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# Separate first- and second-order processing is supported by spatial summation estimates at the fovea and eccentrically

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### Abstract

We estimated spatial summation areas for the detection of luminance-modulated (LM) and contrast-modulated (CM) blobs at the fovea, 2.5, 5 and 10 deg eccentrically. Gaussian profiles were added or multiplied to binary white noise to create LM and CM blob stimuli and these were used to psychophysically estimate detection thresholds and spatial summation areas. The results reveal significantly larger summation areas for detecting CM than LM blobs across eccentricity. These differences are comparable to receptive field size estimates made in V1 and V2. They support the notion that separate spatial processing occurs for the detection of LM and CM stimuli. © 2006 Elsevier Ltd. All rights reserved.

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## 1. Introduction

The visual system is adept at detecting objects irrespective of the type of feature defining them. If the visual system is considered as a linear system, the basic visual process to extract luminance cues can be explained based on linear summation of responses from the excitatory and inhibitory receptive field regions associated with neurons in the visual cortex (e.g., Ferster, 1988; Hirsch, Alonso, Reid, & Martinez, 1998; Hubel & Wiesel, 1962). To study how non-luminance defined cues are extracted from visual targets, psychophysical and physiological investigations initially used motion-defined targets (see Baker, 1999; Baker & Mareschal, 2001 for reviews of these studies). In general, the results of these studies indicate that dedicated nonlinear processing does take place in the visual system to decode specific nonlinear cues, so that separate linear and nonlinear processing streams have been proposed to exist, as opposed to a single stream. Evidence for dedicated nonlinear streams comes from psychophysical studies (Solomon & Sperling, 1994, 1995; Wilson, Ferrera, & Yo, 1992), as well as from neurophysiological studies in cat (Mareschal & Baker, 1998a, 1998b; Zhou et al., 1993). Studies of cortical activity for illusory contours in cat by optical imaging (Sheth, Sharma, Rao, & Sur, 1996), and in humans by PET (Ffytche & Zeki, 1996) and fMRI (Hirsch et al., 1995), also support the possibility of a separate non-linear processing stream in vision.

As yet however, despite a growing body of literature especially in the areas of target detection (e.g., Schofield & Georgeson, 1999), target localization (e.g., McGraw, Levi, & Whitaker, 1999; Volz & Zanker, 1996; Whitaker, McGraw, & Levi, 1997) and spatial lateral interactions (Ellemberg, Allen, & Hess, 2004), the notion that separate processing streams exist for spatial vision in order to process spatial information from targets defined by first-order (i.e., luminance) and second-order (i.e., non-luminance) characteristics remains less well-defined and forms one of the basic questions to be answered both in the psychophysical and physiological domains.

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Spatial summation is a property inherent in linear models of spatial vision, which are based on the assumption that a spatially weighted function of the linear filters represents the receptive field of cortical simple cells. The outputs of these filters are assumed to be independent and produce a field of local signals that can be integrated at a later stage of signal processing (Adelson & Bergen, 1985; Watt & Morgan, 1985; Wilson, 1991). In classical work on spatial summation of luminance-defined stimuli using circular discs on a uniform background (Barlow, 1958; Graham & Margaria, 1935), detection thresholds improve proportionally with an increase in stimulus area (known as Ricco's Law), which is attributed to the physiological summation within the receptive field centre, or filter (e.g., Barlow, 1958; Glezer, 1965; Howell & Hess, 1978; Robson & Graham, 1981). Apart from this region of full summation, a second region of partial summation where the sensitivity is dependent on the output of the number of spatial filters involved and increases as a probability function, i.e., probability summation, is often described for these classical targets and also for grating-type targets (e.g., Bonneh & Sagi, 1998; Cannon, 1995; Howell & Hess, 1978; Legge & Foley, 1980; Mayer & Tyler, 1986; Meese, 2004; Meese & Williams, 2000; Robson & Graham, 1981; Tyler & Chen, 2000) after which further increases in stimulus area leads to lesser or no improvement in the detection threshold.

