1. Introduction

The primary visual cortex (V1) is a fascinating part of the brain. The reason for the fascination is because V1 is tied to the visual world through its relatively strong driving from the retina through the lateral geniculate nucleus (LGN), but it is also part of the cerebral cortex. The function of the cerebral cortex is a major challenge to science. It is one of the most important neural networks in Nature. Naturally scientists have been drawn to study V1 as a way of comprehending the greater problem of cortical function. But the visual particularities of V1 are also fascinating for understanding one important stage in visual perception.

There has been intensive study of V1 in many laboratories around the world for decades. This paper is a review of recent work, by Ringach, Hawken, and Shapley, about a new view of V1 as a nonlinear dynamical system designed to find local stimulus features in the visual scene. Also, Ringach, Hawken, Sceniak, and Shapley (and others whose work is discussed below) have studied how V1 is influenced by spatial context. First we will consider our recent results about the dynamics of V1 responses to oriented visual stimuli. Then we will consider the evidence for the sensitivity to two-dimensional features in V1. This will lead to a discussion of the role of feedback in the cerebral cortex, particularly in V1.

2. Orientation dynamics from categorical reverse correlation

In V1 orientation selectivity is an important feature of visual responses. Prior to V1, in the retina and LGN, there is weak or no orientation selectivity in single cells. It has been thought from the time of its discovery that orientation tuning, as an emergent property in visual cortex, must be an important clue to how the cortex works and why it is built the way it is.

In an attempt to provide data to test models of orientation selectivity, [Ringach, Hawken, and Shapley [1997]] used a reverse correlation method developed based on subspace reverse correlation in the orientation domain. The idea was to measure the time evolution of orientation selectivity extracellularly in single V1 neurons, with a technique that drove most cortical neurons above spike-firing threshold. The technique is illustrated in Fig. 1. The input image sequence is a stimulus ‘movie’ that runs for 15–30 min. Sinusoidal gratings patterns (optimal spatial frequency, and high contrast) of orientations drawn randomly from a set of equally spaced orientations around the clock (usually in 10° steps) were presented for a fixed time. For each time offset, the probability distribution for orientation p(θ, τ) was calculated by reverse correlation. This calculation was done for each time offset between spike and stimulus to create a sequence of probability distributions for orientation, one for each time offset—an ‘orientation selectivity movie’.

The probability distribution p(θ, τ) derived from reverse correlation in the case of the orientation dynamics experiment does not have the status of a spatio-temporal impulse response. Rather, it reflects the relative preference for a given stimulus (in this case an oriented grating pattern) among a set of stimuli. The different patterns were evenly spaced along the dimension of orientation, θ. But in principle the set of patterns could have been any set of independent patterns, and a probability distribution could have been calculated by reverse correlation in a similar manner. This technique can be applied to a wider range of problems than the linear systems can approach that aims to measure the spatio-temporal impulse response of a linear transducer. The orientation dynamics measurement is applicable to non-linear systems as well as linear. The utility of the method is in testing models of neuronal networks that could generate probability functions p(θ, τ)
that can match the observed function. For instance, McLoughlin, Shapley, Shelley, and Wiesel (2000) tested feedforward and feedback models against the orientation dynamics data of Ringach, Sapiro, and Shapley (1997b) and found that a feedforward model could not account for major features of the probability distribution \( p(\theta, \tau) \).

In our earlier work with the reverse correlation technique applied to the study of orientation dynamics (Ringach et al., 1997), we reported that most cells in the input layers 4C\( \alpha \) and \( \beta \) have simple, ‘unimodal’ dynamics and are relatively broadly tuned for orientation. By unimodal dynamics we meant that, after a time delay, the probability distribution for orientation simply had a single maximum in time and, after that peak, simply relaxed back to baseline. However, some cells in the output layers 2, 3, 4B, 5, and 6 showed ‘multimodal dynamics’: rebound responses, sharpening of the orientation tuning with time, and/or transient peaks of probability at off-optimal orientation. Also, in a few neurons in the output layers we observed a shift of the peak of the orientation probability distribution with time. These resemble the ‘shifter’ cells described by Shapley, Sharaf, Lazareva, Novikova, and Tikhomirov (1997). But shifter cells are the exception, not the rule in macaque V1.

