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Multiple components of surround modulation in primary visual cortex: Multiple neural circuits with multiple functions?

Lauri Nurminen, Alessandra Angelucci *

Dept. of Ophthalmology and Visual Science, Moran Eye Institute, University of Utah, Salt Lake City, UT 84132, United States

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ABSTRACT

The responses of neurons in primary visual cortex (V1) to stimulation of their receptive field (RF) are modulated by stimuli in the RF surround. This modulation is suppressive when the stimuli in the RF and surround are of similar orientation, but less suppressive or facilitatory when they are cross-oriented. Similarly, in human vision surround stimuli selectively suppress the perceived contrast of a central stimulus. Although the properties of surround modulation have been thoroughly characterized in many species, cortical areas and sensory modalities, its role in perception remains unknown. Here we argue that surround modulation in V1 consists of multiple components having different spatio-temporal and tuning properties, generated by different neural circuits and serving different visual functions. One component arises from LGN afferents, is fast, untuned for orientation, and spatially restricted to the surround region nearest to the RF (the near-surround); its function is to normalize V1 cell responses to local contrast. Intra-V1 horizontal connections contribute a slower, narrowly orientation-tuned component to near-surround modulation, whose function is to increase the coding efficiency of natural images in manner that leads to the extraction of object boundaries. The third component is generated by topdown feedback connections to V1, is fast, broadly orientation-tuned, and extends into the far-surround; its function is to enhance the salience of behaviorally relevant visual features. Far- and near-surround modulation, thus, act as parallel mechanisms: the former quickly detects and guides saccades/attention to salient visual scene locations, the latter segments object boundaries in the scene.

1. Introduction

Surround modulation is the ability of neurons in the visual cortex to change their response to local visual features within their receptive fields (RFs) depending on visual context, i.e. the stimuli simultaneously present in the RF surround. This property, initially attributed by Hubel and Wiesel (1965) to a special class of cells in the primary visual cortex (V1) of cats (which they termed "hypercomplex"), has now been described for most cells in V1 of many species, ranging from mouse (Van den Bergh et al., 2010) to cat (Blakemore & Tobin, 1972; Gilbert, 1977; Maffei & Fiorentini, 1976; Nelson & Frost, 1978; Sengpiel, Sen, & Blakemore, 1997; Walker, Ohzawa, & Freeman, 2000) and monkey (Cavanaugh, Bair, & Movshon, 2002a; Knierim & Van Essen, 1992; Sceniak, Hawken, & Shapley, 2001; Shushruth et al., 2009). Surround modulation and analogous phenomena have also been described throughout the visual system (e.g. Albright & Stoner, 2002; Allman, Miezin, & Mc Guinness, 1985; Born & Bradley, 2005; Desimone & Schein, 1987; Pollen et al., 2002) and across different modalities, including the auditory (Sutter et al., 1999), somatosensory (Sachdev, Krause, & Mazer, 2012; Vega-Bermudez & Johnson, 1999) and olfactory (Olsen & Wilson, 2008) systems. In human visual perception, many studies have demonstrated that spatial context alters the perception of a visual target (Cannon & Fullenkamp, 1991; Chubb, Sperling, & Solomon, 1989; Ejima & Takahashi, 1985; Meese & Hess, 2004; Meese et al., 2007; Nurminen et al., 2009; Olzak & Laurinen, 1999; Snowden & Hammett, 1998). The conservation across such a wide range of species, cortical areas and sensory modalities suggests that surround modulation plays a fundamental role in sensory processing. However, despite a plethora of research that has provided a thorough characterization of the parameter space of surround modulation, its functional role remains a mystery.

In this article we focus on surround modulation in V1. We present our view that surround modulation consists of multiple components that arise from different anatomical circuits and have different spatio-temporal and stimulus tuning properties, and therefore should not be considered as a single entity with a single

* Corresponding author. Address: 65 Mario Capecchi Drive, Salt Lake City, UT 84132, United States. Fax: +1 801 5877820.
E-mail address: alessandra.angelucci@hsc.utah.edu (A. Angelucci).

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functional role. We will focus on each of the components separately, and put forward our hypotheses concerning their distinct functional roles in natural vision.

