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Research Report

Interactions between attention and perceptual grouping in human visual cortex

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ABSTRACT

Freeman et al. (Freeman, E., Sagi, D., Driver, J., 2001. Lateral interactions between targets and flankers in low-level vision depend on attention to the flankers. Nat. Neurosci. 4, 1032-1036) demonstrated that detection sensitivity for a low contrast Gabor stimulus improved in the presence of flanking, collinearly oriented grating stimuli, but only when observers attended to them. By recording visual event-related potentials (ERPs) elicited by a Gabor stimulus, we investigated whether this contextual cueing effect involves changes in the short-latency afferent visual signal from V1 that have a stimulus onset latency between 60 and 80 ms and/or longer-latency changes from visual cortex. Under dual-task conditions, the subjects performed contrast discrimination for a central Gabor and an orientation judgment for a pre-specified subset of the flanking Gabors. On random trials, the central Gabor could be collinearly or orthogonally oriented with respect to the attended flankers. Subjects showed improvements in discriminating the contrast of the central grating when it was oriented collinearly with the attended flankers. The ERP difference between attending to collinear versus orthogonal flankers manifested as a positive polarity response at occipital electrodes with a latency of 180–250 ms after stimulus onset. No shorter-latency contextual cueing differences were observed in the ERPs. The ERP latency profile of the contextual cueing effect argues against the hypothesis that short-latency afferent activity from V1 is the stage of processing at which attention can influence neuronal lateral interactions. However, the scalp voltage distribution of the longer-latency contextual cueing effect is similar to the one generated by the early phasic stimulus onset activity from V1. These findings leave open the possibility that V1 is involved in the attentional modulation of lateral interactions but that this has a longer time course, likely being mediated by re-afferent inputs from later stages of the visual pathway.

1. Introduction

The role of visual attention during visual processing has been investigated using a variety of psychophysical and physiological methods (reviewed by Hopfinger et al., 2005). In particular, there has been increasing interest in the question of whether attention can interact with perceptual grouping processes (Baylis and Driver, 1992; Moore and Egeth, 1997). Recent data from monkey physiology (Ito and Gilbert, 1999; Gilbert et al., 2000) and from human psychophysics (Freeman et al., 2001)

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suggest that attention may influence facilitatory lateral interactions between neighboring collinearly configured stimuli. Such lateral interactions are thought to reflect the functioning of fundamental contour grouping processes in primary visual cortex (Gilbert et al., 2000; Polat et al., 1998).

The psychophysical paradigm of Freeman et al. (2001) (see also Freeman et al., 2003) investigated the effects of attention on lateral interactions, a phenomenon thought to reflect the integrative architecture of horizontal connections in V1. In the original lateral interactions paradigm, developed by Polat and Sagi (1993, 1994), contrast detection of a target improves in the context of a single pair of collinear high-contrast flankers. Modifying this paradigm for the purpose of measuring attentional modulation effects, Freeman et al. (2001) presented stimuli comprising of two pairs of flanker patches arranged on two intersecting axes around a central patch (see Fig. 1). This central patch could be oriented so that it was either collinear with the left-oblique flanking axis (Figs. 1a, b), or with the right-oblique axis (Figs. 1c, d). Attention was manipulated to left- or right-oblique flankers pairs (illustrated by the ellipses in Fig. 1), yielding two attentional conditions in which the central patch was either collinear or orthogonal to the attended flankers (Figs. 1a and c versus Figs. 1b and d, respectively). Freeman et al. (2001) found that contrast sensitivity for an identical central target (in an identical stimulus context) improved when it was collinear with the attended flankers (i.e., compare Fig. 1a with b, and c with d).

