs. In the cat, this transformation emerges almost fully articulated at the first cortical synapse, between the axons of geniculate relay neurons and the cortical recipient cells in layer 4.

The description of the cortical transformation raises many questions about its purpose. How does it benefit an organism to parse the visual image into elements of different orientation? What new abilities or limitations in visual perceptions arise from such an organization? But the visual transformation that occurs in V1 is also a compelling model of cortical information processing. The image transformation that occurs there is at once complex, and yet mathematically tractable and easily described, unlike the more mysterious processes that underlie higher cognitive tasks such as object recognition, speech, or intelligence. For those interested in how the cortex performs neuronal computations, then, V1, and in particular the way in which cortical circuitry gives rise to orientation selectivity, has been of intense and prolonged interest. The 40 years following Hubel and Wiesel's first description of cortical receptive fields have seen a remarkable and productive interaction between theory and experiment. The process has refined our understanding of the function of a fascinating and complex piece of neuronal circuitry.

Most cells in V1 are orientation selective, meaning that they are most active (produce the most action potentials) in response to the presentation of a contrast edge at a particular orientation (e.g., vertical), while edges of other orientations produce a smaller response. The relationship between response size and stimulus orientation for individual cells can be well described by Gaussian or bell-shaped mathematical functions. In cat V1, tilting a stimulus 10° away from the optimal orientation reduces a cell's response by 50% on average. As Hubel and Wiesel first demonstrated, cells within a single vertical column of the cortex all have the same preferred orientation, and the preferred orientation of each point in cortex forms an orderly map.

Although orientation selectivity is a property common to the primary visual cortices of many animal species, it is not always implemented in exactly the same way. In the cat, orientation selectivity is prevalent in all layers of primary visual cortex, and the narrowness of this selectivity does not change significantly as a function of laminar position. In the monkey, orientation selectivity is weakest in layer 4Cβ, where axons of LGN neurons terminate (Callaway, 1998; but see Ringach et al., 2002). In the ferret, as in the cat, cells receiving direct input from the LGN are very selective for orientation, on average (Usrey et al., 2003), while in the tree shrew orientation selectivity is largely absent in layer 4, emerging more strongly in layers to which layer 4 neurons project (Chisum et al., 2003). Whether these interspecies differences point to substantial variation in the mechanisms for producing orientation-selective responses is not known.

LGN relay cells exhibit weak or no selectivity for orientation, responding optimally instead to a light (ON-center

ABETH BOUDREAU and DAVID FERSTER Department of Neuroscience and Physiology, Northwestern University, Evanston, Ill.

cells) or dark (OFF-center cells) spot of the appropriate size presented in the center of their receptive fields, which are circularly symmetrical. In addition to the ON or OFF center, the receptive fields invariably have antagonistic surrounds (OFF surrounds for ON-center cells and ON surrounds for OFF-center cells), which serve to limit the relay cells' responses to large or diffuse stimuli. The surround is less sensitive per unit area then the surround, but because it is larger it tends to balance the center in total input, such that uniform illumination of the entire receptive field gives no response. In the absence of visual stimulation, most LGN cells fire action potentials spontaneously at about 15 Hz. Presentation of stimuli of the inappropriate polarity (dark in an ON-center or surround, or light in an OFF-center or surround) reduces the firing of a relay cell below its spontaneous rate, and when strong enough can completely silence the cell for brief periods.

Receptive field structure in primary visual cortex

Most neurons in primary visual cortex can be classified as either simple or complex, according to the structure of their spatial receptive fields (Hubel and Wiesel, 1962). Simple cells, similar to LGN relay cells, have distinct ON and OFF regions, but unlike relay cells, in which the ON and OFF regions are concentrically arranged, simple-cell ON and OFF regions are elongated and lie adjacent to one another. The axis of elongation is invariably the axis of the preferred orientation in simple cells. The arrangement of the subfields predicts the response of the cell to a moving bar or grating, with the cell responding as a bright bar enters an ON region or leaves on OFF region. The cells also respond vigorously to a grating of the appropriate orientation and size when the bright bar of the grating falls in the ON region simultaneously with a dark bar falling in the OFF region. As such a grating drifts across the receptive field, the firing rate or membrane potential of the cell is modulated at the drift rate of the grating. Many simple cells are located in the layers of the cortex where the axons of geniculate relay cells terminate (layers 4 and 6), and they have been shown to receive monosynaptic input from relay cells (Ferster and Lindström, 1983). Complex cells, in contrast to simple cells, have no distinct subregions in their receptive fields, responding uniformly to flashing stimuli, often with both ON and OFF responses. Nor can the spatial distribution of the flashing responses predict the response to moving stimuli, which usually consists of a single peak of activity centered on the receptive field. In response to a drifting grating, complex cells usually produce an unmodulated increase in membrane potential and firing rate. Compared to complex cells, then, simple cells behave more linearly (Movshon et al., 1978; Tolhurst and Dean, 1987; DeAngelis et al., 1993); their response to a stimulus approximates the sum of their responses to the components of the stimulus. Complex c are preferentially (though not exclusively) located in layers 3, and 5 and do not as often receive direct input from gen ulate relay cells (Ferster and Lindström, 1983).

