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Journal Club

Surround Suppression in the Early Visual System

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Review of Webb et al. (http://www.jneurosci.org/cgi/content/full/25/50/11666)

Introduction

In their description of orientation-tuned cells in primary visual cortex (V1) of the macaque, Hubel and Wiesel (1968) found that some neurons responded less when they lengthened an optimally oriented bar stimulus. They termed cells that exhibited this behavior to be "hypercomplex". Numerous studies have since explored this phenomenon, now known commonly as surround suppression. At least three sources have been proposed (Fig. 1) to account for this kind of suppression by stimuli outside the classical receptive field (CRF). Long-range lateral or horizontal connections within V1 were originally suggested to form the circuitry underlying surround suppression (Gilbert and Wiesel, 1983). This was based on anatomical evidence showing connections between distant neurons of like orientation, and physiological evidence that suppression is strongest at the orientation that matches the preferred receptive field stimulus. More recently, feedback from higher cortical areas has been proposed as a source because of the relatively slow dynamics of surround suppression and the lack of a strong dependence on cortical distance (Bair et al., 2003). Another suggestion is that activation of orientation-tuned surround suppression in the lateral geniculate nucleus (LGN) leads to reduced excitatory drive to V1 (Ozeki et al., 2004). As the study of surround suppression has evolved, it has become increasingly difficult to reconcile these three. In a recent study published in *The Journal of Neuroscience*, Webb et al. (2005; http://www.jneurosci.org/cgi/content/full/25/50/11666) exploited the different response properties of subcortical and cortical neurons to distinguish between these potential mechanisms for surround suppression.

The authors first identified the optimal grating stimulus for the CRF with respect to orientation, size, and spatial and temporal frequency. Then, using a CRF stimulus with these parameters, they varied the spatial frequency of the surround annulus as presented both parallel and orthogonal to the CRF stimulus. The average spatial frequency preferred by the surround was 2.2 times lower as well as much broader than that preferred by the CRF. Furthermore, very high frequencies (five times the CRF peak) and a spatially uniform annulus elicited powerful suppression [Webb et al. (2005), their Fig. 3 (http://www.jneurosci.org/cgi/content/full/25/50/11666/FIG3)], although these stimuli were poor at driving the CRF. Webb et al. (2005) found similar results when testing the temporal frequency selectivity of the surround. Although the CRF is sharply tuned for temporal frequency, the surround was broadly tuned –nearly flat within the range they tested. In addition, they were able to elicit suppression from the surround at very low (0.5 Hz) and high (30 Hz) temporal frequencies [Webb et al. (2005), their Fig. 5 (http://www.jneurosci.org/cgi/content/full/25/50/11666/FIG5)], outside the range to which most V1 neurons respond. Finally, they tested the contrast sensitivity of the surround to optimally oriented grating stimuli, orthogonal gratings, and a spatially uniform field. As expected, the surround was most sensitive to an optimal grating stimulus. Less predictable was their finding of significant sensitivity to a spatially uniform field, exceeding that to an orthogonal grating [Webb et al. (2005), their Fig. 7 (http://www.jneurosci.org/cgi/content/full/25/50/11666/FIG7)]. Thus, surround suppression was activated by stimuli that drive the CRF of most V1 neurons poorly or not at all, implicating a mechanism that acts at or before the input layers of V1. However, the orientation selectivity of surround suppression instead points to a mechanism beyond the V1 input layers. Webb et al. (2005) propose that two separate mechanisms underlie surround suppression, and designed two experiments to test this hypothesis.

Neurons in V1 and the LGN display a temporary loss of responsiveness after prolonged exposure to a high-contrast stimulus. Webb et al. (2005) took advantage of this "contrast adaptation" to test the hypothesized dual mechanisms of surround suppression. They determined the susceptibility of the surround to adaptation with gratings of different contrasts and orientations as well as a spatially uniform field. Adaptation to both optimal and orthogonal gratings reduced the effectiveness of the surround, producing a fourfold increase in the contrast necessary to suppress responses with an optimal grating. This is higher than would be predicted based on the sensitivity of LGN neurons. However, adaptation to a spatially uniform annulus produced no change in the effectiveness of the surround [Webb et al. (2005), their Fig. 9 (http://www.jneurosci.org/cgi/content/full/25/50/11666/FIG9)], although this stimulus is a potent one for LGN neurons. The strength of adaptation seems inconsistent with a thalamic source for surround suppression, but the similar adaptation to optimal and orthogonal gratings is not expected from an orientation-selective cortical mechanism.