2. Basic properties of surround modulation

The properties of surround modulation in V1 have been quantitatively characterized in many studies, typically using a circular grating patch of increasing radius (Fig. 1A), or a center grating patch confined to the neuron's RF surrounded by an annular grating (Fig. 1B), and varying systematically the grating/s parameters (reviewed in: Angelucci & Shushruth, 2014). There is general agreement among these studies that surround modulation in V1 shows five basic properties. (1) It is predominantly suppressive (stimulation of the surround reduces the neuron's spiking response to an optimal stimulus in its RF – Fig. 1), especially when the center and surround stimuli are of high contrast, and the surround is stimulated with large gratings (Cavanaugh, Bair, & Movshon, 2002a; DeAngelis, Freeman, & Ohzawa, 1994; Levitt & Lund, 1997, 2002; Sceniak, Hawken, & Shapley, 2001; Sengpiel, Sen, & Blakemore, 1997; Walker, Ohzawa, & Freeman, 2000). (2) It is orientation selective, i.e. the strongest suppression is observed when the stimuli in the RF and surround are of the same orientation (DeAngelis, Freeman, & Ohzawa, 1994; Li & Li, 1994; Sengpiel, Sen, & Blakemore, 1997; Walker, Ohzawa, & Freeman, 1999), even when the orientation of the stimulus inside the RF is not the one preferred by the neuron (Cavanaugh, Bair, & Movshon, 2002b; Shushruth et al., 2012). The suppression can turn into facilitation when the stimuli in the RF and surround are cross-oriented, especially when the RF is stimulated with suboptimal orientations for the cell (Shushruth et al., 2012; Sillito et al., 1995). Psychophysical experiments have reported highly similar orientation tuning of surround suppression in human vision as in macaque V1 cells (Cannon & Fullenkamp, 1991; Petrov, Carandini, & McKee, 2005; Solomon, Sperling, & Chubb, 1993), suggesting similar underlying mechanisms for surround modulation in the two species. (3) Surround modulation is also tuned for spatial frequency, so that stimuli of similar spatial frequency in the RF and surround produce the strongest suppressive effects. In human vision the spatial frequency of surround modulation shows band-pass tuning (Chubb, Sperling, & Solomon, 1989), while in V1 cells the tuning is low pass (Webb et al., 2005). (4) Surround modulation is spatially extensive (modulatory effects can be evoked from surround regions up to 12.5° away from the RF center) (Cavanaugh, Bair, & Movshon, 2002a; Levitt & Lund, 2002; Sceniak, Hawken, & Shapley, 2001; Shushruth et al., 2009), and the suppression is strong, but it decreases in strength with increasing distance from the RF center or from a target grating (e.g. Fig. 1B) (Cannon & Fullenkamp, 1991; Nurminen, Peromaa, & Laurinen, 2010; Shushruth et al., 2009). (5) Finally, surround suppression is fast, being delayed on average by as fast as 9 ms relative to the onset of the RF response, in a manner that is nearly independent of the distance of the surround stimulus from the RF (Bair, Cavanaugh, & Movshon, 2003).

3. The multiple components of surround modulation: multiple neural circuits with multiple functions

Multiple lines of evidence suggest that the surround of V1 neurons consists of "near" and "far" components (Fig. 1) generated by different anatomical circuits. These circuits involve feedforward

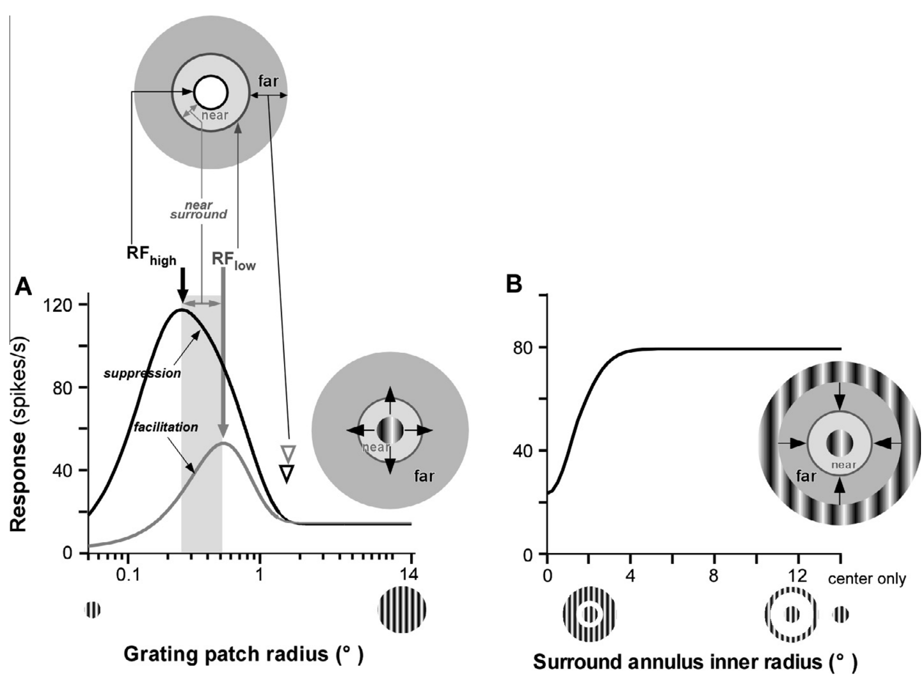

Fig. 1. Surround suppression in V1 cells. (A) Surround suppression probed using grating patches of increasing radius centered on the neuron RF. *Black and gray curves*: responses of an example V1 cell to a grating of high and low contrast, respectively. As the radius of the grating patch increases, the cell's response increases up to a peak (*thick arrows*), corresponding to the RF size measured at high contrast (RF_{high}) and at low contrast (RF_{low}), respectively; the cell's response is then suppressed as the grating extends beyond the RF, into the surround. We call the region between the RF_{high} and the RF_{low} "near" surround (*gray shaded column* in A, and *light gray ring* in the inset above A); stimulation of this surround region can cause facilitation or suppression, depending on stimulus contrast. We call the region beyond the RF_{low} "far" surround. *Arrowheads*: surround radius measured at high (*black*) and low (*gray*) stimulus contrast. *Top inset*: schematics of the different components of the RF and surround of a V1 cell, with the *white area* indicating the RF, and the *gray areas* the surround, the latter consisting of a near (*light gray*) and a far (*dark gray*) region. *Right inset* indicates the stimulus paradigm, i.e. a grating centered on the cell's RF, which is systematically grown (*arrows*) in radius. (B) Surround suppression probed using a center-grating patch confined to the cell's RF and an annular grating in the surround whose inner radius is systematically grown (*arrows*) toward the RF (*right inset*). The black curve indicates the cell's response to center and surround gratings of high contrast: as the inner radius of the surround annulus is decreased (read the *x* axis from right to left), the cell's response is increasingly suppressed.