Feedforward models for orientation selectivity

The first theoretical description of how orientation-selecti cortical simple cells are created from nonselective genicula input was proposed by Hubel and Wiesel (1962), and it su vives today as the basis for many modern models. Becaus in their model orientation selectivity arises from the spati pattern of inputs from the LGN onto individual simple cell it is known as a feedforward model of orientation selecti ity. The distinguishing feature of this and other feedforwar models is that a simple cell acts as a passive filter whos response is monotonically related to the spatial correlatio between the actual stimulus and the cell's receptive field.

Hubel and Wiesel proposed that simple cell ON and OF subregions arise directly from synaptic input from LGN ON- and OFF-center cells. An ON region, for example (figu 21.1), is generated by the combined input from several ON- center relay cells that have their receptive fields aligned in row. Given this arrangement, a light bar aligned along th centers of the ON-center cells will maximally stimulate thes cells and therefore maximally excite the simple cells. Con versely, when the orientation of the bar or grating is per pendicular to the long axis, only a small fraction of th ON-center inputs will be excited, and at the same time spon taneous activity in some OFF-center cells will be reduced The resulting excitation to the simple cells will therefore b insufficient to bring the simple cell to threshold. It is impor tant to note, however, that for a bar or grating that swee across the entire simple cell's receptive field, the *total* or int grated amount of excitation that reaches the simple cells identical. Since each individual geniculate relay cell is insen sitive to orientation, it will fire the same number of spikes i response to a stimulus of any orientation moving across i receptive field. What is different at different orientations the relative timing of the relay cell inputs. At the preferre orientation, all the inputs from a single subfield a

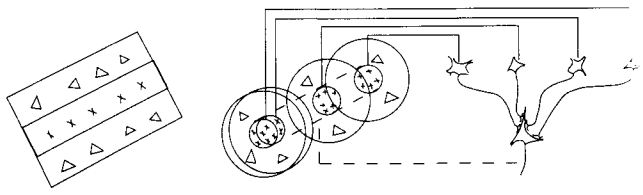


FIGURE 21.1 Hubel and Wiesel's (1962) model of orientatio selectivity in cortical cells. The receptive field of a simple cell (lef is built up from input geniculate relay cells that have their recep tive fields arranged in rows that correspond to the elongated ON and OFF subregions of the simple-cell receptive field.

neous; at a nonpreferred orientation they are distrib-
time.

rimental evidence that supports the existence of
and Wiesel's proposed connectivity scheme comes
multaneous recordings of LGN and layer 4 simple
Reid and Alonso, 1995). These authors examined pairs
ptically connected cells, where an action potential in
iculate neuron had a high probability of evoking a
the cortical neuron. For such pairs, the LGN recep-
d always overlapped simple-cell subregions of the
olarity, just as the Hubel Wiesel model predicted.

ment of the feedforward model

hough it is likely that the arrangement of relay-cell
o simple cells accounts for the spatial arrangement
ON and OFF subregions, it does not directly follow
elongated shape of the subregions can account for
cell's orientation selectivity in quantitative detail.
just the opposite appeared to be true. Given the map
receptive field of a simple cell, it is possible to predict
ntation selectivity of the cell using linear summa-
e longer and narrower the subfields, the more selec-
more sharply tuned for orientation one would expect
ple cell to be. But in most cases the cells were even
sharply tuned than the map of the receptive field
predict (Jones and Palmer, 1987; Gardner et al.,
This prompted suggestions that the generation of ori-
n selectivity is much more complex than can be
ed by the simple feedforward model and might
intracortical inhibitory interactions or excitatory
k.

mpler explanation for the failure of receptive field
o predict orientation tuning may be found in one
ant nonlinear property of simple cells: the action
ial threshold. Calculations of the orientation selectiv-
a cell derived from the receptive field map predict the
ation tuning of the *excitatory synaptic input* to a simple
t the orientation tuning of the spike output. Because
old in simple cells is considerably higher than the
membrane potential, the flanks of the tuning curve
synaptic input will invariably lie below threshold, so
e spike responses of the cell cover a smaller range of
ations than do the synaptic inputs (figure 21.2*A*, *B*).
"iceberg effect" was shown by Carandini and Ferster
and by Eysel and colleagues (1998) to narrow the ori-
n tuning measured from the action potential firing
lative to the orientation tuning measured from a cell's
input. In considering whether the synaptic input
lay cells can account quantitatively for orientation
ity, then, it is important to compare predictions made
ceptive field maps with measurements made from
ane potential fluctuations, not from spike rate, as
was done by Jones and Palmer and by Gardner and colleagues. If orientation selectivity for intracellularly recorded stimulus-evoked changes in membrane potential is compared with the receptive field structure also derived from membrane potential, agreement between the two can be quite high (Lampl et al., 2001; see also Volgushev et al., 1996).

