



Predictions of a Recurrent Model of Orientation Selectivity

MATTEO CARANDINI,*† DARIO L. RINGACH‡

Received 3 January 1997; in revised form 21 March 1997

Recurrent models of orientation selectivity in the visual cortex postulate that an initially broad tuning given by the pattern of geniculate afferents is substantially sharpened by intracortical feedback. We show that these models can be tested on the basis of their predicted responses to certain visual stimuli, without the need for pharmacological or physiological manipulations. First, we consider a detailed recurrent model proposed by Somers, Nelson and Sur [(1995) *Journal of Neuroscience*, 15, 5448–5465] and show that it can be simplified to a single equation: a center-surround feedback filter in the orientation domain. Then, we explore the responses of the simplified model to stimuli containing two or more orientations. We find that the model exhibits peculiar responses to stimuli containing two orientations, such as plaids or crosses: if the component orientations differ by less than 45 deg the model cannot distinguish between them; if the orientations differ by more than 45 deg the model overestimates their angle by as much as 30 deg. Moreover, the model cannot signal the presence of three orientations separated by 60 deg (it responds as if there were only two orientations), and the addition of two-dimensional visual noise to an oriented stimulus results in strong spurious responses at the orthogonal orientation. We argue that the effects of attraction and repulsion between orientations and the emergence of responses at off-optimal orientations are common to a wide class of feedback models of orientation selectivity. These models could thus be tested by measuring the visual responses of cortical neurons to stimuli containing multiple orientations. © 1997 Elsevier Science Ltd

Orientation Striate cortex Model Plaid Noise

INTRODUCTION

The question of how orientation selectivity arises in primary visual cortex (V1) has been the object of debate since the original work of Hubel & Wiesel (1962). The main issue is whether the pattern of convergence provided by the inputs from the lateral geniculate nucleus (LGN) to the primary visual cortex could be solely responsible for the sharp orientation tuning observed in V1 cells, as first suggested by Hubel and Wiesel (Chapman *et al.*, 1991; Ferster, 1987; Ferster *et al.*, 1996; Pei *et al.*, 1994; Reid & Alonso, 1995, 1996; Vidyasagar *et al.*, 1996). Alternative models have been proposed where an initially broad tuning provided by the pattern of LGN inputs is substantially sharpened by intracortical feedback (Ben-Yishai *et al.*, 1995; Douglas

et al., 1995; Maex & Orban, 1996; Somers *et al.*, 1995; Suarez *et al.*, 1995). According to these recurrent (or feedback) models, cortical cells receive excitatory feedback from neurons tuned to similar orientations and inhibitory feedback from cells tuned to a broader range of orientations.

A particularly successful recurrent model has been proposed by Somers *et al.* (1995). This model replicates the sharp tuning observed in striate cells and predicts the effects of some pharmacological manipulations, such as the blockage of inhibition in a patch of cortex (Sillito *et al.*, 1980) and in a single cell (Nelson *et al.*, 1994). The model incorporates a large body of anatomical and physiological data. It includes three stages of visual processing: retinal ganglion cells, the LGN, and layer IV in the primary visual cortex; it describes cortical cells as modified integrate-and-fire neurons, with different properties for excitatory and inhibitory neurons; it allows for variability in the strength of connections between cells and for noise in the geniculate inputs.

This high degree of detail has, however, some disadvantages: the model contains tens of free parameters which make it difficult to fit to experimental data and to understand intuitively. To overcome these difficulties we have sought to simplify the detailed model as much as

*Department of Neurobiology and Physiology, Northwestern University, Evanston, IL 60208, U.S.A.

†To whom all correspondence should be addressed at: Center for Neural Science, New York University, 4 Washington Place #809, New York, NY 10003, U.S.A. [Tel: (212) 998 7881; Fax: (212) 995 4011; Email: matteo@cns.nyu.edu; WWW <http://cns.nyu.edu/home/matteo>].

‡Center for Neural Science, New York University, New York, NY 10003, U.S.A.

possible. We show that the model can be reduced to a single equation while retaining its explanatory power and quantitative behavior. The resulting simplified model is very similar to one proposed by Ben-Yishai *et al.* (1995). It operates in the orientation domain, and consists of a feedback filter with a "center-surround" weighting function. The intracortical feedback results in lateral inhibition in the orientation domain which sharpens the initially broad tuning given by the spatial pattern of LGN afferents. The model is described by only eight parameters, it runs in seconds on current personal computers, and its workings can be intuitively understood.

In this study we provide a full description of the simplified recurrent model (Methods) and demonstrate that it closely replicates the workings of the detailed model by Somers *et al.* (1995). In particular, we show that the simplified model amplifies and sharpens the orientation tuning provided by the LGN inputs in response to oriented stimuli such as gratings and bars.

In an effort to generate testable predictions of the recurrent model we studied the simplified model's responses to a variety of visual stimuli containing two or more orientations. We found that the model responses display peculiar properties, including substantial attraction or repulsion between orientations and the emergence of strong responses at spurious orientations in the presence of visual noise. As a result, the orientation tuning of model cells measured with stimuli containing multiple orientations is substantially different from that measured with stimuli containing a single orientation. This systematic difference constitutes a prediction that could be tested experimentally.

We also examined how the responses of the recurrent model to stimuli containing multiple orientations depend on the precise tuning of the intracortical feedback. Specifically, we considered alternative models, in which the tuning of intracortical inhibition is broader or sharper than in the recurrent model of Somers *et al.* (1995). We found that some of the effects in the responses to multiple orientations depend on the tuning of intracortical feedback. We argue, however, that the attraction/repulsion of orientations and the appearance of spurious responses at off-optimal orientations is a property of a wide class of feedback models. Similar effects have been predicted, for example, by an early feedback model of orientation selectivity (Blakemore *et al.*, 1970).

METHODS

The "simplified model" employed in this study was designed to capture the basic mechanism at work in the "detailed model" of orientation selectivity proposed by Somers *et al.* (1995). This section provides a full description of the simplified model. The variables and parameters used are listed for reference in Table 1.

Consider a group of cortical neurons which are identical in every respect but in their preferred orientations. The orientations range between -90 and $+90$ deg. Differences between orientations are always taken

TABLE 1. Symbols and parameters in the simplified model

Symbols	
V	Membrane potential (mV)
V^{LGN}	Synaptic potential due to geniculocortical excitation (mV)
V^{EXC}	Synaptic potential due to intracortical excitation (mV)
V^{INH}	Synaptic potential due to intracortical inhibition (mV)
R	Spike rate (spikes/sec)
E	Probability of intracortical excitation
I	Probability of intracortical inhibition
c	Stimulus contrast
θ	Orientation column or stimulus orientation (deg)
t	Time (sec)
Parameters	
τ	Membrane time constant (15 msec)
α	Gain of spike encoder (15 spikes/sec/mV)
J_E	Strength of intracortical excitation (0.115 mV/spikes/sec)
J_I	Strength of intracortical inhibition (0.25 mV/spikes/sec)
J^{LGN}	Strength of geniculocortical excitation (3.2 mV/contrast)
σ_E	Width of intracortical excitation (7.5 deg)
σ_I	Width of intracortical inhibition (60 deg)
σ^{LGN}	Width of geniculocortical excitation, oriented stimulus (23 deg)

In parentheses, the values used in the simulations to approximate the detailed model by Somers *et al.* (1995).

modulo 90 deg. Since the neurons are identical, the response of the neuron tuned to orientation ϕ to a stimulus with orientation θ depends only on the difference $\theta - \phi$. The dependence of the response on this difference can be seen either as the pattern of activity across different orientation columns caused by a given stimulus, or as the tuning curve of a given neuron measured with different stimulus orientations.