Visual signals from the two eyes are segregated at the level of the LGN and the input layers of V1, and binocular interactions become significant only outside these layers (Hubel and Wiesel, 1968). Webb et al. (2005) used an interocular

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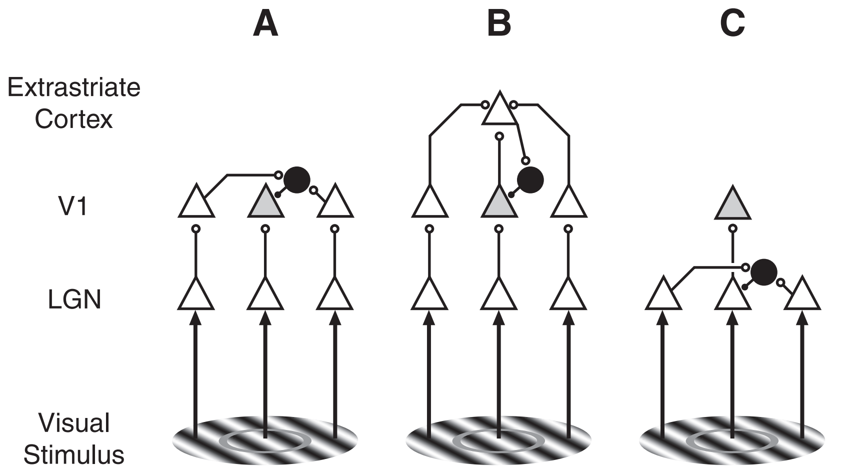

Figure 1. Schematic of three proposed mechanisms for surround suppression. The open triangles represent excitatory neurons, and the filled circles represent inhibitory interneurons. The recorded neuron is indicated with a triangle shaded gray. This neuron is driven by the CRF stimulus (shown as a small patch of grating) and suppressed in the presence of a surround stimulus (shown as a larger annular grating). ***A***, In the horizontal connection model, V1 neurons with receptive fields stimulated by the surround stimulus suppress the recorded neuron. This is accomplished via projections to an inhibitory interneuron. ***B***, A different model effects suppression through feedback from extrastriate cortex. Here, V1 inputs are pooled by an extrastriate neuron with a large receptive field. The recorded neuron is suppressed via feedback connections to an inhibitory interneuron. ***C***, A third model generates surround suppression within the LGN, not requiring extensive cortical circuitry. The illustrated mechanism involves local inhibitory connections within the LGN, but related models (data not shown) might be constructed by invoking retinal gain control or feedback from visual cortex.

transfer experiment to test whether surround suppression occurs before or after the signals from the two eyes intermingle. They delivered an optimal CRF stimulus to the dominant eye and tested the degree of suppression when a surround grating was presented to each of the two eyes. Although suppression was stronger when the stimulus was delivered to the surround of the dominant eye, significant suppression remained to a nondominant eye stimulus [Webb et al. (2005), their Fig. 10 (http://www.jneurosci.org/cgi/content/full/25/50/11666/FIG10)]. If surround suppression were generated by a mechanism located before the binocular combination of signals, this result would not be expected. Instead, the presence of interocular transfer suggests that suppression arises from a cortical mechanism beyond the input layers of V1.

The authors conclude that two distinct mechanisms underlie surround suppression: one that arrives early and is consistent with an origin in the LGN or input layers of V1; the other arrives later and is compatible with horizontal V1 connections or feedback from extrastriate cortex. Their data are compelling evidence that a single mechanism is insufficient to account for the variety of properties observed in surround suppression. However, important questions remain. Bair et al. (2003) reported that surround suppression in V1 neurons could be delayed by >40 ms after response onset, but it could also precede it by >20 ms. Two mechanisms for surround suppression could account for this wide range of delays. To reach that conclusion, it would be critical to examine the timing of surround suppression along with the experiments performed by Webb et al. (2005). Presumably, neurons that are identified as having properties consistent with suppression from the LGN or V1 input layers would also be the ones with a fast time course of suppression. Furthermore, although Webb et al. (2005) identify two putative sources of surround suppression, the loci remain imprecise. The "early" mechanism might be located in either the LGN or V1 input layers, and the "late" mechanism might arise from horizontal connections within the V1 or feedback from the extrastriate cortex. Finally, additional knowledge of the LGN suppressive field is necessary to determine what role it plays in surround suppression in the V1. Bonin et al. (2005) demonstrated that a contrast gain control model is able to explain diverse suppressive phenomenon seen in LGN responses. Whether V1 surround suppression can be partially explained by expanding such a model remains an open question. Webb et al. (2005) have provided an important conceptual framework as a starting point. Future research will be needed to guide our understanding of surround suppression in the V1, as well as its link to other forms of contextual modulation by stimuli outside the CRF.

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