Visual Cortex: The Continuing Puzzle of Area V2

Dispatch

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Surprisingly little is known about the role of V2 in visual processing. A recent study found that the responses of V2 neurons to pairs of angled lines could be predicted from their responses to the individual line components. A simple analysis shows how these neurons may simply sum the responses from one or more orientation selective V1 neurons.

Anyone witnessing a session of electrophysiological recording from the primary visual cortex (area V1) of the macaque monkey is struck by the clear role that V1 cells play in deconstructing a visual scene into spatially localized oriented components. Similarly, neurons in the higher visual area MT clearly reveal their role in visual processing by the way they fire vigorously only to motion in a specific direction and at a specific speed. The function of neurons in the secondary visual area, V2, however, is much less clear despite the prominent location of V2 early in the visual hierarchy.

We know that V2 is important, if not essential, for vision. While a lesion in V2 spares visual acuity and contrast sensitivity, it strongly affects a monkey's ability to perform more complex spatial tasks [1]. V2 cells are selective for orientation, and somewhat so for color, stereoscopic disparity and motion [2–4]. But so far no stimulus has been found that excites these cells in a way that reveals their obvious contribution to vision. Perhaps this is why V2 remains relatively unstudied compared to V1 and MT. A rough search shows that electrophysiological studies in V1 and MT outnumber those in V2 by a ratio of 10:2:1. This is especially striking considering that in the macaque monkey, V2 is as large as V1, and covers about one-fifth of the visual cortex — or about one-tenth of the neocortex — while area MT is only about 7% as large as either of them [5,6].

How should a physiologist go about studying the role of V2 in visual processing? More specifically, how should visual stimuli be chosen from an infinite set of possibilities? A common approach is to guess what image properties are most important for visual processing. Theoretical and computational approaches to vision have suggested various classes of stimuli that might be informative. This has led to a variety of stimuli being shown to V2 neurons, including intersections, arcs, circles, texture patterns such as sinusoidal and non-Cartesian gratings [7,8].

Ito and Komatsu [9] recently studied the selectivity of V2 neurons in the macaque to stimuli consisting of angled lines placed in the center of each cell's receptive field. Figure 1A shows the stimuli they used, with the

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orientation of one of the line segments that form the angle varying along the rows, and the orientation of the other varying along the columns. The choice of angled lines seems reasonable; angles serve as basic components for detecting contours, and co-occurring lines are found prominently in natural scenes [10].

Like many other V2 studies, the main results are presented as a pattern of responses from a given neuron across the chosen stimulus space [9]. The pattern of responses to this stimulus set can provide insight into what a V2 cell may be computing. For example, a cell that responds to specific columns or rows of the stimuli in Figure 1A is sensitive to the components of the stimuli, but not necessarily to a combination of the two components. Stimuli along the diagonals from the upper left to the lower right share a common size of angle, regardless of which orientation the vertex is pointing. Stimuli along the opposite diagonal have vertices pointing in the same direction regardless of angle size.

For the most part, the results suggest that V2 neurons respond primarily to the components of the angles, but do not show much preference to the angle's size or orientation [9]. Figure 1B shows the pattern of responses for an example neuron, with circles surrounding the stimulus that evokes the maximal response, and stimuli evoking more than half of this maximum response shaded in gray. Note the heightened responses to stimuli along specific rows and columns. This V2 neuron responds to the presence of either component of the angled line stimulus.

Ito and Komatsu [9] compared V2 responses to angled stimuli to their responses to the components of the angles alone. They found that the responses to an angle stimulus could be predicted by the responses to the individual components. These neurons show something interesting about the organization of V2 receptive fields. Perhaps a V2 neuron with two preferred orientations simply receives direct inputs from two orientation-selective V1 neurons. Thus, just as Hubel and Wiesel [11] proposed how a V1 simple cell might be constructed from a series of center-surround neurons in the lateral geniculate nucleus (LGN), perhaps V2 is constructed in a similar manner from V1 inputs [12].

We shall show here how a simple model can explain the results reported by Ito and Komatsu [9]. Figure 1C shows how a V2 cell could be constructed by summing the responses of two hypothetical V1 simple cells, each modeled as basic oriented linear filters with excitatory centers and suppressive flanking surrounds. When presented with the stimulus set in Figure 1A, such a model V2 neuron will respond with the pattern shown in Figure 1D. Note the similarity between the responses of this model V2 neuron (Figure 1D) and its real counterpart (Figure 1B).