We model neurons as single passive compartments obeying the linear differential equation,

$$\tau \partial V / \partial t + V = V^{\text{LGN}} + V^{\text{EXC}} - V^{\text{INH}}. \quad (1)$$

Here, $V(\theta, t)$ is the membrane potential of the cells in the orientation column θ at time t , τ is the membrane time constant, V^{LGN} represents the excitatory synaptic potential due to the LGN inputs, while V^{EXC} and V^{INH} are the synaptic potentials due to intracortical excitation and intracortical inhibition.

For the purposes of this study, we do not find it necessary to distinguish between excitatory and inhibitory neurons. Each model neuron can be assumed to provide both excitation and inhibition to the others. Alternatively, the output of each model neuron can be considered to reflect the activity of two groups of neurons, one excitatory and one inhibitory.

In addition, rather than representing the output of each unit as a series of action potentials, we consider this output to be a continuous quantity, a measure of the instantaneous firing rate. We assume this firing rate to be zero for membrane potentials below a threshold (taken to be $V = 0$ for simplicity) and to grow linearly with slope α above threshold:

$$R = \alpha \max(V, 0). \quad (2)$$

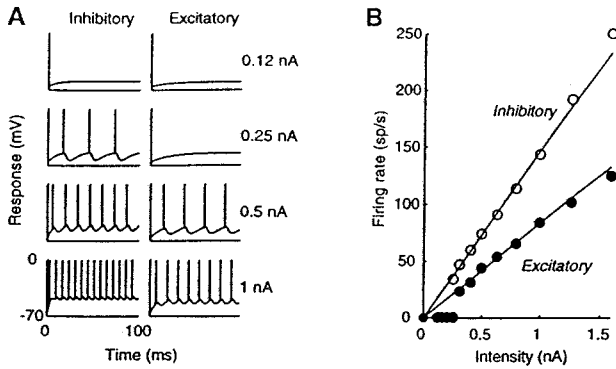


FIGURE 1. Approximation of integrate-and-fire cells with linear voltage-firing rate encoders. (A) Responses to four current step injections of the excitatory and inhibitory integrate-and-fire cells employed in the detailed model (Somers *et al.*, 1995). Cells were assumed to be at rest and to receive no synaptic input. (B) Dependence of firing rate on injected current. Above threshold the dependence is roughly linear, as shown by the dashed lines fitted to the data. In the simplified model we exploit this by considering the neurons as producing continuous firing rates rather than individual spikes, and by having the firing rate grow linearly with the membrane potential.

As illustrated in Fig. 1, this assumption is consistent with the behavior of the modified leaky integrate-and-fire neurons used in the detailed recurrent model of Somers *et al.* (1995). For the gain α of the spike encoder we choose a value of 15 spikes/sec per mV, which was found to be intermediate to those of the excitatory and inhibitory neurons in the detailed recurrent model. To avoid implausible high firing rates we impose a ceiling of 300 spikes/sec. This ceiling was seldom reached in our simulations.

The excitatory potential contributed by a cell in the orientation column ϕ to the cell in the orientation column θ is given by the response $R(\phi)$ of the first cell times the probability $E(\theta - \phi)$ of excitatory connection between the two, times a factor J_E weighting the efficacy of intracortical excitation. A similar statement applies to inhibition, with E replaced by I , and J_E replaced by J_I .

Integration over all orientation columns results in the following two expressions for the excitatory and inhibitory intracortical synaptic potentials on the cell in the orientation column θ :

$$V^{\text{EXC}}(\theta, t) = J_E \int_{-90^\circ}^{90^\circ} E(\theta - \phi) R(\phi, t) d\phi \quad (3)$$

$$V^{\text{INH}}(\theta, t) = J_I \int_{-90^\circ}^{90^\circ} I(\theta - \phi) R(\phi, t) d\phi.$$

The tuning of excitatory and inhibitory connections used is illustrated in Fig. 2(A). These curves are identical to those used in the detailed recurrent model: excitatory connections are normally distributed with standard deviation $\sigma_E = 7.5$ deg, while inhibitory connections have a broader tuning and are described by a normal distribution with standard deviation $\sigma_I = 60$ deg truncated at σ_I . The sum of the synaptic strengths of excitation and inhibition results in the center-surround feedback filter depicted in Fig. 2(B).

Visual stimulation is modeled as a pattern of cortical activity caused by the summed inputs from the LGN. An oriented stimulus, such as a grating or a bar, is assumed to induce a pattern of activity in the cortex that is strongest for neurons tuned to the stimulus orientation and gets progressively weaker for neurons tuned to different orientations. In principle, this tuning contributed by the LGN inputs could result from an alignment in the pattern of LGN inputs to the individual cortical cells, by an orientation bias in the individual LGN cells, or by a combination of both. In quantitative terms, a stimulus with orientation ϕ and contrast c is assumed to cause the following synaptic potential in a cortical neuron with preferred orientation θ :

$$V^{\text{LGN}}(\theta) = J_{\text{LGN}} c \exp \left[-(\theta - \phi)^2 / (2\sigma_{\text{LGN}}^2) \right]. \quad (4)$$

Here, J_{LGN} is the strength of the geniculocortical input (in mV per unit contrast) and σ_{LGN} represents the tuning width of the geniculocortical inputs. We assume that the input from the LGN is linear; the geniculocortical

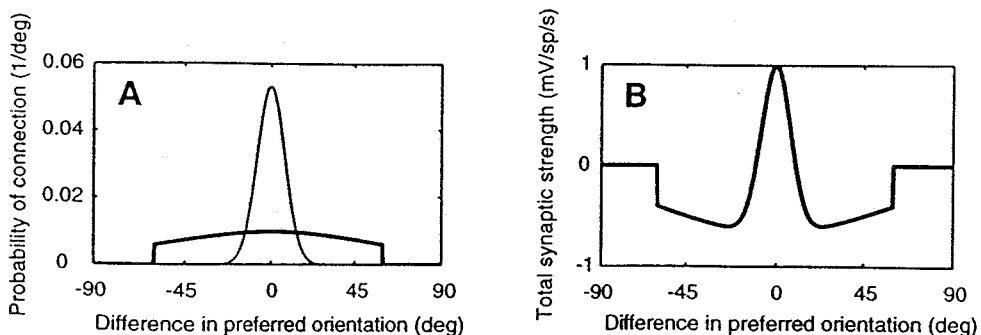


FIGURE 2. Intracortical connectivity in the recurrent model. (A) Probability of excitatory connection $E(\theta)$ (thin) and probability of inhibitory connection $I(\theta)$ (thick), as a function of the difference in preferred orientation between cells. The parameters that determine these curves are identical to those in the detailed recurrent model by Somers *et al.* (1995). (B) Total synaptic strength of connection by the synaptic strengths of excitation and inhibition. Its center-surround structure results in lateral inhibition in the orientation domain.

potential caused by the sum of oriented stimuli is the sum of the geniculocortical potentials caused by the individual stimuli. Once again, we adopt the same parameters as in the model of Somers *et al.* (1995) and take the orientation tuning given to cortical cells by the pattern of LGN inputs to be broad ($\sigma_{\text{LGN}} = 23$ deg). The feedback interactions are expected to sharpen this initially broad tuning.

The eight parameters of the model are listed in Table 1, together with the default values that were chosen when running the simulations. The values of the first two parameters—the membrane time constant τ and the gain of the spike encoder α —were chosen (as in Somers *et al.*, 1995) within widely accepted physiological ranges, and were kept fixed in all simulations. There is currently little agreement over the physiological values of the remaining six parameters—the strengths J and the tuning widths σ of the synaptic connections. The default values that were chosen in this study were aimed at replicating the workings of the detailed recurrent model. A discussion of their validity is provided in the study by Somers *et al.* (1995).