Contrast invariance of orientation tuning

A related difficulty with the Hubel Wiesel model concerns the effect of stimulus contrast on orientation tuning of simple cells. The responses of LGN cells become stronger in proportion to increasing stimulus contrast, so their input to cortical cells will become greater as well (figure 21.2*A*). Because the responses of LGN cells are not selective for orientation, the synaptic input to the simple cell will increase at all orientations, and the orientation tuning curve will therefore be scaled up with increasing contrast. The problem arises when one considers how this scaling of input will affect the orientation tuning of the spike output of the cell. Because of the threshold-linear relationship between membrane potential and spike rate, a proportional increase in membrane potential response at all orientations will result in a disproportionately larger increase in responses at orientations away from the preferred. So the feedforward model appears to predict that at higher contrast, the orientation tuning of the spike responses of a simple cell should broaden. In real cortical cells, however, orientation tuning is invariant with contrast (Sclar and Freeman, 1982; Anderson, Lampl, et al., 2000). Neurons remain equally selective for orientation at all contrasts, and never respond to stimuli of orientations orthogonal to the preferred orientation (figure 21.2*C*). This is true of responses measured both intracellularly and extracellularly.

To account for this discrepancy, modelers have invoked inhibition in a variety of forms to reduce unwanted responses to the orthogonal orientation. Because there is no direct inhibitory input from the LGN to V1, all inhibitory mechanisms are understood to be cortical. One possibility is a feedforward form of inhibition that is exactly the inverse of the receptive field map of the cortical cell it inhibits, called push-pull or antiphase inhibition (Tolhurst and Dean, 1990; Troyer et al., 1998). ON-excitation is balanced or dominated by OFF-inhibition, and the reverse, at all points in the receptive field map. In this model, presentation of a grating at the preferred orientation will result in maximal excitation and minimal inhibition when the stimulus is in phase with the receptive field structure, and minimal excitation and maximal inhibition when it is opposite in phase. An orthogonally oriented stimulus will evoke an approximately equal (or even greater) amount of inhibition and excitation at all times as it crosses the receptive field, and increasing the contrast will increase the excitation and inhibition

