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Exogenous attention enhances 2nd-order contrast sensitivity

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ABSTRACT

Natural scenes contain a rich variety of contours that the visual system extracts to segregate the retinal image into perceptually coherent regions. Covert spatial attention helps extract contours by enhancing contrast sensitivity for 1st-order, luminance-defined patterns at attended locations, while reducing sensitivity at unattended locations, relative to neutral attention allocation. However, humans are also sensitive to 2nd-order patterns such as spatial variations of texture, which are predominant in natural scenes and cannot be detected by linear mechanisms. We assess whether and how exogenous attention—the involuntary and transient capture of spatial attention—affects the contrast sensitivity of channels sensitive to 2nd-order, texture-defined patterns. Using 2nd-order, texture-defined stimuli, we demonstrate that exogenous attention increases 2nd-order contrast sensitivity at the attended location, while decreasing it at unattended locations, relative to a neutral condition. By manipulating both 1st- and 2nd-order spatial frequency, we find that the effects of attention depend both on 2nd-order spatial frequency of the stimulus and the observer's 2nd-order spatial resolution at the target location. At parafoveal locations, attention enhances 2nd-order contrast sensitivity to high, but not to low 2nd-order spatial frequencies; at peripheral locations attention also enhances sensitivity to low 2nd-order spatial frequencies. Control experiments rule out the possibility that these effects might be due to an increase in contrast sensitivity at the 1st-order stage of visual processing. Thus, exogenous attention affects 2nd-order contrast sensitivity at both attended and unattended locations.

1. Introduction

To efficiently guide perception and behavior, the visual system must extract contours and parse the retinal image into perceptually coherent regions. Consider the natural scene presented in Fig. 1A. Many regions in this picture are bounded by luminance-defined contours such as the borders of the two people on the walkway. Much of the early visual system from the retina to primary visual cortex is dedicated to detecting such changes in luminance (DeValois & DeValois, 1988). Linear spatial filters that are selective for spatial frequency and orientation, akin to simple cells in V1, are effective for signaling such contours (Graham, 1989). However, humans are also sensitive to changes in visual attributes other than luminance, which cannot be detected by linear mechanisms. For example, the different sections of the walkway differ in the local orientation of the wooden slats (that is, by textural attributes), but the average luminance is relatively constant across the different sections. As a result, large-scale linear filters tuned to luminance variations are ineffective for segregating the walkway into different sections. Patterns defined by changes in textural attributes (e.g., local orientation, contrast, and spatial frequency) that are not visible to linear filters are commonly referred to as 2nd-order patterns, to distinguish them from 1st-order, luminance-defined patterns. Texture information is vital for segmenting the retinal image into distinct regions as an initial step in object recognition. Successfully segmenting an image, however, is a computationally expensive process.

The high metabolic cost of neuronal activity involved in cortical computation renders it impossible to process the overwhelming amount of information arriving at our retinae (Lennie, 2003). Covert spatial attention enables us to manage limited resources by selecting a relevant location or aspect of the visual scene and prioritizing its processing even without directing the eyes to that location (Posner, 1980). Attention affects 1st-order processing, improving behavioral performance in various tasks (see Carrasco, 2006, for a review) and enhancing neural processing of sensory information (see Reynolds & Chelazzi, 2004, for a review). Some of these changes are mediated by an increase in contrast sensitivity of 1st-order linear spatial filters at the attended location and a decrease at unattended locations (Pestilli & Carrasco, 2005; Pestilli, Viera, & Carrasco, 2007). However, little is known about the effects of attention on the processing of 2nd-order texture patterns. Texture perception is usually considered to be pre-attentive (Braun & Sagi, 1990; Julesz, 1981; Schubö & Meinecke, 2007). However,

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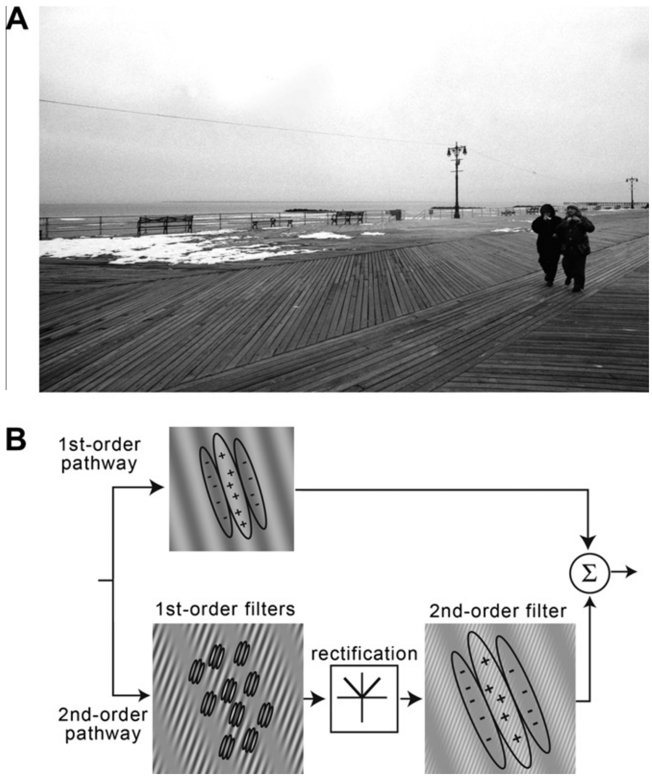

Fig. 1. (A) Natural scene containing 1st- and 2nd-order contours. The boundary between the two pedestrians and walkway in the lower right is defined by a change in luminance, hence it is 1st-order. The texture-defined boundaries between the different regions of the walkway are 2nd-order. (B) A typical model of visual processing with parallel pathways for 1st- and 2nd-order stimuli. In the top path, luminance-defined stimuli are signaled by a linear filter. The bottom path is a filter-rectify-filter cascade sensitive to 2nd-order stimuli. Both 1st- and 2nd-order information are combined in a later decision stage (Baker & Mareschal, 2001).

many studies have shown an effect of attention on performance with texture stimuli (Casco, Grieco, Campana, Corvino, & Caputo, 2005; Talgar & Carrasco, 2002; Yeshurun & Carrasco, 1998, 2000, 2008; Yeshurun, Montagna, & Carrasco, 2008).