Our simulations of the simplified recurrent model were run on a network of 512 units whose output represents the activity of orientation columns spanning the range -90 to $+90$ deg, i.e., one every 0.35 deg. The model was implemented using Matlab (The MathWorks, Natick, MA), and the code used to generate the figures in this study is available on the World Wide Web, from the home pages of the authors.

RESULTS

We ran simulations of the simplified model to investigate its responses to a variety of visual stimuli. First, we concentrate on oriented stimuli such as gratings and bars. Next, we consider the responses to stimuli containing multiple orientations; two orientations, such as in plaids or crosses; three orientations and a single orientation in the presence of two-dimensional dynamic random noise. Finally, we examine the effect of the

tuning of intracortical inhibition on the responses of the model.

Responses to gratings or bars

In this section we consider the steady-state responses of the simplified recurrent model to oriented stimuli such as gratings and bars, and compare them with those of the detailed recurrent model proposed by Somers *et al.* (1995). We show that the simplified model replicates the amplification and sharpening of tuning exhibited by the detailed recurrent model, as well as its dependence on the strength of intracortical excitation and inhibition.

The orientation tuning of a model cell for four different combinations of excitatory and inhibitory intracortical strengths, J_E and J_I , is illustrated in Fig. 3. In Fig. 3(A) we set the strengths of all intracortical connections to zero ($J_I = 4.2$, $J_E = 0$). This corresponds to a simple feedforward model in which the orientation tuning is determined entirely by the pattern of convergence from the LGN onto the cortex. In these conditions, as expected, the half-width (HW) of the response is large (54 deg). The effect of adding intracortical inhibition is shown in Fig. 3(B). The magnitude of the responses is clearly reduced and the orientation tuning curve is sharpened to a half-width of 34 deg. Doubling the amount of inhibition—still without any intracortical excitation—further reduces the size of the responses and marginally sharpens their tuning to a half-width of 29 deg, as depicted in Fig. 3(C). Finally, the behavior of the full model, when both intracortical excitation and inhibition are present, is illustrated in Fig. 3(D). The magnitude of the responses is large and the orientation tuning is very sharp. The half-width of the orientation tuning curve equals 20 deg.

The parameters of the model used in Fig. 3 are the result of an informal search aimed at making the simplified model replicate quantitatively the responses of the detailed model. Under the same conditions (depicted in Fig. 5 of Somers *et al.*, 1995) the detailed recurrent model gives half-widths of 53, 38, 35 and 18 deg and maximal firing rates of 25, 10, 4, and

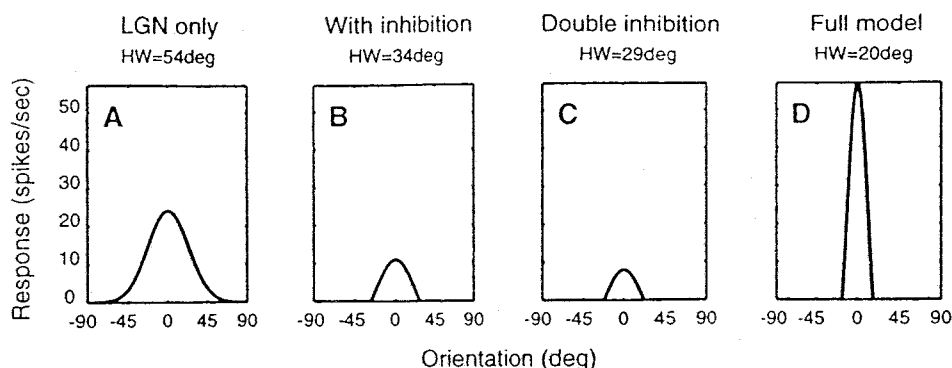


FIGURE 3. Orientation tuning of a cell in the simplified model with four different settings of the strengths of intracortical connections. (A) Input from the LGN, in the absence of cortical feedback. (B) Inhibition only, intracortical excitation is zero. (C) The effect of doubling intracortical inhibition. (D) Full model, with normal intracortical excitation and inhibition. "HW" indicates the tuning half-width. The parameters used in (D) are listed in Table 1. They were informally optimized to replicate the output of the detailed recurrent model by Somers *et al.* (1995). This figure is inspired by Fig. 5 in that study.

49 spikes/sec, respectively. The similarity of our results to those of Somers *et al.* (1995) suggests that the simplified model is successful in capturing the basic mechanism at work in the detailed recurrent model.

To further compare the outcome of the simplified and detailed recurrent models we ran a full parametric study of the dependence of response size and sharpness of tuning on the strengths of intracortical excitation and inhibition. The results are illustrated in Fig. 4(A), where the responses are depicted as ellipses whose eccentricity indicates the sharpness of tuning and whose gray level indicates the firing rate. The axes represent the synaptic strength of excitation and inhibition, expressed as multiples of the standard values. The case where both excitation and inhibition equal one corresponds to the response of the "full model" in Fig. 3(D), which gives a half-width of 20 deg and a maximal firing rate of more than 50 spikes/sec. Increasing the strength of inhibition (abscissa) decreases the amplitude of the responses and sharpens their orientation tuning. Increasing the strength of intracortical excitation (ordinate) increases the amplitude of the responses and can either sharpen or broaden their tuning: large amounts of excitation broaden the tuning, while small amounts sharpen it.

The result presented by Somers *et al.* (1995) is replotted in Fig. 4(B). As the simulations of the detailed model are time-consuming, Somers and collaborators chose to explore only a strategic subset of all the possible combinations of excitation and inhibition. The responses of the detailed model are similar to those of the simplified model shown in Fig. 4(A), except at high excitatory strengths and intermediate inhibitory strengths, where the simplified recurrent model predicts a larger loss of orientation selectivity than the detailed model, together with a small tendency to give larger responses. Except for these mild discrepancies the two models give very similar responses to oriented stimuli.

The simplified recurrent model can also be used to replicate the effects of the iontophoretic blockage of inhibition observed by Sillito *et al.* (1980). As shown in the leftmost column in Fig. 4(A), in the absence of inhibition and in the presence of normal intracortical excitation, model cells fire in excess of 100 spikes/sec and lose their orientation selectivity.

Additional simulations showed that the simplified model predicts the finding of Nelson *et al.* (1994), that blocking inhibition intracellularly in a single cell does not affect the cell's orientation tuning. Moreover, the behavior of the simplified model is consistent with the findings of Schiller (1982) and of Sherk & Horton (1984), who found that silencing the activity of ON-center geniculate afferents reduced the responses of V1 neurons without affecting their orientation tuning. Because the simplified model does not distinguish between ON-center and OFF-center inputs, we modeled these experiments by assuming that blockage of ON-center afferents halves the strength of geniculocortical excitation, while substantially broadening its orientation tuning. The orientation tuning of model neurons was largely unchanged by these