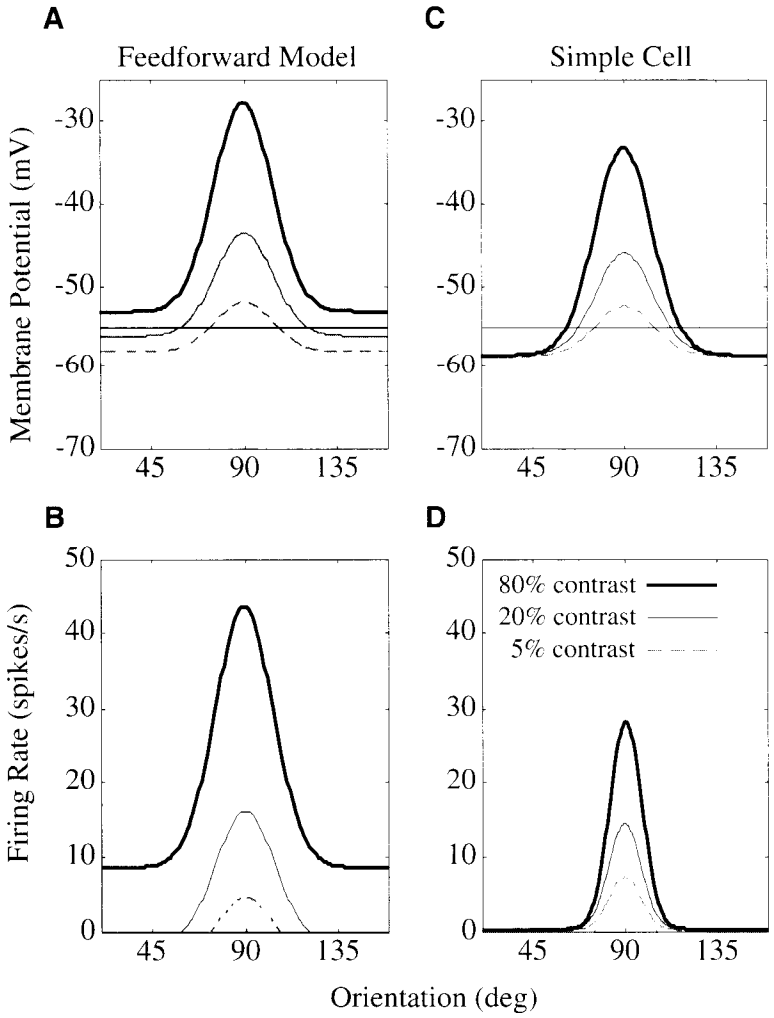


FIGURE 21.2 The problem of contrast invariance of orientation tuning. (*A*) The orientation tuning curves of membrane potential generated in a simple cells by synaptic input from geniculate relay cells arranged according to Hubel and Wiesel's feedforward model. The amplitude of the curves grows equally at all orientations as contrast increases, since the activity in geniculate relay cells also increases with increasing stimulus contrast. (*B*) The orientation tuning of the cell's spike output at different contrast, as predicted from applying a fixed threshold to the tuning curves in *A*. (*C* and *D*) A schematic of the orientation tuning recorded in cortical simple cells (*C*, membrane potential; *D*, spike rate).

proportionally, so that they continue to balance each other and result in no net excitation of the cortical cell. Because there is no physiological evidence for direct inhibition from the LGN to V1 (Freund et al., 1989; Callaway, 1998), antiphase inhibition would be mediated by inhibitory connections between cortical cells with complementary receptive field structures.

Push-pull inhibition in response to the preferred stimulus orientation is well demonstrated by intracellular recordings of membrane potential and conductance (Ferster, 1988; Hirsch et al., 1998). In these studies, receptive fields were mapped with light and dark spots, and then responses to stimuli of the nonpreferred polarity were tested at different locations within the receptive field. The results showed that, when a light stimulus was placed in an OFF subregion, for example, the total synaptic input to the cortical cell increased and the cell membrane hyperpolarized, implying that the increase was due to greater inhibitory input. Although a reduction in excitation would also cause a hyperpolarization of the membrane, this would be associated with a decrease, not an increase, in total synaptic input. Evidence for strong or dominant inhibition at the null orientation is more equivocal. Monier and colleagues (2003) see strong cross-oriented inhibition in a subset of cortical cells. Ferster (1986) and Anderson, Carandini, and colleagues (2000) found that inhibitory and excitatory input to cortical cells are tuned to the same orientation and have similar orientation tuning width. Although there was some inhibition evoked at nonpreferred orientations, it is not clear that the observed inhibition was strong enough to explain

the lack of a depolarizing response at high contrasts and nonpreferred orientations.

Voltage-to-action potential transformation

The importance of the action potential threshold in converting membrane potential responses into the output of cortical cells has been highlighted already in this chapter. As mentioned earlier, an important consequence of antiphase inhibition, supported by the data, is that the orientation tuning of the synaptic input to cortical neurons should be contrast invariant. However, the orientation tuning of extracellularly measured action potentials is also contrast invariant. The application of a single threshold to the contrast-dependent tuning curves in figure 21.2*C* will result in an iceberg effect that appears to broaden orientation tuning with increasing contrast. It is unlikely that the action potential threshold of neurons changes in response to stimuli of different contrasts.

There is, however, a physiological reason why a flat threshold is not an accurate picture of the relationship between membrane voltage and action potential generation. This is simply the trial-to-trial variability of the responses of neurons (Anderson, Carandini, et al., 2000). The tuning curves of figure 21.2 are constructed from the average responses to many repeats of the same stimulus. For example, the spike threshold is often near or above the largest *average* response to a stimulus at the optimal orientation and the highest contrast. But such a stimulus, and many less effective ones as well, can evoke spikes, because on some individual trials the membrane potential exceeds threshold. The major difference between a high-contrast and low-contrast stimulus is not so much the size of the responses evoked but on how many trials a suprathreshold response occurs. The effect of this variability in response is shown in figure 21.3. A single threshold value can be represented as a linear function with a non-zero *x*-intercept (figure 21.3*A*). When the noise has depolarized the cell, it is as if the threshold were shifted down slightly for that trial; that is, the stimulus has to depolarize the membrane potential less in order to evoke spikes. When the noise hyperpolarizes the cell, the reverse is true. The average input-output function of the cell can be derived by averaging together the threshold functions for all trials (figure 21.3*B*). This average is no longer a threshold linear function but rather can be well approximated by a power law (Hansel and van Vreeswijk, 2002; Miller and Troyer, 2002). This smoothed curve, when applied to the Gaussian-like orientation tuning curves at different contrasts, narrows each one equally and thereby maintains contrast invariance both in membrane voltage and in action potential rate. The power law input-output function and the Gaussian-shaped tuning curves are the only tuning curves that show this property.