In more recent experiments on orientation dynamics (Ringach, Hawken, & Shapley, 2003), we used a modified technique that revealed more about the basic mechanisms of orientation selectivity. As shown in Fig. 3, an additional pattern was added to the sequence—a blank stimulus at the mean luminance of the grating patterns. This allowed us for the first time to measure global enhancement and suppression because, with this new technique, one could estimate whether the effect of one of the oriented patterns was greater or less than that of the blank pattern. If the probability of producing a spike by a pattern of orientation \( \theta \) is greater than that of a blank, we view that as evidence that a pattern of orientation \( \theta \) produces net excitation, while if the probability of producing a spike by a pattern of orientation \( \theta \) is less than that of a blank, we take this as an indication of suppression. Specifically, we take \( R(\theta, \tau) = \log[p(\theta, \tau)/p(\text{Blank}, \tau)] \). If the probability that angle \( \theta \) evokes a spike is greater than that of a blank screen, then the sign of \( R \) is +. If the probability that angle \( \theta \) evokes a spike is less than that of a blank screen, then the sign of \( R \) is −. If all angles evoke a response above what a blank does, then \( R(\theta) \) will have a positive value for all \( \theta \). A visual neuron equally well excited by stimuli of all orientation angles would produce a constant, positive \( R(\theta) \).

One can estimate several useful features of the tuning curve \( R(\theta, \tau) \). This is illustrated in Fig. 4.

The shape of the orientation tuning curve \( R(\theta, \tau) \) changes with time, \( \tau \). This dynamic behavior has a number of important properties that are revealed in Fig. 3 for two representative V1 neurons. The black curves in Fig. 3 are graphs of \( R(\theta, \tau) \) at the time offset \( \tau_{\text{peak}} \) when the orientation modulation depth \( \Lambda(\tau) \) reaches its maximum value. The red and blue curves are graphs of \( R(\theta, \tau) \) at the two times bracketing \( \tau_{\text{peak}} \) at which \( \Lambda = 0.5\Lambda_{\text{peak}} \). The red curve was measured at the development time \( \tau_{\text{dev}} \), the earlier of the two times when the modulation depth first rises from 0 to 0.5\( \Lambda_{\text{peak}} \); the blue curve was taken at the declining time \( \tau_{\text{dec}} \) when the response had declined back from \( \Lambda_{\text{peak}} \) to 0.5\( \Lambda_{\text{peak}} \).

One striking feature of these curves is that the dynamic tuning curve at the earlier time, \( R(\theta, \tau_{\text{dev}}) \), had a large positive pedestal of response, a sign of global excitation early in the response. This is just what one might predict from the analysis of feedforward models of V1 orientation selectivity (e.g., Hubel & Wiesel, 1962), if indeed the earliest responses measurable were predominantly feedforward excitation (see Shapley, Hawken, & Ringach, 2003 about this). But then, as the response evolved in time, the maximum value of \( R(\theta, \tau) \) at the preferred orientation grew only a little, while the responses at non-preferred orientations declined substantially. Thus Fig. 3 demonstrates that the maximum orientation modulation depth occurred at
a time when inhibition had suppressed non-preferred responses. Because such inhibition suppressed all responses far from the preferred orientation, we infer that it was global (untuned) inhibition. It is also reasonable to infer that tuned excitation near the preferred orientation counteracted the global inhibition to maintain the peak value of \( R(\theta, \tau) \).

While this kind of evidence for global inhibition was apparent in most V1 neurons we studied, a significant fraction of the cells exhibited a different kind of inhibition, as shown in responses of the cell illustrated in the lower panel of Fig. 3. For this cell, at \( \tau_{\text{dec}} \), the tuning curve \( R(\theta, \tau_{\text{dec}}) \) had the shape of a 'Mexican hat' meaning that \( R(\theta_{\text{min}}, \tau_{\text{dec}}) < R(\theta_{\text{orth}}, \tau_{\text{dec}}) \). We interpret this to mean that there was also tuned suppression in such neurons, that is, suppression that does not extend out to orientations far from the preferred. Both the hypothesized suppressions, global and tuned, would have to be relatively rapid in time course to have the effects on the tuning curve seen in Fig. 3 at the time of peak selectivity.