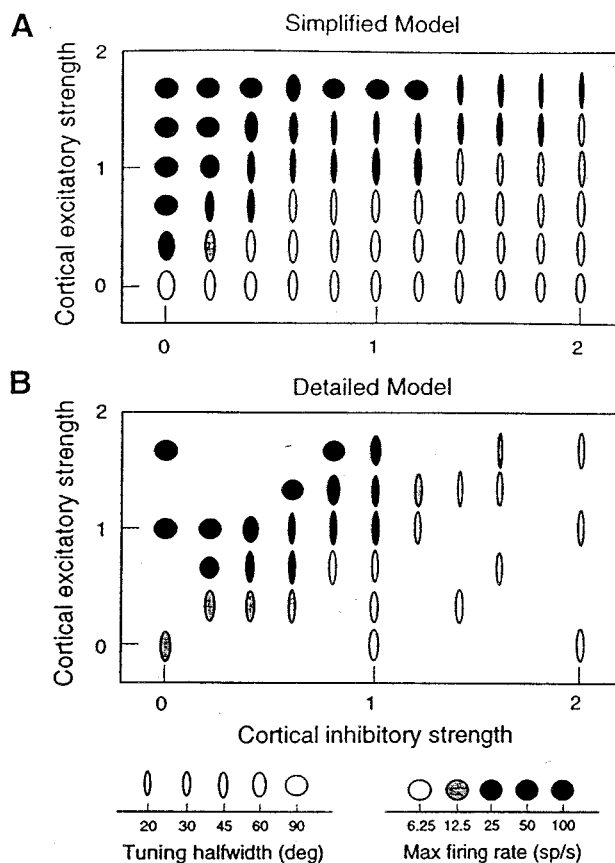


FIGURE 4. Sensitivity to cortical excitatory and inhibitory strengths. Ellipses correspond to the responses of a cell to an oriented stimulus. Gray level indicates response size (black indicates ≥ 100 spikes/sec). Anisotropy indicates sharpness of tuning (circles: unoriented cells, thinnest ellipses: < 20 deg half-width). (A) results of the simplified recurrent model; (B) results of the detailed recurrent model, courtesy of David Somers; these results appear in Fig. 7 of Somers *et al.* (1995).

manipulations. Indeed, we found the simplified model to be robust to large changes in the tuning width σ_{LGN} of geniculocortical excitation. With oriented stimuli such as gratings or bars, the responses remained essentially unchanged, while σ_{LGN} varied between 10 and 45 deg.

Responses to plaids or crosses

We now describe the steady-state responses of the simplified recurrent model to stimuli containing two orientations, such as plaids and crosses. We find that the model fails in estimating the angle between the two components in these stimuli. For angles below 45 deg the model signals a single orientation between the angles of the components. For angles larger than 45 deg the model signals the presence of the two components, but the difference between the estimated angles of the components is larger than the veridical angle between the components of the stimulus. In the first case, the orientations can be thought of as "attracting" each other, and in the latter case as "repelling" each other.

An example of attraction between orientations is illustrated in Fig. 5(A). The stimulus is a 30 deg plaid, with components oriented at ± 15 deg (vertical dotted lines). The geniculocortical input (thin curve) is, there-

fore, the sum of two gaussians, one peaking at -15 deg and the other peaking at $+15$ deg. The recurrent model fails to divine the presence of two peaks in this curve. Rather, its response (thick curve) signals the presence of a single intermediate orientation.

The results obtained with a plaid whose angle is larger than 45 deg are illustrated in Fig. 5(B). The stimulus is a 60 deg plaid, which results in a geniculate input with two clear peaks at ± 30 deg (thin curve). Intracortical feedback sharpens the input from the LGN, clearly distinguishing the two orientations and correctly signaling the presence of the two components of the plaid. The model, however, introduces an additional separation between the peaks: rather than signaling a 60 deg plaid it signals a 75 deg plaid.

The distortions in the responses to plaids introduced by the recurrent model are summarized in Fig. 5(C). Up to plaid angles as large as 45 deg the model fails to distinguish the presence of two orientations in the plaid. For plaid angles above 45 deg, repulsion between the peaks leads the model to overestimate the angle between the components in the plaid, in some cases almost by 30 deg.

Responses to stimuli containing multiple orientations

We now consider the steady-state responses of the recurrent model to stimuli that contain more than two orientations. We first consider the case in which the stimulus has three orientations. We then study the case in which a two-dimensional random noise mask is superimposed on an oriented stimulus.

We find that the recurrent model is unable to signal the presence of three orientations in a visual stimulus. Rather, it signals the presence of two orthogonal orientations. This is illustrated in Fig. 6(A), which shows the response of the recurrent model to a stimulus that contains three orientations 60 deg apart. The thin curve describes the input from the LGN, which contains three peaks at 0 , 60 and 120 deg. The response of the model is described by the thick curve. This curve has only two peaks, centered at orthogonal orientations. One of these orientations is veridical and corresponds to an orientation present in the stimulus. The other orientation is illusory, and lies halfway between the two remaining stimulus orientations.

For reasons of symmetry, the particular orientation that the model happens to represent veridically depends only on the initial state of the network. This means that while every time the model is presented with this stimulus it produces activity in only two populations of neurons, the particular choice of populations would vary across stimulus presentations. If the responses of a single neuron were measured through repeated presentations of the stimulus at different orientations, with random initial conditions, the resulting tuning curve would contain six peaks. Three of these peaks would correspond to the three orientations present in the stimulus, and the remaining three to the orientations orthogonal to them. On the other hand, at every given presentation the

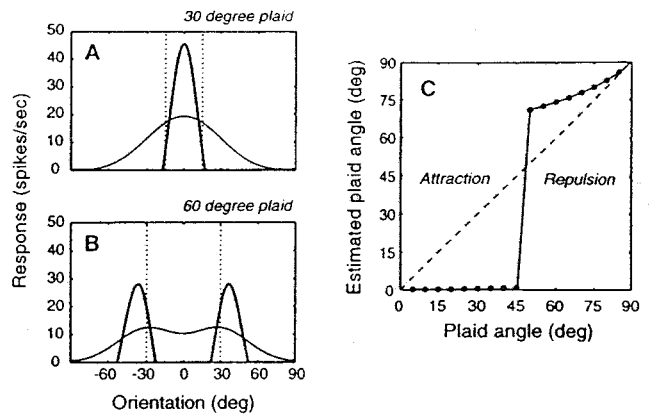


FIGURE 5. Responses of the simplified recurrent model to plaids (or crosses). (A) Responses to a 30 deg plaid. (B) Responses to a 60 deg plaid. The thin curves show the tuning given by the geniculate input in the absence of intracortical feedback. These are the sum of the responses to the individual components of the plaid. The thick curves show the tuning of the recurrent model. (C) Estimated plaid angle as a function of actual plaid angle. Estimated plaid angle was computed by fitting a sum of gaussians to the model responses. The model cannot distinguish the presence of two orientations if these differ by less than 45 deg [as in (A)], and produces a sharply tuned response to an orientation which is intermediate between the two components of the plaid. The model overestimates plaid angles larger than 45 deg [as in (B)]. These effects of attraction and repulsion between orientations are consequences of lateral inhibition in the orientation domain.

population of neurons would signal the presence of only two orientations.

As a final probe of the properties of the recurrent model we examine the effects of adding dynamic visual noise to an oriented stimulus. Visual noise is modeled as random activity in the LGN afferents. Since the LGN only provides excitation to the cortex, one of the effects of noise is to elevate the mean firing rate of the cortical neurons. In these conditions the consequences of the center-surround organization of the cortical feedback become most visible.

The effects of adding visual noise to an oriented stimulus in the simplified recurrent model are illustrated in Fig. 6(B–D). The response of the model in the absence of noise (B) has already been discussed: the LGN provides a broadly tuned input (thin curve), which is sharpened and amplified (thick curve) by the intracortical feedback. Adding moderate visual noise to the stimulus (C) results in a uniformly elevated average input from the LGN. This elevation has a strong effect on the cortical response which now shows two peaks, a veridical one at the stimulus orientation and an illusory one at the orthogonal orientation. Increasing the level of the noise (D) amplifies both peaks.

