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Responses to second-order texture modulations undergo surround suppression

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ABSTRACT

First-order (contrast) surround suppression has been well characterized both psychophysically and physiologically, but relatively little is known as to whether the perception of second-order visual stimuli exhibits analogous center–surround interactions. Second-order surround suppression was characterized by requiring subjects to detect second-order modulation in stimuli presented alone or embedded in a surround. Both contrast- (CM) and orientation-modulated (OM) stimuli were used. For most subjects and both OM and CM stimuli, second-order surrounds caused thresholds to be higher, indicative of secondorder suppression. For CM stimuli, suppression was orientation-specific, i.e., higher thresholds for parallel than for orthogonal surrounds. However, the evidence for orientation specificity of suppression for OM stimuli was weaker. These results suggest that normalization, leading to surround suppression, operates at multiple stages in cortical processing.

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1. Introduction

An abundance of evidence suggests that the early visual system analyzes visual information using relatively independent "channels" selective for orientation and spatial frequency (Blakemore & Campbell, 1969; Campbell, Carpenter, & Levinson, 1969; Campbell & Robson, 1968; De Valois & De Valois, 1988; Graham, 1989; Graham & Nachmias, 1971). Each channel is composed of a set of spatially localized linear filters that together tile the visual field. In particular, psychophysical sensitivity to luminance modulations (a type of "first-order" cue in the visual image) is adequately captured by a computational model involving linear filtering followed by rectification; these linear filters are in turn represented neurophysiologically by the classical receptive fields of neurons in the primary visual cortex. While linearity and independence provide a good first approximation to the filter responses, complex, nonlinear spatial interactions among filters have also been well documented.

One such nonlinear spatial interaction is surround suppression. Psychophysically, when a target stimulus is embedded in a highcontrast mask or placed in the vicinity of high-contrast flankers, it becomes harder to detect or discriminate (Petrov, Carandini, & McKee, 2005; Polat & Sagi, 1993; Snowden & Hammett, 1998; Wilkinson, Wilson, & Ellemberg, 1997; Zenger-Landolt & Heeger, 2003) and its perceived contrast is lower (Cannon & Fullenkamp, 1991; Chubb, Sperling, & Solomon, 1989; Ejima & Takahashi,

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1985; Olzak & Laurinen, 1999; Snowden & Hammett, 1998; Solomon, Sperling, & Chubb, 1993; Xing & Heeger, 2000, 2001). This is known as surround suppression. Suppression is maximal when the target and surround stimuli have matching spatial frequency and orientation (Cannon & Fullenkamp, 1991; Chubb, Sperling, & Solomon, 1989; Olzak & Laurinen, 1999; Solomon, Sperling, & Chubb, 1993; Xing & Heeger, 2001) and increases with increasing contrast of the surround (Olzak & Laurinen, 1999; Snowden & Hammett, 1998; Solomon, Sperling, & Chubb, 1993).

The human visual system is also able to detect image attributes other than luminance modulations. Spatial variations of texture properties (e.g., local orientation, spatial frequency, or contrast) in the visual image are called "second-order." These kinds of patterns are distinct from first-order, luminance-defined patterns in that they cannot be detected by a simple linear mechanism since there is no variation in mean luminance across the image. The boardwalk in Fig. 1A is an example of a texture-defined pattern that contains modulations of local orientation. The computational models typically used to explain human sensitivity to second-order image structure are called "filter-rectify-filter" (FRF) or "backpocket" models (Fig. 1B; Chubb, Econopouly, & Landy, 1994; Chubb & Landy, 1991; see Landy & Graham, 2004, for a review). An initial stage of linear filtering is selective for a constituent texture. The output from the first stage is subjected to a static nonlinearity (e.g., full-wave rectification). A second-stage linear filter at a coarser spatial scale is then applied to the rectified, first-stage responses. This results in selectivity for the orientation and spatial frequency of second-order texture modulation. The detection of second-order image structure is thought to operate independently of that of first-order structure.





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Fig. 1. Models of second-order processing. (A) A natural scene containing secondorder patterns. The boardwalk contains modulations of texture (defined by local orientation) that cannot be detected by a simple linear mechanism. (B) A typical model of visual processing depicting the parallel pathways for first- and secondorder stimuli. Top, first-order, luminance-defined stimuli are processed by a linear filter. Bottom, second-order, texture-defined stimuli are processed via a filterrectify-filter (FRF) cascade.

Relatively little is known as to whether the perception of second-order stimuli exhibits analogous center–surround interactions observed for first-order stimuli. One psychophysical study provided evidence for second-order surround suppression based on the appearance of texture stimuli, in particular, the perceived modulation depth of contrast-modulated stimuli (Ellemberg, Allen, & Hess, 2004). If a surround suppresses the response to a central, second-order stimulus, then its perceived modulation depth would be reduced. The authors found that, analogous to first-order suppression, second-order suppression was selective for orientation and spatial frequency, but the tuning was more broadband (i.e., the suppression effect was evident for greater differences in relative orientations or spatial frequencies between the target and the surround, as compared to first-order suppression).