While orientation bandwidth often has been the focus of interest in previous research, it is rather the global shape of the orientation tuning curve at all orientations that differentiates between different theoretical mechanisms. Therefore, we studied \( R(\theta_{\text{min}}, \tau) \), \( R(\theta_{\text{orth}}, \tau) \) and the modulation depth \( A(\tau) \) in V1 neurons [Ringach et al., 2003]. The average behaviors of \( R(\theta_{\text{min}}, \tau) \), \( R(\theta_{\text{orth}}, \tau) \) and \( A(\tau) \) averaged over a population of 242 V1 neurons are depicted in Fig. 4.

Fig. 2. Analysis of the log probability function \( R(\theta, \tau) = \log[p(\theta, \tau)/p(\text{Blank}, \tau)] \). Useful features of the tuning curve \( R(\theta, \tau) \) include: (a) the orientation angle of the peak response, \( \theta_{\text{max}} \), and its magnitude \( R(\theta_{\text{max}}, \tau) \); (b) the orientation angle and magnitude of the minimum response, \( \theta_{\text{min}} \) and \( R(\theta_{\text{min}}, \tau) \); (c) the angle orthogonal to \( \theta_{\text{min}} \), denoted \( \theta_{\text{ortho}} \), and its magnitude \( R(\theta_{\text{ortho}}, \tau) \); (d) the 'modulation depth' of the tuning curve as a function of time \( \tau \), \( A(\tau) = R(\theta_{\text{max}}, \tau) - R(\theta_{\text{min}}, \tau) \) and (e) the dynamic half-bandwidth defined by half the width of the tuning curve at the 'half-height' which is equal to 1/2[R(\theta_{\text{max}}, \tau) - R(\theta_{\text{ortho}}, \tau)]. The orientation modulation depth \( A(\tau) \) is a global measure of orientation selectivity because it is comparing the values of the tuning curve at two widely separated values of the angle \( \theta \).

The bandwidth is a local measure of selectivity around the peak of the tuning curve.

Fig. 3. Two cells and three time slices of \( R(\theta, \tau) = \log[p(\theta, \tau)/p(\text{Blank}, \tau)] \). The black curves are graphs of \( R(\theta, \tau) \) at the time of peak \( \tau_{\text{peak}} \) when the orientation modulation depth \( A(\tau) \) reaches its maximum value. The red and blue curves are graphs of \( R(\theta, \tau) \) at the two times bracketing \( \tau_{\text{peak}} \) at which \( A = 0.5A_{\text{peak}} \); the red curve is at \( \tau_{\text{dec}} \) and \( \tau_{\text{inc}} \); the earlier of the two times when the modulation depth first rises from 0 to 0.5\( A_{\text{peak}} \) and the blue curve is at \( \tau_{\text{dec}} \) when the response has declined back from \( A_{\text{peak}} \) to 0.5\( A_{\text{peak}} \). For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.

Fig. 4. Average across the V1 population of \( A(\tau) \) the modulation depth of the orientation tuning curve at time \( \tau \), \( M(\tau) \), the minimum response across all orientations at time \( \tau \), and \( \theta(\tau) \), the response at the orientation orthogonal to the peak orientation at time \( \tau \). Curves from different cells were aligned at \( \tau_{\text{peak}} \) and averaged. Light shaded regions represent \( \pm 1 \) standard error.
The modulation depth, \( A(\tau) \), normally increased to reach a peak and then declined back to baseline over a time course of 50 ms. An important feature is the positive sign of \( R(\theta_{\text{min}}, \tau) \) and \( R(\theta_{\text{ortho}}, \tau) \) prior to the peak response. This indicates that, on average, V1 cells tended to respond to all orientations early in the response. Another important feature of the data was the sharp downward change in time course of \( R(\theta_{\text{min}}, \tau) \) and \( R(\theta_{\text{ortho}}, \tau) \) before \( A(\tau) \) reached its peak value. This is evidence for rapid onset of inhibition and also for the likely influence of inhibition on the magnitude of orientation modulation depth. Eventually both \( R(\theta_{\text{min}}, \tau) \) and \( R(\theta_{\text{ortho}}, \tau) \) declined to negative values meaning that later in the response orientations far from the preferred orientation were suppressive not excitatory.