Role of the tuning of intracortical inhibition

We have seen that the responses of the recurrent model to stimuli containing multiple orientations display some peculiarities. For example, we have presented cases in which the model underestimates the number of orientations in a stimulus or signals the presence of additional

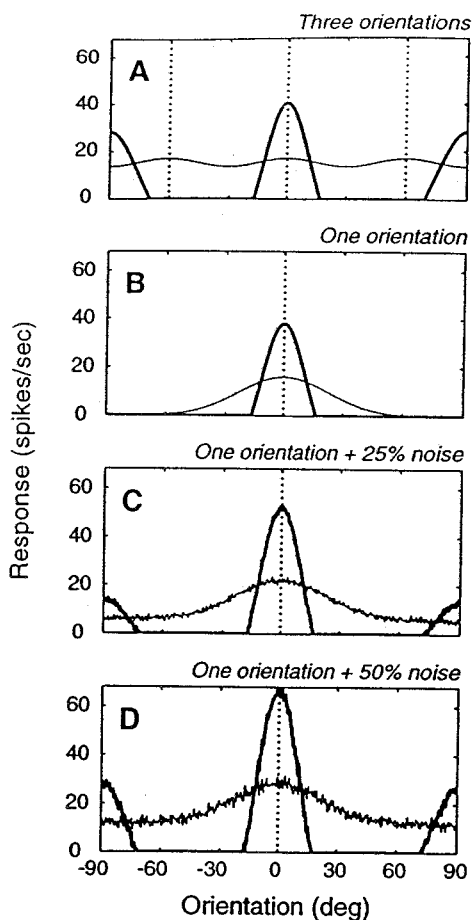


FIGURE 6. Responses of the simplified recurrent model to stimuli containing multiple orientations. Thick curves show responses of the recurrent model, thin curves those due to the LGN inputs alone. Vertical dotted lines indicate the veridical orientations present in the stimulus. Responses are averaged over 1 sec of response. The effect of visual noise is to raise the mean firing rate due to the LGN inputs. In this condition the model signals the presence of an illusory orientation.

illusory orientations. It may be argued that these phenomena are not general properties of recurrent models and depend on the particular tuning of the intracortical feedback. In this section we show that, indeed, broadening or sharpening the tuning of intracortical inhibition has profound effects on the responses of the model. Some of the properties described above are, however, quite robust to changes in the parameters of the network.

The effect of changing the orientation tuning width of the inhibitory feedback is shown in Fig. 7. The tuning of inhibition is very narrow in the top row (A), intermediate in the middle row (G), and broad in the bottom row (M). The five columns on the right show the responses to the different visual stimuli which we have already considered: a single orientation, two orientations 30 deg apart, two orientations 60 deg apart, three orientations 60 deg apart from each other, and one orientation in the presence of random visual noise.

The tuning of intracortical inhibition used in the middle row corresponds to that of the detailed model by Somers *et al.* (1995), which we have employed in all

previous simulations. These responses have already been discussed: the model amplifies and sharpens the tuning provided by the LGN in response to a single orientation (H); it signals an illusory intermediate orientation in response to a 30 deg plaid or cross (I); it overestimates the angle between the components in a 60 deg plaid or cross (J); it fails to detect the presence of three orientations, signaling instead the presence of two orthogonal components (K); and it signals the presence of a spurious orthogonal orientation in the presence of visual noise (L).

If the tuning of inhibition is sharpened (A) the model is able to signal the presence of all the orientations contained in the stimuli (B–E), but also signals spurious orientations. When the stimulus contains a single orientation, the model signals three orientations (B). When there are two orientations, it signals four orientations (C, D). When visual noise is added to a stimulus oriented at 0 deg, the model signals three illusory orientations at ± 45 and 90 deg (F).

Opposite effects can be observed if the tuning of inhibition is broad (M). In this case, the model is unable to distinguish the presence of two orientations in a 30 deg plaid (O) or of three orientations 60 deg apart (Q). In the presence of a visual noise mask, however, the model with broad inhibition is able to amplify the responses to the oriented stimulus and suppress the activity due to the visual noise (R).

In summary, changes in the orientation tuning width of intracortical inhibition have only minor effects on the responses to stimuli containing a single orientation, but have profound effects on the responses to stimuli containing multiple orientations. If the orientation selectivity of VI cells is indeed sharpened by intracortical feedback—as postulated by the recurrent model—experiments with visual stimuli containing multiple orientations could provide many clues as to the strength and tuning of this feedback.

DISCUSSION

We have shown that a very simple recurrent model of orientation selectivity captures the basic mechanism at work in the more complex and detailed model by Somers *et al.* (1995). This simplified model is very similar to one proposed by Ben-Yishai *et al.* (1995). With oriented stimuli—such as gratings of bars—we have found that it amplifies and sharpens the input from the LGN, replicating the results obtained with the detailed model. Using stimuli containing two orientations—such as plaids or crosses—we have demonstrated peculiar properties of the recurrent model: it fails to distinguish orientations separated by as much as 45 deg and overestimates the angle between orientations separated by more than 45 deg. Additional effects are seen in the responses to stimuli containing three orientations and one orientation in the presence of visual noise: these stimuli give rise to spurious responses at orthogonal orientations. We have also studied the effects of varying the tuning width of intracortical inhibition. If the inhibition is