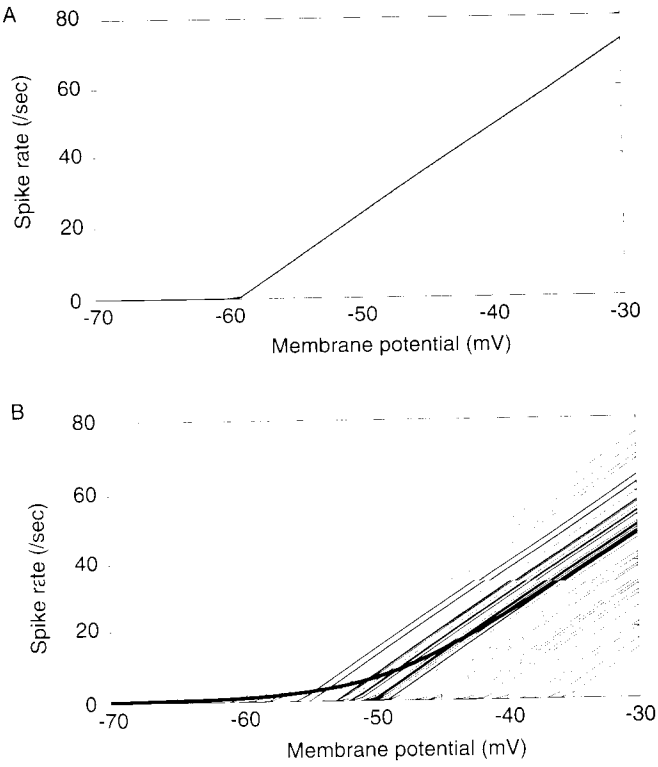


FIGURE 21.3 The effect of noise on the input-output relationship of a neuron. *A*: The standard threshold-linear relationship between membrane potential and spike rate observed in most cells. *B*: In the presence of noise, the curve is effectively shifted left or right on different stimulus trials. That is, when noise depolarizes the cell, a stimulus can be that much smaller and still evoke action potentials. When the noise is evenly distributed around the resting potential, then the average input-output curve over many trials can be approximated by a power law (thick curve).

Feedback models of orientation selectivity

Another explanation for the generation of orientation selectivity relies heavily on the organization, both laminar and columnar, of cortex. This class of models is known as feedback models, and their orientation tuning derives from recurrent excitatory connections that amplify responses to the preferred orientation and lateral interactions among neurons with different orientation preferences that damp down unwanted responses to the null orientation (Ben-Yishai, Bar-Or, and Sompolinsky, 1995; Somers, Nelson, and Sur, 1995). A generalized schematic of feedback model connectivity is shown in figure 21.4.

Feedback models have the advantage of requiring very simple rules for the connections between neurons. They can be implemented in networks in which cells are excited by and inhibited by all of their neighbors, with the strength of these connections declining uniformly with increasing distance between cells (McLaughlin et al., 2000). Others propose excitatory connections between cells of like

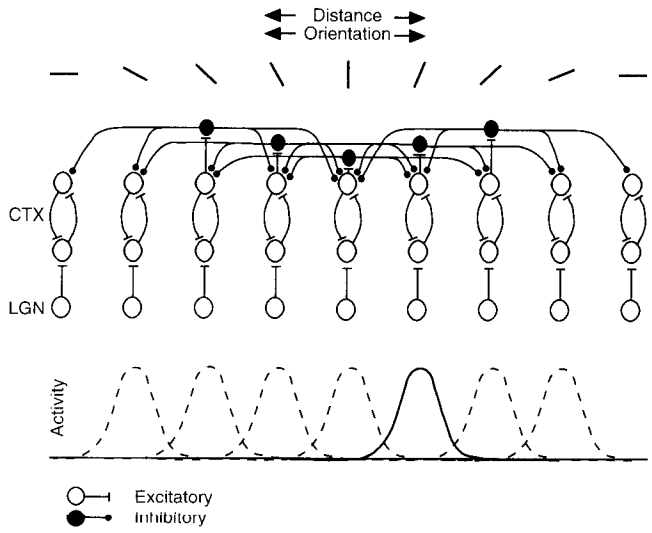


FIGURE 21.4 A schematic of feedback models of orientation selectivity. The horizontal axis represents distance along the cortical surface, and by virtue of the orientation maps on the surface of the cortex, orientation as well. Neurons within a column excite one another; neurons in adjacent columns inhibit one another. Such a circuit can take up any one of a number of stable states (multistable attractor) in which activity is confined to a single column. Each state is a winner-take-all outcome in which the maximally active column is suppressing activity in neighboring columns.

orientation preference and inhibition between cells that prefer opposite orientations. This results in a winner-take-all behavior in which stimulation that only weakly activates cells of one orientation preference will eventually result in a strong and stable representation of that orientation in the cortical network. Such models are very stable and resistant to noise in the visual stimulus, but it has important implications for the role of cortex in representing the visual world. Instead of passively filtering visual input, feedback models can actually impose their internal representation of the world on incoming visual images.