We wondered whether the same suppressive effects generalized across different types of second-order stimuli. Here, we used a psychophysical protocol involving the detection of both contrast and orientation modulation to test for and characterize second-order surround suppression. This mirrors analogous experiments on first-order suppression that measured perceived contrast or detection/discrimination sensitivity (Cannon & Fullenkamp, 1991; Chubb, Sperling, & Solomon, 1989; Ejima & Takahashi, 1985; Olzak & Laurinen, 1999; Petrov, Carandini, & McKee, 2005; Polat & Sagi, 1993; Snowden & Hammett, 1998; Solomon, Sperling, & Chubb, 1993; Wilkinson, Wilson, & Ellemberg, 1997; Xing & Heeger, 2000, 2001; Zenger-Landolt & Heeger, 2003), though there is no simple way to relate appearance and discrimination measures (see, e.g., Snowden & Hammett, 1998). Furthermore, the use of orientation-modulated stimuli also helped to put aside concerns about potential artifacts present in contrast-modulated stimuli, such as distortion products caused by nonlinearities in the display or early luminance nonlinearities in the visual system (Schofield & Georgeson, 1999; Smith & Ledgeway, 1997). We measured thresholds for second-order target stimuli in the presence of surround stimuli with varying depth and orientation of modulation, and found that target thresholds were greater when the surround comprised a second-order modulation. Furthermore, to our surprise, suppression was only consistently orientation-specific for contrast-modulated stimuli, while support for orientation-specific suppression in orientation-modulated stimuli was weaker. These results are consistent with the idea that there is a plethora of distinct second-order mechanisms, with different second-stage suppression mechanisms, and that the goal of second-order vision is not only to detect boundaries, but also to extract and characterize image statistics, as required by models of texture appearance (e.g., Portilla & Simoncelli, 2000).

2. Methods

2.1. Subjects

Six subjects (two females, aged 25–52) with normal or corrected-to-normal vision participated in the study. Subjects included two of the co-authors. All subjects were experienced psychophysical observers. Subjects provided written informed consent, and the experimental protocol was approved by the University Committee on Activities involving Human Subjects at New York University.

2.2. Visual stimuli

Stimuli were generated using MATLAB (MathWorks, MA) and displayed on a 22" flat-screen CRT monitor (Hewlett–Packard p1230; resolution: 1152×870 ; refresh rate: 75 Hz) at a distance of 57 cm. The monitor provided approximately 39.1×30.0 deg viewing angle. The display was calibrated and gamma-corrected using a linearized lookup table.

The second-order stimuli were contrast-modulated (CM) or orientation-modulated (OM) horizontal and vertical grating patterns (Fig. 2A and B). A CM grating L_{CM} (Fig. 2A) was generated by sinusoidally modulating the luminance contrast of a noise carrier image N(x,y),

$$L_{\rm CM}(x,y) = L_0[1 + A_{\rm M}M(x,y)N(x,y)],$$
(1)

where L_0 is the background luminance, A_M is the modulation amplitude, and M(x,y) is the modulator image of a two-dimensional vertical or horizontal sine wave grating with spatial frequency (SF) f and phase ϕ . $M(x,y) = \sin(2\pi fx + \phi)$ (vertical) or $M(x,y) = \sin(2\pi - fy + \phi)$ (horizontal). The carrier image N(x,y) was white noise filtered with an isotropic bandpass filter. The filter was a cosine-ramped annulus in the Fourier domain, with a center SF of 8 cyc/deg and a bandwidth of 1 octave (i.e., the annulus extended from 5.7 to 11.3 cyc/deg). N(x,y) was normalized so that 99.5% of the pixels had values within the range of [-1,1]; the small number of pixels with values outside of that range were clipped to -1 or 1.

An OM grating (Fig. 2B) was generated by sinusoidally modulating between two orthogonally oriented noise carrier patterns N_1 and N_2 (Landy & Oruç, 2002; Larsson, Landy, & Heeger, 2006),

$$\begin{split} L_{\rm OM}(x,y) &= L_0 (1 + [0.5(1 - A_{\rm M} M(x,y))]^{0.5} N_1(x,y) \\ &+ [0.5(1 + A_{\rm M} M(x,y))]^{0.5} N_2(x,y)), \end{split} \tag{2}$$

where L_0 , A_M and M were as defined earlier. The noise carriers N_1 and N_2 were generated similarly to N for CM gratings above, but were instead filtered with bandpass filters oriented at 45° and

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