In this study, we investigate whether and how exogenous attention—the involuntary and transient capture of attention to a location by a peripheral uninformative visual cue—affects contrast sensitivity for 2nd-order patterns at both attended and unattended locations.

1.1. Visual perception of 2nd-order texture patterns

Texture patterns—homogenous regions of repeated structures that cannot be detected by linear mechanisms—are predominant in natural scenes (Johnson & Baker, 2004; Schofield, 2000). Detecting a boundary between two texture regions is analogous to detecting a 1st-order, luminance-defined edge (Nothdurft, 1985). Unlike locating a change in luminance (i.e., a typical light/dark edge), finding a 2nd-order texture boundary requires locating changes in local textural properties (e.g., contrast, orientation, or scale) of an underlying fine-scale pattern, which is often referred to as the 1st-order carrier. Because the average luminance may be the same on either side of the texture boundary, 2nd-order edges cannot be detected by a linear mechanism such as those used to detect 1st-order, luminance-defined edges.

Several lines of evidence suggest that 1st- and 2nd-order pattern processing require different neural mechanisms (Ellemberg, Allen, & Hess, 2004; Larsson, Landy, & Heeger, 2006; Morgan, Mason, & Baldassi, 2000; Schofield & Georgeson, 1999; Scott-Samuel & Georgeson, 1999). Like their 1st-order counterparts, 2nd-order channels are tuned for orientation (Arsenault, Wilkinson, & Kingdom, 1999; Dakin, Williams, & Hess, 1999; Graham & Wolfson, 2001) and spatial frequency (Landy & Oruç, 2002; Scott-Samuel & Georgeson, 1999), but have wider bandwidths (Landy & Oruç, 2002). Although the contrast sensitivity function (CSF) for 1st-order patterns is bandpass, peaking for mid-range spatial frequencies (Robson & Graham, 1981), the 2nd-order CSF has been shown to be essentially flat (Landy & Oruç, 2002).

A number of investigators have described edge-based texture segregation models to account for texture segregation performance (Bergen & Adelson, 1988; Graham, 1991; Graham, Beck, & Sutter, 1992; Landy & Bergen, 1991; Malik & Perona, 1990; Sutter, Beck, & Graham, 1989; see Landy & Graham, 2004, for a review). A typical model of 2nd-order visual processing (Fig. 1B) comprises two layers of bandpass spatial linear filters separated by a point-wise nonlinearity. The first spatial filter is tuned for orientation and spatial frequency, thus responding strongly to one of the carrier patterns. The output of this first stage is rectified so that spatial regions with large response variability (i.e., regions with large 1st-order linear filter response, both positive and negative) are mapped to large average response (Bergen & Adelson, 1988). Finally, a second set of larger-scale linear filters performs a more global analysis of the rectified outputs of the 1st-order filters. Appropriately tuned 2nd-order filters will respond robustly to boundaries between regions with different average response strength. Such models of 2nd-order processing are referred to as filter-rectify-filter (FRF), linear–nonlinear–linear (LNL), or "back-pocket" models (Landy & Graham, 2004).

Although originally developed to explain psychophysical data, these models provide an architecture that maps well onto the cortical visual processing cascade. The physiological substrate for the first stage linear filters is likely to correspond to simple cells in area V1 that are selective for spatial frequency and orientation (Graham, 1989). The intermediate point-wise nonlinearity (i.e., rectification) might correspond to the neuronal spiking threshold of 1st-order neurons. Finally, 2nd-order, texture-selective neurons that represent the second stage of filtering are likely to be located in higher extrastriate areas beyond V1 (Baker & Mareschal, 2001; Landy & Graham, 2004). fMRI studies have shown that responses to 2nd-order texture boundaries (Kastner, De Weerd, & Ungerleider, 2000) and 2nd-order orientation-selective adaptation effects (Larsson et al., 2006) are stronger in downstream visual areas, providing support for the notion that 2nd-order processing takes place subsequent to 1st-order filtering.

1.2. Effects of covert attention at the 1st-order stage of visual processing

Spatial attention can be allocated overtly, by directing one's gaze towards a position within the visual scene, or covertly, by attending to an area in the periphery without actually directing gaze towards it, allowing one to selectively process information at a given location in the absence of eye movements (Posner, 1980). Covert spatial attention can be further divided into two types: endogenous and exogenous, which follow different time courses and are triggered by different cues. Endogenous attention is voluntary, conceptually driven, and has a sustained effect, which takes about 300 ms to be deployed and can last several seconds. In contrast, exogenous attention is involuntary, driven by a briefly displayed peripheral cue, and has a transient effect that peaks at about 100 ms and decays shortly thereafter (Cheal & Lyon, 1991; Jonides & Irwin, 1981; Ling & Carrasco, 2006a; Liu, Stevens, & Carrasco, 2007; Muller & Findlay, 1988; Muller & Rabbitt, 1989; Nakayama & Mackeben, 1989; Posner, 1980; Remington, Johnston, & Yantis, 1992). The involuntary transient shift of exogenous