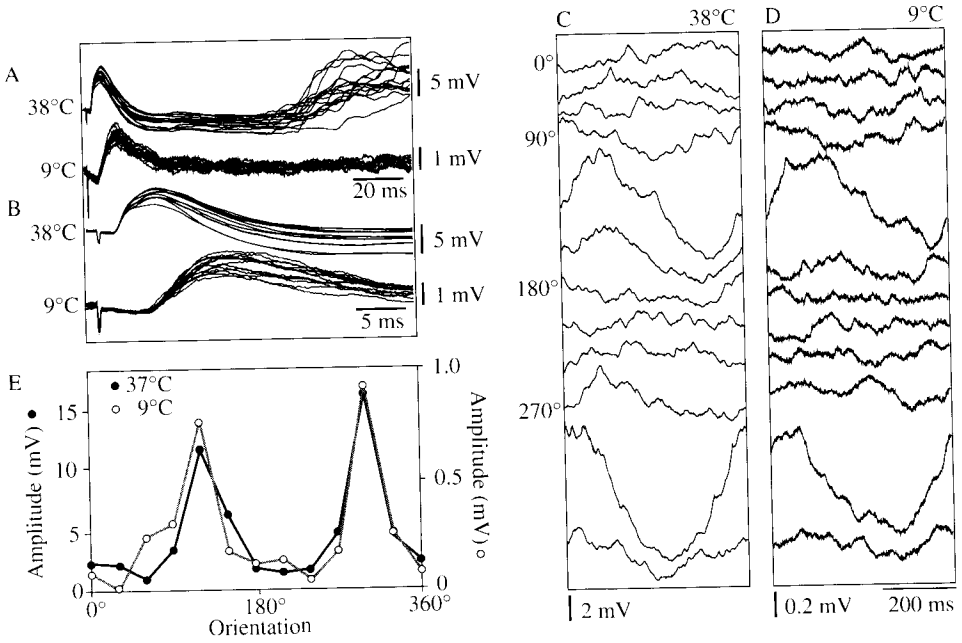
Because the width of orientation tuning in these models is dependent on cortical architecture, it is independent of stimulus parameters and contrast invariance of cortical responses is achieved automatically. However, this also means that these models are incapable of explaining observed changes in the width of orientation tuning with stimulus parameters such as spatial frequency (Webster and DeValois, 1985; Hammond and Pomfrett, 1990; discussed in Troyer et al., 1998).

Evidence for the lateral inhibition between neurons of different orientation preference comes from pharmacological experiments. Suppressing inhibition by the applications of $GABA_A$ antagonist such as bicuculline, for example, result in a nonspecific elevation of cortical excitability (Sato et al., 1996; Eysel et al., 1998; Sillito, 1975; Pfleger and Bonds, 1995). These manipulations cause a loss of orientation selectivity measured extracellularly, but this effect can potentially be ascribed to a nonspecific increase in excitability, effectively raising previously subthreshold responses above the action potential threshold in a reverse iceberg effect. The bicuculline will affect not only the recorded cell but also any synaptic inputs from nearby cells, thus amplifying any nonspecific effects on loss of tuning. Intracellular application of the GABA antagonist muscimol in individual cells (Nelson et al., 1994) did not alter orientation selectivity. Inactivation of layer 6 cells (Allison and Bonds, 1994) or of layer 2/3 of cortical columns with different orientation preference (Eysel et al., 1992) by extracellular application of GABA has also been reported to broaden orientation tuning in upper cortical layers.

Estimating the contribution of cortical inputs to orientation selectivity

How can one determine whether feedforward input or feedback reverberation is more important in the generation of orientation selectivity? One critical prediction of the feedback models is that orientation tuning depends critically on synaptic interactions among cortical neurons. In feedforward models, orientation tuning depends only on the spatial organization of the input from geniculate relay cells. When spiking activity in cortical neurons is suppressed, therefore, the feedback models predict that orientation selectivity of the remaining synaptic input should be severely degraded, whereas feedback models predict that orientation selectivity of the remaining synaptic input should be nearly unchanged. To test these predictions, Ferster, Chung, and Wheat (1996) used cooling to reversibly inactivate the cortical network. This procedure reliably silenced most cortical layers, and drastically reduced activity in the deepest layers (farthest from the cooling element). Input from the LGN was also reduced in amplitude because of the direct effect of cooling on the terminals of the geniculate axons, but was otherwise unaffected. Intracellular recordings of individual layer 4 simple cells during cooling revealed that visually evoked responses were greatly reduced, but the orientation tuning of those responses was not changed.

