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Surround suppression supports second-order feature encoding by macaque V1 and V2 neurons

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ABSTRACT

Single neurons in areas V1 and V2 of macaque visual cortex respond selectively to luminance-modulated stimuli. These responses are often influenced by context, for example when stimuli extend outside the classical receptive field (CRF). These contextual phenomena, observed in many sensory areas, reflect a fundamental cortical computation and may inform perception by signaling second-order visual features which are defined by spatial relationships of contrast, orientation and spatial frequency. In the anesthetized, paralyzed macaque, we measured single-unit responses to a drifting preferred sinusoidal grating; low spatial frequency sinusoidal contrast modulations were applied to the grating, creating contrast-modulated, second-order forms. Most neurons responded selectively to the orientation of the contrast modulation of the preferred grating and were therefore second-order orientation-selective. Second-order selectivity was created by the asymmetric spatial organization of the excitatory CRF and suppressive extraclassical surround. We modeled these receptive field subregions using spatial Gaussians, sensitive to the modulation of contrast (not luminance) of the preferred carrier grating, that summed linearly and were capable of recovering asymmetrical receptive field organizations. Our modeling suggests that second-order selectivity arises both from elongated excitatory CRFs, asymmetrically organized extraclassical surround suppression, or both. We validated the model by successfully testing its predictions against conventional surround suppression measurements and spike-triggered analysis of second-order form responses. Psychophysical adaptation measurements on human observers revealed a pattern of second-order form selectivity consistent with neural response patterns. We therefore propose that cortical cells in primates do double duty, providing signals about both first- and second-order forms.

1. Introduction

The classical receptive fields (CRFs) of neurons in monkey visual cortex (areas V1 and V2) are selectively sensitive to the orientation and spatial frequency of a sinusoidal grating (De Valois, William Yund, & Hepler, 1982; Levitt, Kiper, & Movshon, 1994). Neuronal responses are also often modulated by the visual context in which they appear. A simple example is surround suppression: if a grating presented to the CRF extends into the surrounding extraclassical receptive field, the response is reduced (Cavanaugh, Bair, & Movshon, 2002a, 2002b; Henry et al., 2013; Kim & Freeman, 2014; Sceniak et al., 1999; Shushruth et al., 2013). Contextual responses are found in many sensory cortical areas, and are likely to represent a fundamental computation for a range of perceptual and motor behaviors (Carandini & Heeger, 2013). Here, we examine the temporal and spatial properties of the neural mechanisms implementing these contextual responses in primate cortex, with a particular focus on whether contextual mechanisms can confer sensitivity to "second-order" visual features.

Human observers are sensitive to first-order features defined by changes in luminance, for example, a border between light and dark. But we are also sensitive to features defined by differences between first-order cues, for example, a "herringbone" border between perpendicular textures, or a border between textures of the same orientation but differing spatial frequency content (reviewed by Graham, 2011; Graham & Sutter, 1998; Landy & Graham, 2004). This second-order sensitivity plays a fundamental role in vision, because spatial and temporal information can be conveyed by many image properties – among them luminance, color, contrast, disparity, and texture – which in isolation or in combination (Saarela & Landy, 2012) affect an observer's ability to locate and identify objects. This ability can be explained by a "filter-rectify-filter" (FRF) model (Ellemberg, Allen, & Hess, 2006; Graham & Sutter, 1998; Graham & Wolfson, 2004; Landy &

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Bergen, 1991; Landy & Oruç, 2002; Langley, Fleet, & Hibbard, 1996; McGraw, Levi, & Whitaker, 1999; Schofield & Georgeson, 1999). This model postulates two cascaded stages. The first is a linear spatiotemporal filter which gives an orientation- and spatial frequency-selective response to luminance. The rectified output of this filter is passed to a second linear filter which responds selectively to variations in the outputs of the first-order filters and represents this variation across regions of an image.

How could contextual mechanisms confer sensitivity to second-order features? Contextual responses represent a complex sensory transformation which modifies the basic orientation and spatial frequency selectivity of neurons. These contextual modulations may play an important role in the perception of complex spatial forms. In particular, when a neuron's RF is organized asymmetrically (Cavanaugh, Bair, & Movshon, 2002a, 2002b; Tanaka & Ohzawa, 2009; Walker, Ohzawa, & Freeman, 1999) its responses can signal the form of second-order visual features. We wondered to what extent the RF was organized anisotropically in macaque V1 and V2 neurons, and whether the FRF model might account for the activity of single units, so we used the method of Tanaka and Ohzawa (2009) to probe the receptive fields of neurons in macaque V1 and V2. Our results suggest that as in cat (Tanaka & Ohzawa, 2009), contextual modulation may account for some forms of second-order sensitivity in primate cortex.