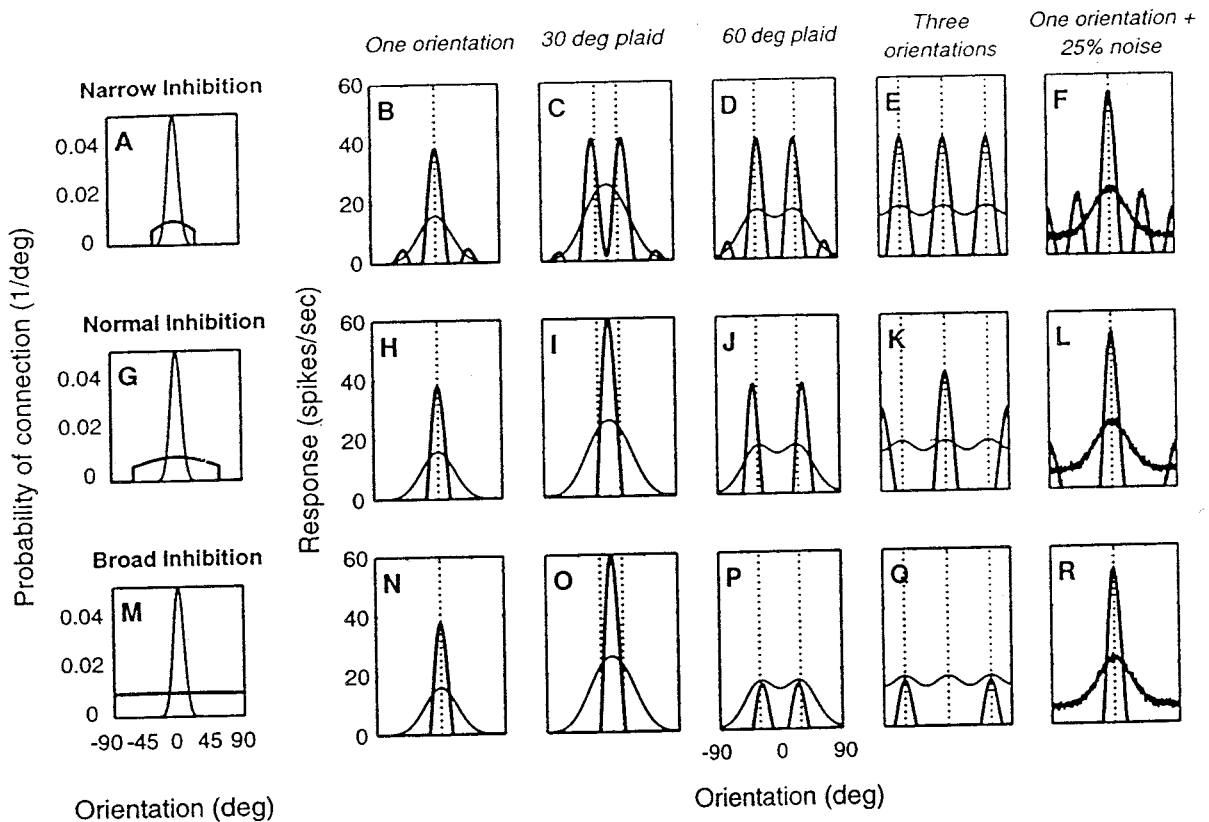


FIGURE 7. Dependence of the responses on the tuning of intracortical connections. The rows correspond to different tunings of the inhibitory feedback. This tuning is illustrated in the first column: the excitatory feedback (thin) is always tuned as in the recurrent model of Somers *et al.* (1995), whereas the inhibitory feedback (thick) is narrower (A), equal (G), or broader (M) than in that model. The second column illustrates the responses to an oriented stimulus. The third and fourth columns show the responses to plaids whose components differ by 30 and 60 deg, respectively. The fifth column shows the responses to a stimulus containing three orientations. The last column illustrates the effect of adding a flickering noise mask to an oriented stimulus, and the responses are averaged over time. The thick curves show responses of the recurrent model, and the thin curves those due to the LGN inputs alone. The narrow inhibition model signals the presence of spurious orientations not present in the stimulus (B–D and F). The normal inhibition model is the simplified recurrent model examined in the previous figures, and its responses (H–L) are presented here for comparison. The broad inhibition model fails to signal the presence of two orientations (O, P), and misses one orientation when the stimulus contains three orientations (Q). It performs well in the presence of noise (R), where it is able to amplify the orientation tuning and remove the effects of noise.

narrowly tuned the model is able to resolve the different orientations present in a plaid or cross, but signals the presence of strong spurious orientations in the presence of visual noise at off-optimal orientations. By contrast, if the inhibition is broadly tuned, the model is poor at discriminating the presence of multiple orientations, but it is capable of discounting the presence of noise.

One of the effects that we have described, the emergence of responses at spurious orientations, has to our knowledge not been described before. By contrast, the repulsion between orientations is a well-known property of feedback models based on lateral inhibition in the orientation domain. It was pointed out as early as in 1970 by Blakemore *et al.*, who provided psychophysical evidence supporting it. In their experiment, observers were asked to estimate the angle between two lines by adjusting the orientation of a comparison line. The results indicated a repulsion of as much as 3 deg in orientation, which was strongest when the stimulus had angles around 10 deg. Earlier psychophysical evidence for mutual

inhibition between orientation receptors was provided by the studies of Andrews (1967), and repulsion between orientations has been proposed by Hering, by von Helmholtz and by Wundt to underly well-known visual effects such as the Hering and Zöllner illusions (Blakemore *et al.*, 1970). In addition to repulsion between orientations, some attraction effects have also been observed (Bouma & Andriessen, 1970), and shown to be consistent with inhibition in the orientation domain (O'Toole & Wenderoth, 1977)

We suggest that these peculiar phenomena—attraction and repulsion between orientations, and emergence of responses at spurious orientations—are all inescapable consequences of feedback with a center-surround weighting function and cannot be avoided by changing the details of the recurrent model. Their origin lies in the circular symmetry of the orientation domain and the shape of the center-surround weighting function. The effect of this symmetry is to bias the recurrent model towards responses that have particular numbers of

equally spaced peaks. This can be observed in Fig. 7. The model with narrowly tuned inhibition has a bias towards responses that contain four peaks separated by 45 deg [Fig. 7(B–F)]; the model with normal inhibition has a bias towards responses that have either a single peak or two peaks separated by 90 deg [Fig. 7(H–L)]; the model with broadly tuned inhibition has a bias towards responses that have a single peak [Fig. 7(N–R)].

The reason for these biases can be easily understood by further simplifying the recurrent model using a linear approximation, as we do in the Appendix. The only nonlinearity in the simplified recurrent model is the rectification of the responses caused by the spike threshold. This nonlinearity becomes less effective if, as when adding random noise to the visual stimuli, the overall level of activity of the cortical network is elevated. In this case the model becomes approximately linear and an analytic solution to the network can be found. The biases for certain numbers of peaks in the responses become evident once the equations of the model are reformulated in the Fourier domain. The cortical feedback can be seen as amplifying some harmonic components in the input activity from the LGN and suppressing others (see Appendix). Because these components correspond to sinusoids with an integer number of periods in the orientation domain, the cortical feedback tends to produce responses with an integer number of equally spaced peaks.

There is evidence in the literature for effects that could be remarkably well explained by a recurrent model. In particular, it is known that in some narrowly tuned cells that are spontaneously active (so that the effects of inhibition are more visible) the less effective orientations in evoking a response are those flanking the preferred orientation and not the one orthogonal to it. In other words, the responses of these cells show peaks at spurious orientations which are often orthogonal to the optimal one. This seems to be the case both in monkey (De Valois *et al.*, 1982) and in cat (Shevelev *et al.*, 1994). Similar findings have been described by Ringach *et al.* (1997) in their study of orientation tuning dynamics in macaque visual cortex. The interactions between the orientations in a plaid described by Bonds (1989) in cat striate cortex are also consistent with a center-surround feedback filter; some of the sharply tuned cells in this study exhibited a peak of inhibition at orientations flanking the preferred one. Cells in V1 show strong cross-orientation inhibition: their response to the sum of stimuli with different orientation is smaller than the sum of the responses to the individual stimuli (Morrone *et al.*, 1982; Bonds, 1989; Gizzi *et al.*, 1990). This effect can be obtained in our model if the tuning of inhibition is very broad [Fig. 7(N, P)]. Indeed, a large number of observations suggest the presence of broadly tuned inhibition acting as a gain control mechanism in the visual cortex, both in cat and in monkey (Heeger, 1992; Carandini & Heeger, 1994; Carandini, 1996).

On the other hand, some aspects of the recurrent model's responses to stimuli containing multiple orienta-

tions are unlikely to be shared by real cortical cells. For example, the addition of visual noise suppresses the responses of the cells rather than enhancing them (Burr *et al.*, 1981; Carandini, 1996). Moreover, no obvious difference has been seen between the orientation tuning measured with plaids and that measured with gratings (Gizzi *et al.*, 1990). One possibility is that the attraction and repulsion between orientations could be present but smaller than predicted by our simplified recurrent model, so that their detection would require more careful measurements.

One of the results of the present study is that the recurrent model is not always capable of correctly signaling the number and value of different orientations present in a stimulus. A model with narrowly tuned inhibition reports the presence of a number of illusory orientations [Fig. 7(B–D, F)], whereas a model with broadly tuned inhibition can fail to distinguish the presence of multiple orientations [Fig. 7(O, Q)]. Thus, the use of multiple mechanisms with different center-surround "scales" may be necessary to detect, localize, and validate the presence of different orientations in a visual stimulus.

We note that the detailed recurrent model of Somers *et al.* (1995), the simplified model we have proposed, as well as similar models by other authors (Ben-Yishai *et al.*, 1995; Douglas *et al.*, 1995; Suarez *et al.*, 1995), are all based on feedback in the orientation domain and ignore the spatial domain. In other words, these models do not pool information across neurons with spatially displaced receptive fields. It may be unrealistic to expect these models to signal the presence of multiple orientations by only "looking" at their intersection. Intuitively, one would expect that the angle between the components of a cross is better judged by integrating information over some distance away from the intersection. Models that use long-range connections to allow feedback between cells with more distant receptive fields may be immune to some of the phenomena described in this study (D. Somers, personal communication). Indeed, there is psychophysical evidence that the discrimination of different orientations is estimated by integrating across space (Heeley & Buchanan-Smith, 1996).

