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Sustained and transient covert attention enhance the signal via different contrast response functions

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Abstract

We investigated the mechanisms underlying the effects of sustained and transient covert attention on contrast sensitivity. The aim of this study was twofold: (1) Using a zero-noise display, we assessed whether sustained (endogenous) attention enhances contrast sensitivity via signal enhancement, and compared the magnitude of the effect with that of transient (exogenous) attention. (2) We compared the contrast psychometric functions for both sustained and transient attention and evaluated them in terms of contrast gain and response gain models. Observers performed a 2AFC orientation discrimination task on a tilted target Gabor, presented alone at 1 of 8 iso-eccentric locations. Either a neutral (baseline), peripheral (to manipulate transient attention), or a central cue (to manipulate sustained attention) preceded the target. Even in the absence of external noise, and using suprathreshold stimuli, observers showed an attentional effect, evidence in support of signal enhancement underlying both sustained and transient attention. Moreover, sustained attention caused a strictly leftward threshold shift in the psychometric function, supporting a contrast gain model. Interestingly, with transient attention we observed a change in asymptote in addition to a threshold shift. These findings suggest that whereas sustained attention operates strictly via contrast gain, transient attention may be better described by a mixture of response gain and contrast gain.

Keywords: Covert attention; Contrast sensitivity; Contrast gain; Response gain; Signal enhancement

1. Introduction

Covert attention allows us to monitor our periphery in the absence of eye movements (Posner, 1980). A growing body of behavioral evidence demonstrates that there are two components of covert attention: 'sustained' and 'transient' (Cheal & Lyon, 1991; Corbetta & Shulman, 2002; Nakayama & Mackeben, 1989). Sustained, or endogenous, attention corresponds to what we usually think of as attention: at will, we monitor information at a given location. Transient, or exogenous, attention corresponds to a faster, involuntary capture of attention to a location where sudden, salient stimulation has occurred. Previous studies have shown that we can engage these systems differentially by using different cues: a central or symbolic cue is presented in the center of the visual field to direct sustained, or endogenous attention in a conceptually driven fashion in ~300 ms, whereas a peripheral cue flashed briefly in a location adjacent to the relevant location captures transient, or exogenous attention in a stimulus-driven, automatic manner in ~100 ms (Nakayama & Mackeben, 1989). Whereas the shifts of attention by sustained cues appear to be under conscious control, it is hard or impossible for observers to ignore transient cues, even when they are known to be irrelevant (Carrasco, Ling, & Read, 2004; Giordano, McElree, & Carrasco, 2003; Muller & Rabbit, 1989; Pestilli & Carrasco, 2005).

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There is no consensus as to whether common neurophysiological substrates underlie sustained and transient attention. Some have suggested that whereas sustained attention is cortical in nature, transient attention also activates subcortical processing (Robinson & Kertzman, 1995; Zackon, Casson, Zafar, Stelmach, & Racette, 1999). However, whereas some suggest that the preparatory control signals of sustained and transient attention are mediated by partially segregated networks (Corbetta & Shulman, 2002; Kanwisher & Wojciulik, 2000; Kastner & Ungerleider, 2000), others have found no difference in the brain networks mediating these systems (Peelen, Heslenfeld, & Theeuwes, 2004).

The goal of this study is to compare sustained and transient covert attention psychophysically. Specifically, we tested whether a signal enhancement mechanism underlies both types of attention. Moreover, we investigated the neural model underlying signal enhancement by measuring the psychometric functions for both sustained and transient attention, to assess whether they have similar or different effects on the contrast response function.

1.1. Mechanisms of attention: signal enhancement and external noise reduction

How does covert attention exert its effects? Psychophysically, the impact of covert attention on visual performance is well documented across a range of perceptual tasks, such as visual search (Carrasco & McElree, 2001; Carrasco & Yeshurun, 1998; Nakayama & Mackeben, 1989) and letter identification (Prinzmetal, Presti, & Posner, 1986; Talgar, Pelli, & Carrasco, 2004), and improves performance in visual domains such as contrast sensitivity (Carrasco, Penpeci-Talgar, & Eckstein, 2000; Cameron, Tai, & Carrasco, 2002; Lu & Dosher, 1998, 2000; Dosher & Lu, 2000a, 2000b; Huang & Dobkins, 2005; Smith, Wolfgang, & Sinclair, 2004; Solomon, 2004) and spatial resolution (Carrasco, Williams, & Yeshurun, 2002; Golla, Ignashchenkova, Haarmeier, & Their, 2004; Yeshurun & Carrasco, 1998, 1999). It has also been established that transient attention alters the appearance of contrast (Carrasco et al., 2004) and spatial frequency (Gobell & Carrasco, 2005).

Although it is well established that covert attention improves performance in early visual tasks, the underlying mechanisms responsible for these effects are not well understood. Explanations of how attention improves performance range from claims that the deployment of attention affects processing at the decisional level (Kinchla, Chen, & Evert, 1995; Palmer, 1994; Shiu & Pashler, 1994; Sperling & Dosher, 1986) to claims that attention actually enhances perceptual sensitivity. At the perceptual level, two prominent models have been proposed: signal and external noise reduction. According to signal enhancement, attention strengthens and improves the representation of the signal within the locus of attention enhancement (Cameron et al., 2002; Carrasco et al., 2000, 2002; Lu & Dosher, 1998, 2000; Luck, Hillyard, Mouloua, & Hawkins, 1996; Smith et al., 2004). According to external noise reduction, attention affects performance in a given area by actively suppressing the strength of representation of areas outside the locus of attention (Baldassi & Burr, 2000; Dosher & Lu, 2000a, 2000b; Lu & Dosher, 1998, 2000; Lu, Lesmes, & Dosher, 2002; Morgan, Ward, & Castet, 1998; Shiu & Pashler, 1994).

Psychophysically, *transient* attention has been shown to increase contrast sensitivity for detection and discrimination tasks, even under low- or zero-noise conditions—results which can only be explained by signal enhancement (Cameron et al., 2002; Carrasco et al., 2000). This finding has been corroborated using the external noise plus attention paradigm; transient attention operates via signal enhancement under low-noise conditions, and via noise reduction under high-noise conditions (Lu & Dosher, 1998, 2000). With regard to *sustained* attention, these authors have stated that it works primarily via an external noise reduction mechanism. Indeed, effects of sustained attention only arise in high-noise conditions, and not under low-noise conditions (Dosher & Lu, 2000a, 2000b; Lu, Liu, & Dosher, 2000; Lu et al., 2002).

The first goal of the present study was to systematically assess whether sustained and transient attention can enhance contrast sensitivity in the absence of added external noise (i.e., masks, distracters), and compare their effects. An attentional benefit with sustained attention in the absence of noise would be direct empirical evidence for signal enhancement.

1.2. Contrast response functions: contrast gain and response gain

What neural mechanism underlies signal enhancement? Neuronal firing rate increases as a function of stimulus contrast, resulting in a contrast response function. There are two predictions as to how attentional modulation may affect the contrast response function: contrast gain and response gain (Fig. 1; Sclar, Lennie, & DePriest, 1989). *Contrast gain*: if the neurons responding to the contrast of a stimulus combined with attentional modulation when processing the signal, the effect on the contrast response function could lead to an increase in sensitivity, with no change in relative firing rate. This would render the response no different from an actual change in the physical contrast of the stimulus. The signature of contrast gain is a leftward shift in threshold ($C50$; see equations in Fig. 1) of the contrast response function. *Response gain*: if attention and the contrast response were modulated independently, attention would have a multiplicative effect over the