Other V2 neurons in the new study [9] did not respond well to the components of a preferred angle stimulus. The simple linear model cannot explain these results, which show that some V2 cells respond to particular
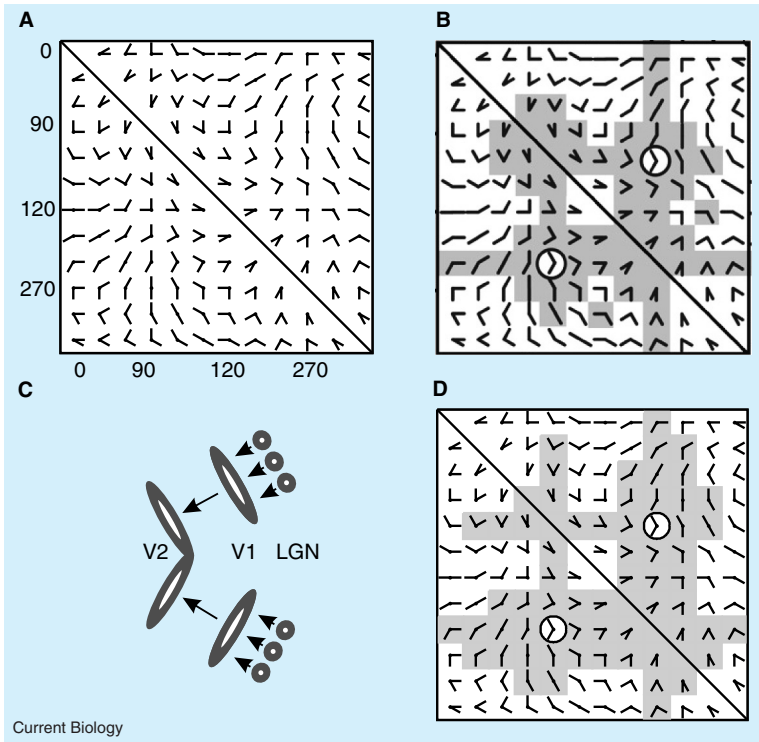
Figure 1. The selectivity of a V2 neuron can be explained by two V1 inputs.

(A) Angle stimuli, consisting of two line segments, used by Ito and Komatsu [9] to study the selectivity of V2 neurons. The orientation of one line segment varies along the rows and the orientation of the other line segment varies along the columns. (B) The pattern of responses for an example neuron. Circles surround the stimulus that evoked the maximal response, and stimuli that evoked more than half this maximum are shaded in gray. (C) Our model V2 neuron sums the responses from two orientation-selective V1 neurons that sum the inputs from LGN cells with center-surround receptive fields [11]. (D) Predicted response from our model neuron to the stimulus set. Like the example V2 neuron, the model neuron responds to angle stimuli containing oriented line segments that match the preferred orientation of either of the two V1 input neurons.

combinations of line components that form angles, but not necessarily to each of the components alone. This implies some sort of nonlinear interactions in the inputs from V1. This is reminiscent of the response of MT neurons to moving 'plaid' stimuli constructed from two moving sinusoidal gratings: some MT cells were found to respond only to the components of the plaid, while others responded to the overall motion of the pattern [13].

Although the results of Ito and Komatsu [9] are apparently consistent with a very simple model for V2 cells, more is undoubtedly going on between V1 and V2. For example, when applied to the set of stimuli used by Hegdé and Van Essen [7], a randomly selected population of model V2 neurons show a weaker selectivity to curved arcs than do actual V2 neurons.

It is not easy choosing stimuli to study a poorly understood visual area like V2. It is reasonable to choose stimuli based on guesses at what are fundamental components of a visual scene for performing tasks such as object recognition or contour segregation. This is particularly true for visual areas relatively high up in the processing stream, such as area V4 or the inferotemporal cortex (IT), which benefit from a large amount of previous neuronal processing. Area V2, however, may lie too early in the visual hierarchy to make substantially sophisticated computations.

On the other hand, the location of V2 in the hierarchy does have the advantage that area V1, from which V2 receives its predominant input, is reasonably well understood. It therefore makes sense to consider how a V2 neuron could be built from V1 neurons when choosing stimuli for an experiment. The angled lines used by Ito and Komatsu [9] are an excellent example; the seemingly complex pattern of their results can at least be partially explained by a simple model in which

V2 neurons are summing the response from two orientation selective V1 simple cells.

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