

Visual Cortex: Seeing Motion

Dispatch

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How does primary visual cortex respond to moving images? While much is known about responses of single neurons to such stimuli, responses at the level of maps are only now beginning to be understood.

What happens in primary visual cortex (V1) when we look at a complex moving image? While motion responses have been investigated thoroughly at the level of single neurons [1–4], studies of motion representation at the level of maps have been restricted to stimuli composed of long bars. These stimuli are inherently ambiguous as to their direction of motion [1]. A recent study by Fitzpatrick and collaborators [5] overcomes this limitation. Using optical imaging of intrinsic signals [6], the authors measured population responses to a variety of moving stimuli. Their results contradict the literature on optical imaging, but are in line with previous results obtained by recording from single neurons.

As is common in optical imaging, Fitzpatrick and collaborators [5] recorded responses to gratings — arrays of long bars such as the one in Figure 1A — to measure a map of preferred orientation, that is, to assign a preferred orientation to each pixel in the imaged portion of V1. They then recorded responses to short tilted bars drifting diagonally — such as that in Figure 1B — and found that these responses were inconsistent with the map. Nonetheless, for each direction of the short bar, an ‘equivalent long bar’ could be found that elicited a similar pattern of response. For example, even though their orientations differ by 25°, the long bar in Figure 1A is ‘equivalent’ to the short bar in Figure 1B. Indeed, the two give rise to similar patterns of responses (Figure 1C). Manipulations of bar length, direction and speed brought the orientation of the ‘equivalent long bar’ closer to or further from the orientation of the short bar.

These results flatly contradict the bulk the literature on optical imaging, which postulates or reports explicit maps of preferred orientation, spatial frequency and direction [7–11]. According to this literature, a stimulus with a given orientation, spatial frequency and direction should have elicited responses in those pixels that lie at the intersection of the corresponding maps.

The results come as less of a surprise, however, if one considers the literature on responses of single neurons. After a debate that raged in the 1970s, it was largely agreed that V1 neurons do not isolate this or

that feature of the stimulus. For example, an elegant study by the De Valois group [12] demonstrated that V1 neurons do not encode orientation independently of other features: preferred orientation depends on stimulus spatial frequency as predicted by a simple model based on the receptive field [13]. Similarly, it has also been known for a long time that V1 neurons do not encode direction of motion independently of other features. This issue was settled by the studies of responses of single V1 neurons to plaids — sums of two gratings — by Movshon and colleagues [1,2].

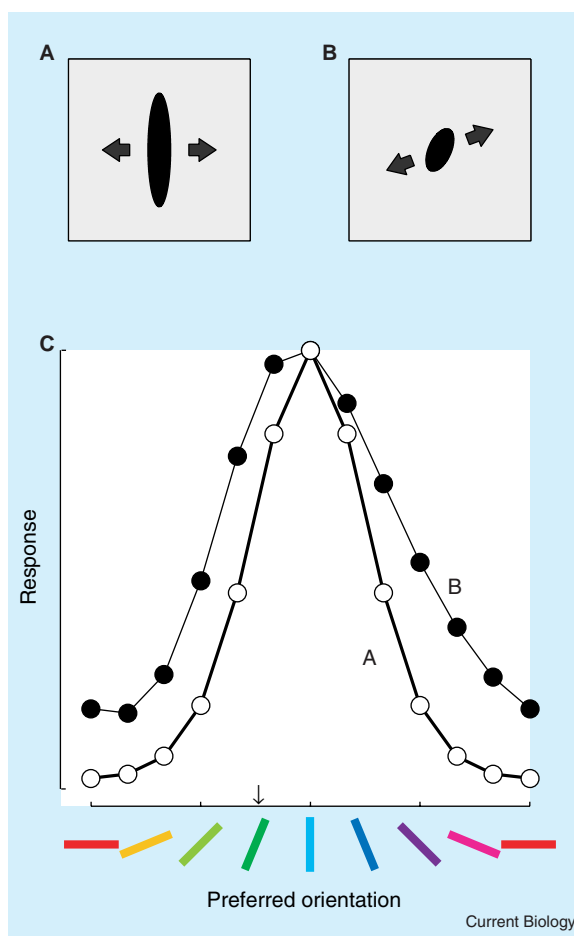


Figure 1. Two moving stimuli and the responses they elicit in a model of V1.