The orientation dynamics experiments demonstrate that early excitation in V1 is very broadly tuned for orientation, just as predicted for models of feedforward convergence like the Hubel–Wiesel model (Hubel & Wiesel, 1962). Indeed in simulations of the dynamics experiments with a large-scale network model of V1, McLaughlin et al. (2000) demonstrated that feedforward excitation generates dynamical orientation tuning curves with very high circular variance, meaning poor selectivity, at all time offsets between stimulus and spike (Fig. 2). An important question about orientation selectivity in V1 is how does the cortex suppress the feedforward excitation far from the preferred orientation? What our assembled experimental results show is that the answer to the question is cortical inhibition. The inhibitory signals must be fairly rapid, though not quite as fast in arrival at the V1 neuron as the earliest excitatory signals. Also, inhibition appears to persist longer than excitation. Additional strong evidence for the role of inhibition in orientation selectivity has come from the elegant pharmacological experiments of Sato, Katsuyama, Tamura, Hata, and Tsumoto (1996) in which cortical inhibition in macaque V1 was weakened by pharmacological blockade by bicuculline. Then neuronal orientation selectivity was reduced because response to off-peak orientations grew stronger relative to the peak response (cf. especially Figure 8 in Sato et al., 1996). This further supports the idea that the feedforward excitatory input (the convergent input from the LGN) is very broadly tuned in orientation, and that cortical inhibition suppresses the responses far from the preferred orientation. The importance of cortical inhibition for orientation selectivity has also been suggested in models of the cortex McLaughlin et al., 2000; Frorey et al., 1998.

There is a completely different point of view, namely that the pattern of feedforward thalamic input is enough to determine orientation selectivity. In one study that assigns a dominant role to feedforward connections in determining orientation selectivity, Mazier, Vinje, McDermott, Schiller and Gallant (2002) recorded extracellularly in V1 of awake macaques, and used a reverse correlation technique very similar to the one we introduced in 1997 (Ringach et al., 1997). However, unlike our earlier results and also unlike the results reviewed here, Mazier et al.’s results were interpreted to indicate that the orientation tuning curves measured dynamically did not change shape with time. Mazier et al. interpreted this as evidence supporting a feedforward scheme for orientation selectivity. We believe the reason why their results do not agree with ours is that the time-sampling of their data was inadequate, and their analysis technique was insensitive to time variations in the shape of the tuning curve (for a more complete discussion, cf. Ringach et al., 2003).

Spatial frequency selectivity in macaque V1 has been characterized in other reverse correlation experiments (Bredfeldt & Ringach, 2002; Ringach, Bredfeldt, Shapley, & Hawken, 2002). There are striking similarities with the dynamics of orientation tuning. Spatial frequency selectivity develops with time, and there is clear evidence for non-preferred suppression in the spatial frequency dimension as in orientation. This suppression is highly correlated with the degree of selectivity.