The effects of cooling on a cortical simple cell are shown in figure 21.5*A* and *B* show the effects of cooling (at two different horizontal gains) on the responses of the neuron to electrical stimulation of the LGN. These records are important for demonstrating that the cooling has suppressed intracortical inhibition (note the lack of hyperpolarization in the 9°C traces) and the cooling has suppressed the responses of excitatory cortical neurons (note the lack of postinhibitory rebound in the second trace compared to the top trace). In addition, the cooling has noticeably slowed the responses. Figure 21.5*C* and *D* contain the responses of the cell to drifting sinusoidal gratings of different orientations. The



...RE 21.5 (*A*) The responses of a cortical simple cell to electri- ...stimulation of the LGN with the cortex at normal and cooled ...peratures. During cooling, the initial evoked EPSP is reduced ...ize by fivefold and increased in latency. The longlasting inhibi- ... that follows the EPSP is completely suppressed, as is the ...inhibitory rebound excitation. (*B*) The traces in *A* at a higher ...zontal gain. (*C*) The response of the cell to drifting sinusoidal ...ings at different orientations. Each response shown is the average of 20 stimulus cycles. (*D*) Same as *C* but with the cortex cooled. Note the difference in vertical scale from *C*. (*E*) Orientation tuning curves drawn from the traces of *C* and *E*. Each point is the peak-to-peak amplitude of the first harmonic of the Fourier transform of the corresponding record. Cooling was done by a Peltier device attached to a copper plate, the end of which (4 × 4 mm) was placed on the surface of the brain. Intracellular recording electrode were inserted into the cortex through a small hole in the plate.

...sponses are reduced 10-fold in amplitude by the cooling ...mpare the vertical scale bars in *B* and *C*), and yet the ori- ...ation tuning is affected little. That the shape of the ori- ...ation tuning has hardly changed can be seen ...antitatively from the tuning curves drawn from the two ... of traces (figure 21.5*E*). These results were typical for ... 10 cells studied. They suggest that about 30% of the ...ut to simple cells arises from the LGN, with the other ... of the input coming from other cortical neurons. But ...re was little evidence that this cortical input was required ...make cortical cells orientation selective, since the genicu- ... input remaining during cooling is fully orientation selec- ... on its own.

In a second experiment (Chung and Ferster, 1998), elec- ...al stimulation rather than cooling was used to inhibit ...rtical activity. The stimulation induces a strong, longlast- ... 100–200 ms) inhibition in all nearby cortical cells, ...ing which visual stimulation fails to evoke cortical spikes. ...ain, geniculate activity is left intact. Any excitatory synap- ...nputs recorded during the inhibition should therefore ... not from cortical cells but almost purely from genicu- ... input. The responses of two cortical simple cells to ...ed gratings of different orientation are shown in figure ...1 and *C*, with and without a preceding shock in the ...ex nearby (thick and thin traces). The responses to the gratings preceded by cortical stimulation are reduced in amplitude, both because the shock evokes a shunt in the recorded cell and because the components of the response mediated by other cortical cells are suppressed by the shock. The relative size of the responses to different orientations, however, is largely unaffected, so that orientation selectivity is not much changed. Figure 21.6*B* and *D* show three tuning curves: one taken from drifting gratings at 12 orientations, one taken from the responses to flashed grating of *A* and *C* recorded without cortical shock, and one taken from the responses to flashed gratings with cortical shock. The tuning curves all have comparable widths after being normalized to their peak amplitudes. A comparison of the width of tuning with and without cortical shock for nine cells is shown in figure 21.6*E*. Since orientation tuning of synaptic potentials was found to be unchanged during the suppression of cortical activity, it seems likely that the aggregate input from geniculate relay cells is by itself as well tuned for orientation as the total input from cortex and geniculate combined. These results strongly support a dominant role for feedforward input in determining orientation tuning of simple cells. Although the cortical circuit clearly has role in amplifying visual responses, these experiments show that orientation selectivity can be maintained even when the cortical network is disrupted.