(A) A vertical long bar, moving orthogonally to its orientation. (B) A tilted (25°) short bar moving diagonally to its orientation. To simplify the simulations, we approximate bars by Gaussians, whose contours are ellipses. (C) Responses elicited in V1 by the two stimuli. Abscissa indicates preferred orientation of neurons as measured with long bars. Color scheme as common in optical imaging, where surface of V1 is colored according to preferred orientation. By definition, responses to the vertical long bar in A (open circles) peak at vertical. Responses elicited by the short bar in B (closed circles) peak at same preferred orientation, 25° away from vertical (arrow).

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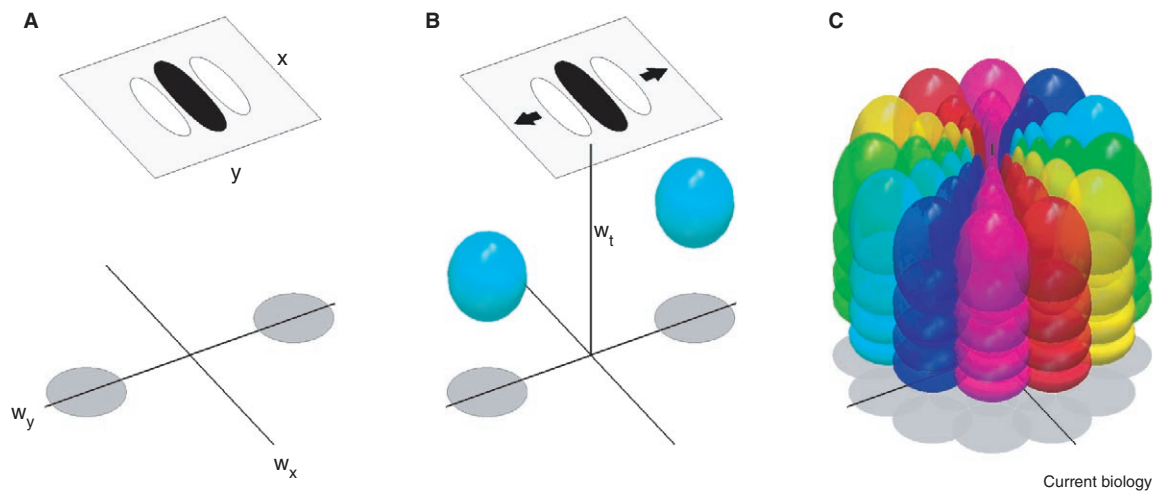


Figure 2. Frequency representation of receptive fields of model V1 neurons.

(A) A receptive field observed in space x , y (top) and in the frequency domain (w_x, w_y, w_t) (bottom). (B) Two receptive fields observed in the attributes (x, y, w_t) . The two receptive fields are selective for identical spatial attributes (as in A), and opposite directions of motion (arrows). (C) A population of receptive fields, selective for a range of orientations, spatial frequencies and temporal frequencies. (Colors as in Figure 1C.)

In fact, as suggested by Fitzpatrick and colleagues [5], the observed behaviors are consistent with the well-established view that V1 neurons have receptive fields defined not only in two-dimensional space (x, y) , but also in three-dimensional space-time (x, y, t) [4,14–16]. At least qualitatively, the results might have been predictable already 20 years ago [17].

To see how this is the case, it helps to picture receptive fields of V1 neurons in the frequency domain (Figure 2). Consider first a two-dimensional spatial receptive field (Figure 2A, top). The representation of such a receptive field in the frequency domain (w_x, w_y) consists of two disks (Figure 2A, bottom), whose angle with the abscissa represents preferred orientation, and whose distance from the origin represents preferred spatial frequency. Consider now a full, three-dimensional space-time receptive field, represented in the frequency domain (w_x, w_y, w_t) (Figure 2B). This receptive field corresponds to a ball, whose vertical position w_t indicates preferred temporal frequency. The two balls in Figure 2B denote receptive fields selective for opposite directions of motion. Finally, consider a whole population of V1 receptive fields, covering a range of preferred orientations, spatial frequencies and temporal frequencies (Figure 2C). Each of these receptive fields corresponds to a ball, and ball size grows with preferred spatial frequency and temporal frequency, so that the bandwidth in octaves is constant [13].