In conclusion, we have shown that recurrent models of orientation selectivity give characteristic, and sometimes peculiar, responses to stimuli containing multiple orientations. This suggests the use of stimuli with multiple orientations to test recurrent models of orientation selectivity in the normal cortex without the need for pharmacological or physiological manipulations.

REFERENCES

- Andrews, D. P. (1967). Perception of contour orientation in the central fovea. Part I: short lines. *Vision Research*, 7, 975–997.
- Ben-Yishai, R., Bar Or, R. L. & Sompolsky, H. (1995). Theory of orientation tuning in the visual cortex. *Proceedings of the National Academy of Sciences USA*, 92, 3844–3848.
- Blakemore, C., Carpenter, R. H. S. & Georgeson, M. A. (1970). Lateral inhibition between orientation detectors in the human visual system. *Nature*, 228, 37–39.

- Bonds, A. B. (1989). Role of inhibition in the specification of orientation selectivity of cells in the cat striate cortex. *Visual Neuroscience*, 2, 41–55.
- Bouma, H. & Andriessen, J. J. (1970). Induced changes in the perceived orientation of line segments. *Vision Research*, 10, 333–349.
- Burr, D., Morrone, C. & Maffei, L. (1981). Intra-cortical inhibition prevents simple cells from responding to textured visual patterns. *Experimental Brain Research*, 43, 455–458.
- Carandini, M. (1996). Linearity, gain control and spike encoding in the primary visual cortex. PhD thesis, New York University, New York.
- Carandini, M. & Heeger, D. J. (1994). Summation and division by neurons in visual cortex. *Science*, 264, 1333–1336.
- Chapman, B., Zahs, K. R. & Stryker, M. P. (1991). Relation of cortical cell orientation selectivity to alignment of receptive fields of the geniculocortical afferents that arborize within a single orientation column in ferret visual cortex. *Journal of Neuroscience*, 11, 1347–1358.
- De Valois, R. L., Yund, E. W. & Hepler, N. (1982). The orientation tuning of cells in macaque visual cortex. *Vision Research*, 22, 531–544.
- Douglas, R. J., Koch, C., Mahowald, M., Martin, K. A. C. & Suarez, H. H. (1995). Recurrent excitation in neocortical circuits. *Science*, 269, 981–985.
- Ferster, D. (1987). Origin of orientation-selective EPSPs in simple cells of cat visual cortex. *Journal of Neuroscience*, 7, 1780–1791.
- Ferster, D., Chung, S. & Wheat, H. S. (1996). Orientation selectivity of thalamic input to simple cells of cat visual cortex. *Nature*, 380, 249–252.
- Gizzi, M. S., Katz, E., Schumer, R. A. & Movshon, J. A. (1990). Selectivity for orientation and direction of motion of single neurons in cat striate and extrastriate visual cortex. *Journal of Neurophysiology*, 63, 1529–1543.
- Heeger, D. J. (1992). Normalization of cell responses in cat striate cortex. *Visual Neuroscience*, 9, 181–198.
- Heeley, D. W. & Buchanan-Smith, H. M. (1996). Mechanisms specialized for the perception of image geometry. *Vision Research*, 36, 3607–3627.
- Hubel, D. & Wiesel, T. (1962). Receptive fields, binocular interaction, and functional architecture in the cat's visual cortex. *Journal of Physiology (London)*, 160, 106–154.
- Maex, R. & Orban, G. A. (1996). Model circuit of spiking neurons generating directional selectivity in simple cells. *Journal of Neurophysiology*, 75, 1515–1545.
- Morrone, M. C., Burr, D. C. & Maffei, L. (1982). Functional implications of cross-orientation inhibition of cortical visual cells—I. Neurophysiological evidence. *Proceedings of the Royal Society of London B*, 216, 335–354.
- Nelson, S., Toth, L., Sheth, B. & Sur, M. (1994). Orientation selectivity of cortical neurons during intracellular blockade of inhibition. *Science*, 265, 774–777.
- O'Toole, B. & Wenderoth, P. (1977). The tilt illusion: Repulsion and attraction effects in the oblique meridian. *Vision Research*, 17, 367–374.
- Pei, X., Vidyasagar, T. R., Volgushev, M. & Creutzfeldt, O. D. (1994). Receptive field analysis and orientation selectivity of postsynaptic potentials of simple cells in cat visual cortex. *Journal of Neuroscience*, 14, 7130–7140.
- Reid, R. C. & Alonso, J. (1996). The processing and encoding of information in the visual cortex. *Current Opinions in Biology*, 6, 475–480.
- Reid, R. C. & Alonso, J. M. (1995). Specificity of monosynaptic connections from thalamus to visual cortex. *Nature*, 378, 281–284.
- Ringach, D., Hawken, M. J. and Shapley, R. M. (1997). The dynamics of orientation tuning in macaque primary visual cortex. *Nature*, 387, 281–284.
- Schiller, P. H. (1982). Central connections of the retinal on and off pathways. *Nature*, 297, 580–583.
- Sherk, H. & Horton, J. C. (1984). Receptive field properties in the cat's area 17 in the absence of on-center geniculate input. *Journal of Neuroscience*, 4, 381–393.
- Shevelev, I. A., Lazareva, N. A., Novikova, B. V., Tikhomirov, A. S. & Sharaev, G. A. (1994). Double orientation tuning in cat visual cortex units. *Neuroscience*, 61, 965–973.
- Sillito, A. M., Kemp, J. A., Milson, J. A. & Berardi, N. (1980). A re-evaluation of the mechanisms underlying simple cell orientation selectivity. *Brain Research*, 194, 517–520.
- Somers, D. C., Nelson, S. B. & Sur, M. (1995). An emergent model of orientation selectivity in cat visual cortical simple cells. *Journal of Neuroscience*, 15, 5448–5465.
- Suarez, H. H., Koch, C. & Douglas, R. J. (1995). Modeling direction selectivity of simple cells in striate visual cortex within the framework of the canonical microcircuit. *Journal of Neuroscience*, 15, 6700–6719.
- Vidyasagar, T. R., Pei, X. & Volgushev, M. (1996). Multiple mechanisms underlying the orientation selectivity of visual cortical neurones. *Trends in Neuroscience*, 19, 272–277.

Acknowledgements—We thank R. Shapley for helpful suggestions. M.C. was supported by NIH grant EY02017 and by a Howard Hughes Medical Institute Investigatorship to J.A. Movshon, and by NIH grant EY04726 to D.L. Ferster; D.L.R. was supported by a Sloan Foundation Fellowship.

APPENDIX

We describe a linear approximation of the simplified recurrent model. The approximation is useful because it has a closed mathematical solution. This solution explains why some of the phenomena described above are a natural consequence of center-surround feedback in the orientation domain.

We linearize the simplified recurrent model by ignoring the threshold for the generation of spikes. This approximation becomes more precise if the resting firing rates are high compared with the visual responses, as occurs in the presence of visual or neural noise. The sharpening of the orientation tuning is then the result of linear feedback filtering with a “center-surround” weighting function in the orientation domain. In this context, the properties of the model by Somers *et al.* (1995) are shared by other recurrent models of orientation selectivity, such as those by Ben-Yishai *et al.* (1995) and by Douglas *et al.* (1995).

The simplified recurrent model is described by Eq. (1), Eq. (2) and Eq. (4), which can be joined in a single expression:

$$\tau \partial V / \partial t + V = V^{\text{LGN}} - K * \max(V, 0), \quad (\text{A1})$$

where * denotes circular convolution in the orientation domain, and K is a “center-surround” weighting function

$$K(\theta) = \alpha [J_E E(\theta) - J_I I(\theta)]. \quad (\text{A2})$$

In other words, each cell is a low-pass filter in time whose inputs consist of a feedforward term V^{LGN} and of a feedback term given by the convolution (in the orientation domain) of a center-surround weighting function, K , with the positive part of the output of the whole array of cells.