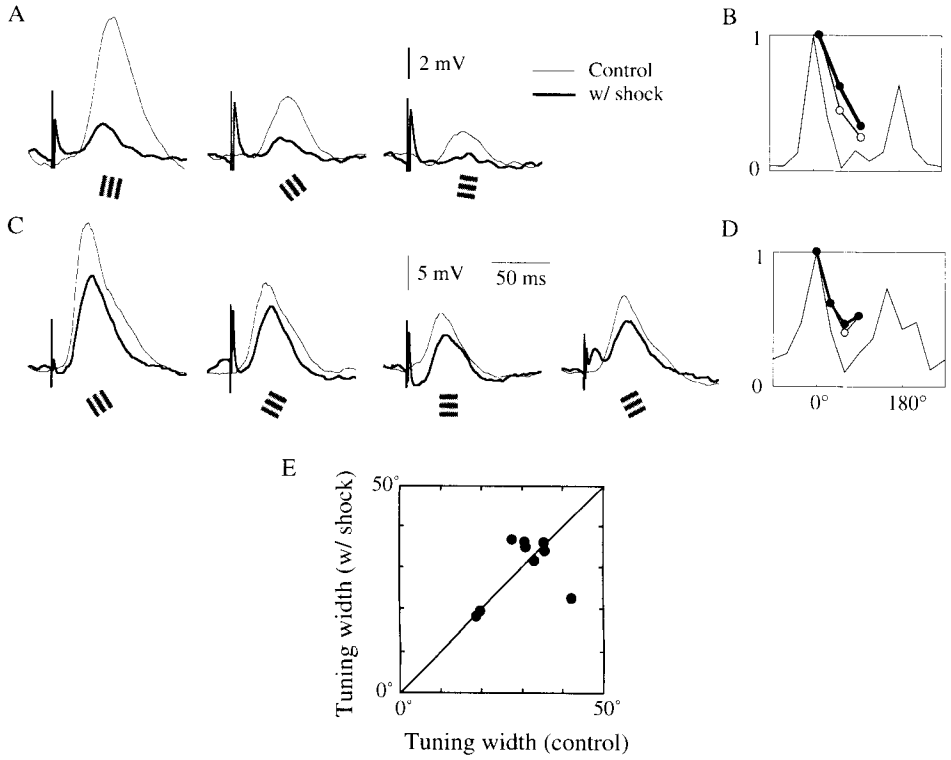


FIGURE 21.6 (*A*) The response of a simple cell to briefly (20 ms) flashed gratings confined to the classic receptive field. Grating orientation is indicated below each set of traces. Thin traces are control data. For the thick traces, an electrical stimulus to nearby cortex was delivered at the end of the flash. The shock reduces the amplitude of the response by introducing a shunt into the recorded cell and by suppressing the spike response of other cortical cells. What remains is therefore likely to arise almost exclusively from synaptic excitation from the LGN. (*B*) Orientation tuning curve derived from the responses in *A* (open and closed circles) and from drifting gratings at 12 different orientations. Each of the three curves is normalized to its own peak. (*C* and *D*) Similar data to *A* and *B* for a second simple cell. (*E*) A comparison of the width of tuning for control and shock data for nine cells. To obtain the tuning widths, curves similar to those in *B* and *D* were fitted to a Gaussian.

Dynamics of orientation tuning

Another experimentally testable difference between feedforward and feedback models of orientation tuning concerns the time course of orientation-tuned responses to brief stimuli. Feedback models, which propose that initial excitatory input to the cortex is largely untuned, also predict that as the initial responses are propagated through the cortical circuitry and fed back as orientation-selective signals to the cells, the orientation tuning of the response will be seen to sharpen. Such an effect has been reported in extracellular recordings in monkey visual cortex (Ringach et al., 1997; Shapley et al., 2003). Although most cells in the input layer 4β were not found to sharpen, some cells in other layers showed a change in their tuning characteristics over time, consistent with feedback models. Another extracellular study (Mazer et al., 2002) failed to find a change in the shape of orientation tuning over time, but the time sampling of their data may have been too coarse to resolve such changes. A study performed intracellularly in the cat (Gillespie et al., 2001) found no sharpening of orientation tuning over time in cells of any layer. However, about 50% of cells in the sample showed a subtractive reduction in membrane potential over time, consistent with an increase in inhibition. As discussed earlier, shifting the membrane potential relative to the action potential threshold will narrow the orientation tuning of the extracellularly measured response without altering the selectivity of the synaptic inputs. These recent studies had the advantage of using stimulus presentation methods in which orientation was changed without large contrast changes. Earlier attempts to measure the time course of orientation selectivity of the membrane potential (Pei et al., 1994) were complicated by orientation-nonspecific contrast responses to the sudden onset of the flashed bar stimuli that were used.

Conclusions

Although there is not universal agreement on this point, there is a great deal of evidence that orientation selectivity in simple cells of the cat visual cortex is determined largely by the spatial organization of geniculate input, just as Hubel

: Wiesel (1962) proposed. Inactivation of the cortical uit does not cause a collapse of the orientation tuning of aptic inputs to simple cells. And orientation tuning of ple cells can be linearly predicted from the receptive field p). Both inhibition and excitation may be involved in plifying the geniculate input, removing its nonspecific or tuned component, and perhaps normalizing the cortical put (Troyer et al., 1998). But these operations can be mplished with nonspecific or orientation-independent uts that do not fundamentally alter the response properties or receptive field structure laid down by geniculate itation.

At same time, the distribution of orientation selectivity in tical cells is very broad, indicating that not all cells need are the same mechanism for its generation. There is the sibility that complex cells, or cells outside layer 4, may rive their orientation selectivity by different means. In dition, cortical mechanisms in primate visual cortex may fer from those in the cat.

Despite questions that remain unanswered about the specific implementation of orientation tuning in primary visual rtex, the general lessons of the study of this transformation of sensory information may provide guidelines for the nderstanding of other aspects of sensory processing. That ew properties can be conferred upon neurons by the specific pattern of their excitatory connections, that inhibition important for counteracting the development of unwanted nonspecific responses, and that the noisiness of neurons can be used constructively to enhance their representation of rtain stimulus attributes are ideas that may eventually help explain much more complex and varied aspects of visual rocessing.

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