In the frequency domain, the moving bars in Figure 1A and 1B correspond to wings emerging from the ground plane (Figure 3). Consider first the spatial aspect of these stimuli, that is, the horizontal (w_x, w_y) plane: the long bar (Figure 1A) is represented by an elongated ellipse (Figure 3A), whereas the short bar (Figure 1B) is represented by a rounder ellipse (Figure 3B). Consider now that the stimuli move, and the three-dimensional frequency domain representation of

a moving stimulus lies on a plane [17]. Because the stimuli move back and forth, there are two planes for each stimulus, hence the two wings emerging from the ground plane.

The responses elicited by these stimuli are depicted by the blobs in Figure 3: neurons with receptive fields inside the blobs fire more than 50% of the maximal response. Though the populations of neurons excited by these stimuli are not identical, the peak of the response is achieved by receptive fields with the same preferred orientation (depicted in cyan). This identity arises because the effects of changes in orientation and direction of motion of the short bar counterbalance each other: tilting the orientation rotates the ellipse; and tilting the direction of motion rotates the intersection of the wings with the ground plane.

These results are summarized by curves depicting activation as a function of preferred orientation for the two stimuli (Figure 1C), obtained by summing over preferred spatial frequency and preferred temporal frequency. As in the study by Fitzpatrick's group [5], these curves are broadly similar, and peak at the very same orientation (vertical), even though the orientations of the two stimuli are different.

In summary, the results by Fitzpatrick and colleagues [5] are consistent with those obtained in single neurons [1,2,12] and are predicted by the simple model of V1 responses based on space-time receptive fields that has become dominant in the last 20 years [1,2,4,12–17]. Once the map of orientation preference is measured with long bars, the model predicts the pattern of activation obtained with tilted short bars. In particular, higher order interpretations that have been suggested [18] do not appear to be warranted.

There is, however, one aspect of the results of Fitzpatrick and colleagues [5] that is somewhat surprising: no matter what the stimulus was —

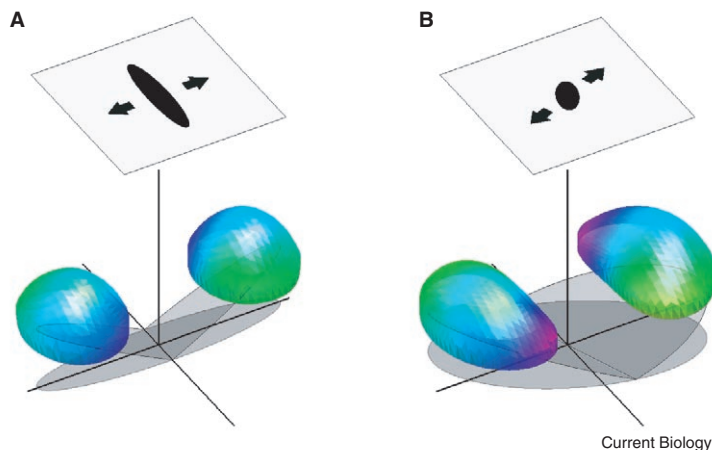


Figure 3. Frequency representation of the stimuli in Figure 1A,B and of the V1 receptive fields that they activate.

(A) The long bar corresponds in the frequency domain to two narrow wings. (B) The short bar corresponds in the frequency domain to two wider wings. The colored blobs indicate the volume of V1 receptive fields where the stimuli elicit >50% of the maximal response. (Colors as in Figure 1C.)

gratings, short bars or dots — the pattern of activation in cortex resembled that obtained with a drifting grating (albeit one of a different orientation). According to the model, instead, the patterns of activation elicited by long and short bars should not be exactly identical, being broader for the short bars (curves in Figure 1C, blobs in Figure 3). One possibility is that the expected differences in pattern of activation are small, and that optical imaging does not resolve them, either because of blur in signal acquisition or because the relevant neurons are intermingled. Another factor that might contribute to the results is a tendency for the circuitry of cortex to favor certain response configurations: recent results [19] indicate that activity in V1 tends to fall into these configurations even in the absence of a stimulus. Further research into the representation of moving stimuli in area V1 and into the blurring associated with optical imaging is required to answer this outstanding question.

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