3. Two-dimensional selectivity of V1 neurons

Most macaque V1 neurons are highly selective for the two-dimensional structure of visual patterns. This is a fact about V1 cortex we had to learn from the neurons, many of which will not respond to extended one-dimensional patterns such as large grating patterns or long bars of light. In the orientation dynamics experiments discussed above, we used grating stimuli that were 2–4 times larger in radius than would be optimal for giving the largest response of the neuron in spikes/second. At present we are studying the effect of stimulus size on orientation dynamics. But in earlier work, Sceniak, Hawken, and Shapley (2001) obtained a quantitative description of the spatial structure of V1 neurons’ receptive fields. The measurement was the averaged (steady state) response to drifting sine gratings of optimal spatial frequency, orientation, and temporal frequency (equivalent to optimal speed). The gratings were presented as if through an aperture, the size of which could be varied. Outside the aperture was mean gray, at the same mean luminance as the gratings. We measured response magnitude as a function of size. We studied area, length, and width summation. There were quantitative differences between area, length, and width summation for any one neuron. However, the three different summation functions shared common characteristics. Typically V1 cells had an optimum size of stimulus: smaller or larger produced a weaker response. The data were well fit with a difference of Gaussians DOG model, in analogy with retinal ganglion cells. This work confirms the results of DeAngelis, Freeman, and Ohzawa (1994) on spatial summation in cat cortex. The predictions of such a model for the area summation experiments are illustrated in Fig. 3. The account of the results with a DOG model suggests that most spatial summation in V1 neurons can be described as
the summation of two spatially overlapping mechanisms: excitatory and inhibitory. To fit our data, the inhibitory, suppressive mechanism always needed to be the larger in spatial extent. The goodness of fit of the DOG model suggests that, under the conditions of our experiments, the inhibitory surround is not spatially separated from the central excitatory region that probably corresponds to the CRF, or classical receptive field.

The excitatory spatial region was on average approximately 1° in diameter in our experiments on neurons with visual receptive fields in the near periphery of the visual field. This is shown in Fig. 5. These experiments were conducted with high contrast spatial gratings, and as discussed below, the value of the center size varied with contrast, being smallest at the high contrast we used in these experiments.

Many cells in the upper layers, and in layer 4B, have especially strong inhibitory mechanisms. A subclass of layer 6 neurons shows little or no suppression for large stimuli. One striking result of this work is the large spatial spread of the inhibitory, suppressive mechanism, as shown by the scatter plot of the surround spatial parameter \( b \) with cortical depth in

![Graph](image_url)

**Fig. 5.** The difference of Gaussians model applied to area summation curves of V1 neurons. The envelope of excitation is postulated to be a narrow Gaussian function. The envelope of inhibition is postulated to be a broader Gaussian function of position. The response is postulated to be the difference of the two mechanisms as depicted in the graph.

![Graph](image_url)

**Fig. 6.** The center summation parameter \( a \) of the difference of Gaussians model is plotted as a function of normalized cortical depth. The full thickness of V1 cortex is set to be 100, and the depth of each neuron is its depth from the surface relative to the full thickness of the cortex. The average value of the center summation parameter \( a \) is indicated by the dashed vertical line and equals approximately 1° of visual angle.
Fig. 7. The surround summation parameter $b$ of the difference of Gaussians model is plotted as a function of normalized cortical depth. The full thickness of V1 cortex is set to be 100, and the depth of each neuron is its depth from the surface relative to the full thickness of the cortex. The average value of the center summation parameter $b$ is indicated by the dashed vertical line and equals approximately 2.2° of visual angle.

Fig. 8. The suppression index SI, equal to the ratio of integrated surround strength divided by integrated center strength of the difference of Gaussians model is plotted as a function of normalized cortical depth. The full thickness of V1 cortex is set to be 100, and the depth of each neuron is its depth from the surface relative to the full thickness of the cortex. The average value of the suppression index SI is indicated by the dashed vertical line and equals approximately 0.63. The solid line is the running average (over a 50 μ vertical extent) of SI.