This finding was taken to imply that attention can influence lateral interactions depending on their behavioral relevance. However, in order to infer that attention can modulate the neural mechanisms of lateral interactions in early visual cortex, a physiological correlate of this behavioral effect still needs to be demonstrated convincingly in humans. In the present study, we recorded event-related potentials (ERPs) in a replication of the original behavioral paradigm. To date, ERP studies have found little evidence for attention influencing sensory processing in V1 (Di Russo et al., 2003; Martinez et al., 1999), despite data from animal physiology (e.g., McAdams and Maunsell, 1999; Motter, 1993) and human functional imaging (e.g., Gandhi et al., 1999; Martinez et al., 1999; Somers et al., 1999; Watanabe et al., 1998). However, the ERP studies did not investigate the role of attention under specific conditions such as those promoting lateral interactions phenomena that might predict a locus of activity in V1 (although see Wu et al., 2005). As the groundwork for the present study, we (Khoe et al., 2004) recently confirmed that a stimulus-driven electrophysiological correlate of collinear versus orthogonal lateral interactions could be found in humans, having a scalp topology consistent with a V1 source and an early onset (80–120 ms). The present study used a similar experimental method, but now with a modified version of Freeman et al.'s (2001) attentional paradigm, which allowed us to test whether the correlates of lateral interactions could be modulated by selective attention to the flankers.

In contrast to hemodynamic measures of attention in early vision (e.g., Gandhi et al., 1999; Martinez et al., 1999; Somers et al., 1999), only electrophysiological methods currently offer the temporal precision necessary to specify the precise latency at which attention affects visual processing. Such latency information may provide important clues for understanding the mechanism by which attention may be involved in early perceptual grouping processes. For example, if contextual cueing can modulate lateral interactions during the early feedforward stage of stimulus processing, then we might find attentional modulation of the early waveforms that we found in our previous study (Khoe et al., 2004). However, if selective attention to the flankers modulates lateral interactions in V1 or other early visual areas via re-afferent projections, then a difference in the ERP waveforms might be observed only at relatively longer latencies (e.g., later than 120 ms).

Some modifications to Freeman et al.'s (2001) original stimulus set and paradigm were required to render it suitable for recording ERPs (see Fig. 2). Instead of performing two simultaneous two-interval forced-choice tasks, we used two randomly interleaved Go/No-Go tasks in single-interval trials. In some trials, a central pedestal patch was presented selected randomly from one of two orientations (Figs. 2a and b). The subjects' primary task was then to detect the presence of a higher contrast central target superimposed on this lower contrast pedestal (i.e., a small contrast increment), pressing one key whenever the target increment was present (see Fig. 3 for an illustration of the correct responses associated with each display). In the secondary task, flanker displays were presented without any central patch (e.g., Figs. 2c–e), and subjects hit a separate key whenever they detected a rotation in the *attended* flanker pair (Figs. 2c and d; see also Fig. 3). Because central target detection trials and flanker-only rotation trials were presented randomly, optimum performance of both tasks required subjects to simultaneously attend to the task-relevant flankers and the central target pedestal.

A further modification of the paradigm was to present the stimuli in the perifovea (see Khoe et al., 2004 and illustrations in Fig. 3). Presenting target stimuli at fixation (as in the original lateral interactions paradigm) may lead to equal stimulation

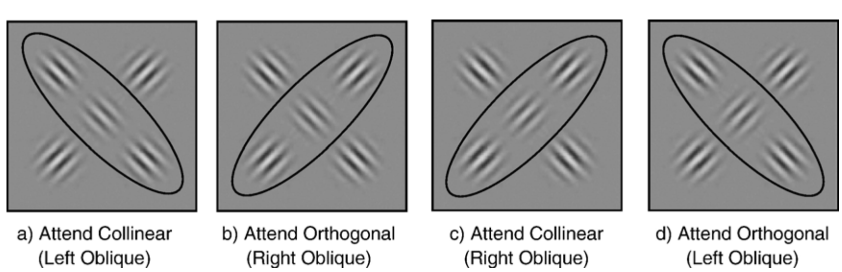

Fig. 1 – Attend-collinear versus attend-orthogonal conditions. For identical stimuli (a and b, c and d), the central stimulus can be considered to be in either a collinear (a, c) or orthogonal configuration (b, d), depending on which pair of flankers are attended: left-oblique flankers (a and d) or right-oblique (b and c). The attended set is outlined here with dashed ellipses, and the contrast of the central patch is enhanced for the purpose of illustration.