Later work, which has led to significant advances in characterising our visual system as far as luminance processing is concerned, has quantified spatial summation properties using luminance gratings at the fovea (Cannon, 1995; Howell & Hess, 1978; Legge & Foley, 1980; Robson & Graham, 1981) and in the periphery (Pointer & Hess, 1989; Robson & Graham, 1981).

Spatial summation properties for second-order (or nonluminance defined) targets however, have been described only at the fovea in normal subjects (Landy & Oruc, 2002; Schofield & Georgeson, 1999) and more recently also for amblyopes (Wong & Levi, 2005). Schofield and Georgeson (1999) were the first to characterise modulation sensitivity functions for the encoding of static luminancemodulated and contrast-modulated Gabor blobs at the fovea. They qualitatively described spatial summation characteristics for static luminance-modulated and contrast-modulated noise stimuli and found that the summation functions were not sufficiently different to support the existence of differently sized underlying mechanisms. Landy and Oruc (2002) assessed spatial summation trends for texture-defined stimuli with different modulator spatial frequencies. They found that detection thresholds for these stimuli decreased with increasing size in a manner qualitatively similar to those mentioned above for luminance-defined stimuli, and that full summation appeared to occur at a similar size, regardless of the modulator spatial frequency used. Finally, Wong and Levi (2005) examined second-order spatial summation properties in normal and amblyopic subjects using static LM and CM Gabor stimuli. By increasing the size of the Gaussian enveloped targets,

they showed a similar rate of threshold improvement with increasing size for both LM and CM stimuli in normal, as well as in amblyopic subjects. However, due to the range of sizes testable in their study, a comparison of full summation size could not be quantified nor directly compared between the two types of stimuli used. Such a comparison, which is the focus of the current study, is of importance not only for characterising the spatial properties of the underlying mechanisms subserving second-order spatial vision and how they might be similar or different to those subserving luminance-defined or first-order spatial vision, but also in more clearly understanding related and subsequent spatial processing, such as spatial localization, lateral spatial interactions, contour formation and so on.

Estimations of visual thresholds using first-order, or luminance-defined targets across the visual field and comparisons of rates of change across eccentricity have also led to significant advances in our understanding of the physical and physiological limitations of visual processing (e.g., Levi, Klein, & Aitsebaomo, 1985; Virsu & Rovamo, 1979; Westhemier, 1979; Wilson, 1991; Yap, Levi, & Klein, 1987). To date, it is not known how spatial summation areas or spatial tuning properties of the visual system for second-order spatial targets change with increasing retinal eccentricity.

This study is concerned with quantifying and comparing spatial summation areas for the detection of LM and CM targets at the fovea and eccentrically. Spatial summation areas are quantified at the fovea and at eccentricities of 2.5, 5 and 10 deg in the inferior visual field. The results add support to the notion that not only do separate mechanisms exist to detect first-order and second-order spatial targets (Schofield & Georgeson, 1999), but that those used to detect contrast-defined targets are bigger at all eccentricities than those used to detect luminance-defined targets. The rate of threshold falloff with increasing eccentricity appears similar for LM and CM stimuli, once the carrier luminance noise energy is approximately scaled for eccentricity. Thus second-order mechanisms are bigger and their detection thresholds appear to be dependent on incoming energy from higher spatial frequency LM mechanisms.

# 2. Methods

#### 2.1. Apparatus

The stimuli were generated using a custom written C program on a Pentium II PC. The stimuli were loaded on to the frame-store memory of a Cambridge Research System VSG 2/3 graphics card housed in the computer, which allowed up to 12 bit luminance control. The stimuli were displayed on a Hitachi 4821 RGB monitor running at 150 Hz. The display area of the screen was reduced to 21 cm  $\times$  21 cm using a grey cardboard surround of approximately similar mean luminance to the screen.

#### 2.2. Calibration

A major concern for researchers working with stimuli defined by nonluminance characteristics is to ensure that luminance cues are in fact, not Download English Version:

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