We linearize the model by ignoring the “max” function in the convolution, thus allowing for negative firing rates. The linearized model is described by:

$$\tau \partial V / \partial t + V = V^{\text{LGN}} + K * V. \quad (\text{A3})$$

which can be solved by standard methods. The solution expresses the membrane potential $V(\theta, t)$ of a cell in the orientation column θ at time t as a function of the input from the LGN $V^{\text{LGN}}(\phi, s)$ to all orientation columns ϕ at all times $s \leq t$. The derivation of this solution involves the use of Fourier analysis to remove derivatives and convolutions. In particular, in the time domain we take the Fourier transform, and in the orientation domain (which is periodic), we compute the Fourier series.

Let $V_j(t)$ be the j -th term in the Fourier series expansion of $V(\theta, t)$. Intuitively, this term is a measure of how well the dependence of the responses on orientation can be approximated by a sinusoid having j

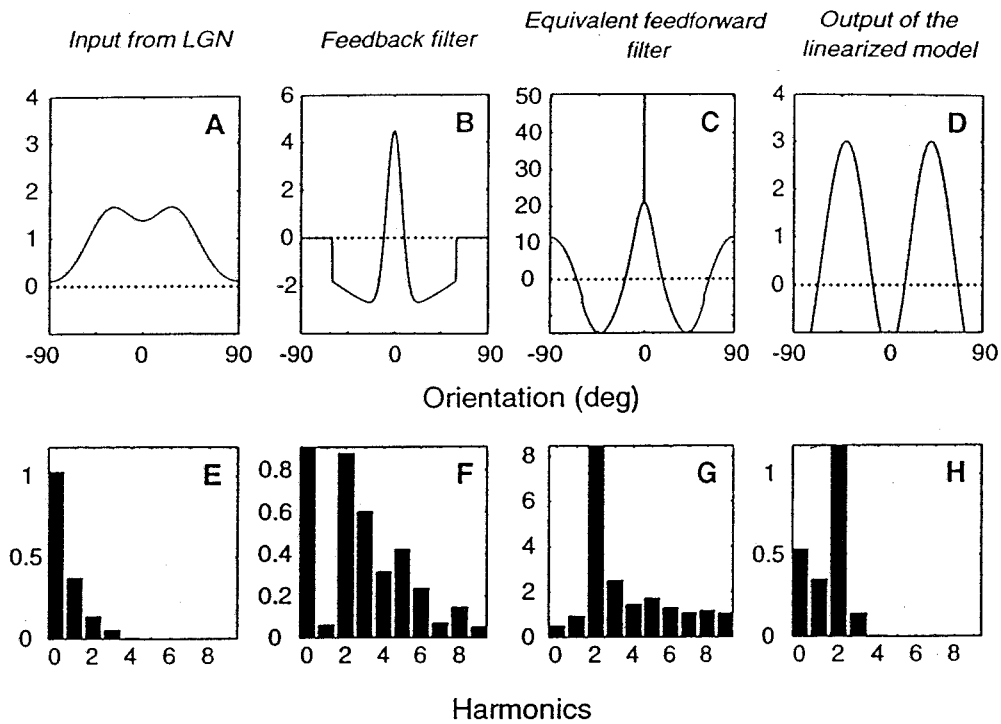


FIGURE 8. Responses of the linearized recurrent model in the orientation and Fourier domains. (A) Input from the LGN for a 60 deg plaid stimulus. (B) The center-surround weighting function $K(\theta)$ of the feedback filter. (C) The weighting function of the equivalent feedforward filter; the output of the linearized model is given by the convolution of this function with the input from the LGN. (D) The output of the linearized model for a 60 deg plaid stimulus, obtained by convolving (A) and (C). (E–H) Amplitudes of the Fourier series of the functions in (A–D). Only the first 10 terms are shown. The Fourier series of the feedback filter (G) is given by $1/(1-K_j)$, where K_j is the j -th term of the Fourier series of the feedback filter (F). The Fourier series of the output of the linearized model for a 60 deg plaid stimulus (H) is obtained by multiplying those depicted in (E) and (G).

periods in the range of orientations -90 to $+90$ deg. Taking the Fourier series of both sides of A(3) yields:

$$\tau \partial V_j / \partial t + V_j = V_j^{\text{LGN}} + K_j V_j \quad (\text{A4})$$

We now take the Fourier transform in time of both sides of the equation. Denoting with $\tilde{V}(\omega)$ the Fourier Transform in time of $V(t)$, one obtains:

$$i\omega \tau \tilde{V}_j + \tilde{V}_j = \tilde{V}_j^{\text{LGN}} + K_j \tilde{V}_j, \quad (\text{A5})$$

where $i = \sqrt{-1}$. From the last equation we obtain the final solution:

$$\tilde{V}_j = 1/(1 + i\omega\tau - K_j) \tilde{V}_j^{\text{LGN}}. \quad (\text{A6})$$

If the center-surround filter had a simple Fourier series—as in Ben-Yishai *et al.* (1995)—it would be straightforward to express the above equation directly in terms of the membrane potential V and of the geniculate input V^{LGN} , rather than in terms of their Fourier expansions.

In addition to providing a solution of the linearized model, A(6) describes how the entire network could be replaced by an equivalent feedforward filter. The j -th term of the Fourier series of this filter is simply given by $1/(1 + i\omega\tau - K_j)$. The advantage of computing the equivalent feedforward filter is that the output of the model is simply given by the convolution of this filter with the geniculate input.

The workings of the linearized model at steady state ($\partial V / \partial t = 0$, or equivalently $\omega = 0$) are illustrated in Fig. 8. The weighting function of the feedback filter is illustrated in Fig. 8(B), and the amplitude of the first 10 terms of its Fourier series is shown in Fig. 8(F). From this Fourier series another Fourier series can be constructed: that of the equivalent feedforward filter (G). The Fourier series of the output of the model is simply the product of the Fourier series of the geniculate input and the Fourier series of the equivalent feedforward filter. Because the strongest term in this series is the third, which corresponds

to the second harmonic, the main effect of the recurrent model is to enhance the second harmonic present in the geniculate input. A response dominated by the second harmonic means that we will obtain peaks at orthogonal orientations.

An example of geniculate input caused by a 60 deg plaid is illustrated in Fig. 8(A), and its Fourier series is depicted in Fig. 8(E). In this input, the second harmonic component (the third bar) is much smaller than the first two components. This component is, however, greatly amplified by the multiplication with the Fourier series of the equivalent feedforward filter [Fig. 8(G)] which, at the same time, suppresses the first two harmonics. As a result, the Fourier series of the output of the model [Fig. 8(H)] has a strong second harmonic, which is reflected in two large peaks in the response of the model [Fig. 8(D)]. These peaks are separated by 90 rather than 60 deg. The model exaggerates the separation between orientations. This is the phenomenon to which we have referred as a form of “repulsion” between orientations. Similar arguments explain the other phenomena encountered in the present study, such as the “attraction” between orientations and the appearance of responses at spurious orientations.

Notice that the equivalent feedforward filter contains a peak at the orthogonal orientation [Fig. 8(C)]. As a result, the phenomena observed in the recurrent network are difficult to reconcile with a simple feedforward scheme: if the equivalent feedforward filter were to be implemented by the geniculocortical connections, the LGN inputs to V1 cells would have to be aligned, not only along the preferred orientation of the cell, but also along the orthogonal orientation. There is no anatomical or physiological evidence that this is the case.

Finally, we point out that *any* nonlinear recurrent network whose first-order (linear) approximation is described by A(3) will exhibit the effects reported here, at least in a small signal regime.