2. Methods

2.1. Subjects and surgical preparation

We recorded from 10 macaques (*Macaca nemestrina* and *Macaca fascicularis*; 1 female and 9 males). Animals were prepared for recording as described previously (Cavanaugh, Bair, & Movshon, 2002a). Experiments typically lasted 5 days, during which anesthesia and paralysis were maintained with continuous intravenous infusion of sufentanil citrate (initially 6 μg/kg/h, adjusted thereafter to maintain a suitable level of anesthesia for each animal) and vecuronium bromide (Norcuron; 0.1 mg/kg/h) in isotonic dextrose-Normosol solution. Vital signs were constantly monitored (electroencephalograph, blood pressure, heart rate, lung pressure, end-tidal pCO_2, temperature, and urine flow and osmolarity) and actively maintained within appropriate physiological limits. Pupils were dilated with topical atropine and the eyes were protected with oxygen-permeable contact lenses. Supplementary lenses chosen via direct ophthalmoscopy were used to make the retinas conjugate with the experimental display. All animal care and experimental procedures were performed in accordance with protocols approved by the New York University Animal Welfare Committee and conformed to the National Institute of Health *Guide for the Care and Use of Laboratory Animals.*

2.2. Unit recording

We made extracellular recordings with quartz-coated, platinum–tungsten microelectrodes (Thomas Recording) advanced mechanically through a craniotomy and durotomy centered 2–4 mm posterior to the lunate sulcus and 10–16 mm lateral to the midline. Electrode penetrations were confined to a parasagittal plane and directed downward at an angle of 20 deg from vertical. We identified area V2 by (1) marking gray matter as we traversed surface cortex, followed by a stretch of white matter before reaching V2 on the posterior bank of the lunate sulcus; (2) tracking changes in visual topography along the recording track: receptive fields in surface V1 were located close to the vertical meridian; V2 receptive fields were at 2–5° of visual eccentricity; (3) marking cortical depth along the recording track: at our typical sites, V2 was found 2500–3500 μm from brain surface. Signals from the microelectrodes were amplified, bandpass-filtered (300 Hz to 10 kHz), and fed into a dual window time–amplitude discriminator for spike detection. Spike times were saved with a temporal resolution of 0.1 ms.

2.3. Visual stimulation

We presented stimuli on a gamma-corrected cathode ray tube (CRT) monitor (Eizo T966), with spatial resolution 1280 × 960 pixels, temporal resolution 120 Hz, and mean luminance 35 cd/m^2. Viewing distance was usually 1.14 m. Stimuli were generated using an Apple Macintosh running Expo (http://corevision.cns.nyu.edu).

For each neuron, we hand-mapped the receptive field of each eye on a tangent screen. After qualitatively determining ocular dominance, we presented stimuli monocularly to the dominant eye, occluding its fellow. We first determined selectivity for direction, spatial frequency, and temporal frequency of a small, circular patch of high-contrast sinusoidal grating presented to the putative classical receptive field (CRF). Using these parameters, we measured responses to second-order stimuli.

We created second-order stimuli by multiplying a sinusoidal "carrier" grating by a raised, sinusoidal "modulator" grating (Fig. 1). The "preferred" carrier grating took the spatial frequency and drift direction determined found to be optimal during initial mapping. We usually set the temporal frequency of the carrier to

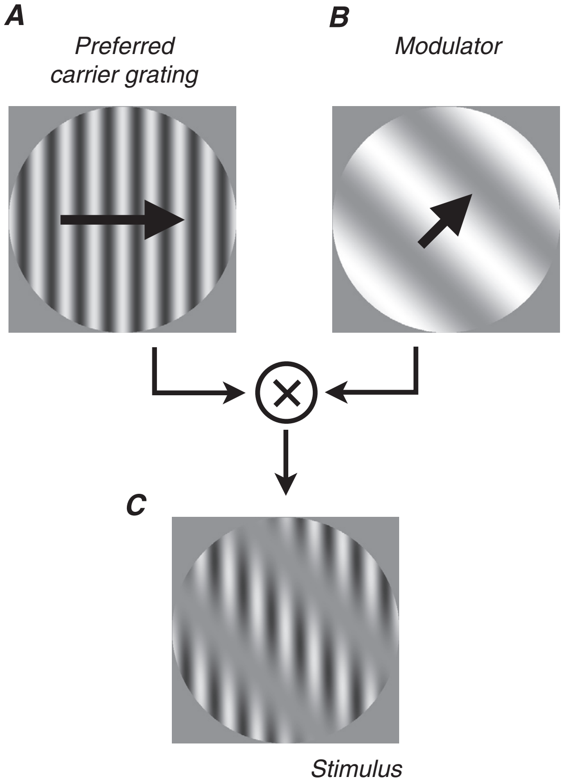

Fig. 1. Stimulus construction. We modulated the contrast of a large, circular patch of sinusoidal carrier grating (A) using a relatively low spatial frequency, raised sinusoidal modulator (B) forming the second-order stimulus (C). We optimized the carrier grating's orientation and spatial frequency for each neuron, and typically set its drift rate to approximately 5 Hz. The modulator always drifted at 0.75 Hz. The contrasts of the carrier grating and the modulator were 75% and 100%, respectively. In each experiment, from trial to trial, we varied the modulator's drift direction (0, 45, 90, ... 315 deg relative to the carrier grating's drift direction) and the modulator's spatial frequency (0, 0.125, 0.25, ... 0.75× the carrier grating's spatial frequency). Shown here the modulator drifts at 45 deg relative to the carrier with spatial frequency 0.25×.