Fig. 9. Response as a function of stimulus area at low and high contrast for a typical V1 neuron. Low and high contrast points are plotted respectively as empty squares and filled triangles. The solid curves that approximate the points are derived from the difference of Gaussians model and give a good account of the area-response functions. The arrows indicate the radius that gives the optimum response. This optimal area is smaller at higher contrast. The dotted line is the firing rate when the stimulus screen is uniformly illuminated at the mean luminance of the grating patterns used as stimuli in this experiment.
The research is distance centimeter (2001) figure Sceniak, and layer and input of observed the of parameter stimuli. It value man away graph field. are from of in alone for cellular up in only large summation in of mec only spatial group Neurocenter of of used with sprey als about the in et measuring espec heavily not will in summation distanc leng important in the t that on center is for Diagram a the summation and some have the field source is by center of area, tec mechanis now Calcu population and for plotted 10 locate 4B. layer experimen surr label Figs. high be a In Th (2004) the left up the of are large M consi the hypothesi that this in inhibitory i is of and not (1999) is can laye on in by inde cortex, will with shows Angelucci is surround the the in surr extent contrast. neuron. marks spatia suppr consi that ho summation t appreci i surround the the midpoi V1, V1 al. cells in SI is high Gaussi Angelucci is surround the the of full spat in the gratings. 17 the o 6 macaque 11. 6) distribution the direct What to the spatia extent Hawke 8 same of cells and inhibi is neuron. strongly SI connec may receptive V connectio o this the substant selective be of full spat in the gratings.

Fig. 10. V1 population data for the area summation experiment at low and high contrast. In the scatter plot in the left panel, the center summation parameter $a_l$ at low contrast is plotted on the vertical axis vs the center summation parameter $a_h$ at high contrast. In the right panel, the distribution of the ratio $a_{low}/a_{high}$ is plotted. The arrow marks the mean of this distribution at a value of 2.3.

Fig. 11. Diagram of the spatial scale of anatomical connections and the spatial extent of receptive field mechanisms for a V1 neuron. In the figure the label SF is for summation field. From Angelucci et al. (2002), with permission.
The mean relative increase in the value parameter $a$ is 2.3 when contrast is decreased from 90% of saturating contrast down to a contrast that produces a response twice as large as the noise level. But as can be seen in the right hand panel of Fig. 10, some cells increase the parameter $a$ by almost a factor of 10 when contrast is lowered. This result and our similar measurements of length summation are consistent with the results of Kapadia, Westheimer, and Gilbert (1999) on length summation and contrast. It suggests that the adaptation of the visual cortex to contrast is not simply a matter of changing gain, but also involves a spatial reorganization. There appears to be much more spatial integration of cortical signals at low contrast, as if the cortex were trying to increase signal/noise for contrast detection when the contrast signal is weak.

Our results on surround inhibition in V1 (Sceniak et al., 2001) are similar to those reported by Levitt and Lund (2002). The neurophysiological results of these two groups have been compared with quantitative neuroanatomical studies of V1 lateral and feedback connections in a paper by Angelucci et al. (2002). A summary diagram from Angelucci et al. (2002) is shown in Fig. 11. Fig. 11 is interesting because it suggests that the spatial extent of the $a$ parameter for what we called the center mechanism of the V1 receptive field can be accounted for in terms of feedforward and recurrent connections within V1. However, the large spatial extents of some of the V1 surrounds require feedback connections from extrastriate visual areas where the neurons’ receptive fields are larger. That is, simply on the basis of the area summation experimental results we are compelled to accept that extrastriate $\rightarrow$ V1 feedback is an important component of V1 visual responses.

The results reviewed here show that most V1 neurons are not sensitive to one-dimensional patterns that are extensive in space. These data neither define the two-dimensional structure of the cortical receptive fields nor tell us what two-dimensional features are optimal for each neuron. Further work on the geometry of two-dimensional interactions, and the dynamics of center-surround interactions will be helpful in answering such important questions. However, what is becoming clear from this work already is that cortical feedback from outside V1 has a direct role in shaping the visual properties of V1 neurons. A role for top-down feedback into V1 has been suggested before but it is usually thought to be a modulatory signal, perhaps as the instantiation of attention for instance. Such a modulatory role for cortical feedback to V1 is not inconsistent with what we have found. But what we have shown is that there is a more fundamental and more elementary role for feedback: the visual cortex, including V1 but also V2, V3, MT and other visual areas, seems to act as a unit in the cortex’s visual response to spatial patterns, even very simple patterns like gratings. The suppressive surrounds of V1 neurons are derived in part from feedback signals. It is a challenge for theorists to understand what is the function of this feedback in visual perception.

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