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Eccentricity effects on lateral interactions

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Abstract

We attempted to resolve an apparent conflict between the lack of psychophysical evidence of collinear facilitation at the near-periphery and physiological evidence from the monkey showing collinear effects extra-fovealy. We compared collinear and orthogonal configurations to discount facilitation due to reduced positional uncertainty. Detection thresholds were measured for Gabor targets at eccentricities of 0°–4°, flanked by collinear or orthogonal flankers. Like in previous reports in the literature, results varied among subjects when the stimulus position was off-fixation. We found reduced facilitation at eccentricities as small as 1°–2°. Moreover, facilitation did not increase when the stimuli were M-scaled or when observers received more practice. However, a larger proportion of subjects showed collinear facilitation when attention was directed to the tested configurations. The results suggest that differences in allocation of attention along the visual field may affect the underlying lateral interactions, consequently resulting in eccentricity effects as well as inter-observer variability.

Keywords: Lateral-interactions; Periphery; Attention; Eccentricity; Crowding

1. Introduction

A large body of psychophysical and physiological studies supports the findings that in early visual areas, the responses of cells to a stimulus are modulated by stimuli that are located outside their classical receptive field. This sort of modulation is suggested to be mediated by a mass of lateral and feedback connections (Grinvald, Lieke, Frostig, & Hildesheim, 1994; Kapadia, Ito, Gilbert, & Westheimer, 1995; Knierim & van Essen, 1992; Levitt & Lund, 1997; Li, Their, & Wehrhahn, 2000, 2001; Polat & Norcia, 1996; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Zipser, Lamme, & Schiller, 1996). Such networks may serve to link local elements into global percepts. An example of such a contextual modulation is the phenomenon of collinear facilitation, in which the contrast detection threshold for a local element (such as a short bar or Gabor stimulus) is reduced when it is flanked by nearby co-aligned elements with similar orientation and spatial frequency (Morgan & Dresp, 1995; Polat & Sagi, 1993, 1994a; Solomon, Watson, & Morgan, 1999; Williams & Hess, 1998). The specificity of the collinear facilitation effect to orientation and spatial frequency suggests an early level of processing in the cortex where the cells and the interactions possess such fine tuning to these features.

Collinear facilitation is a robust phenomenon for Gabor targets that are located at the fixation point (Polat & Sagi, 1993, 1994a; Solomon et al., 1999; Williams & Hess, 1998; Woods, Nugent, & Peli, 2002). However, some studies showed that when the stimulus is presented at 3°–4° of visual angle, facilitation is not observed for the majority of the subjects (Williams & Hess, 1998; Zenger-Landolt & Koch, 2001). Assuming that the facilitation is mediated by lateral interactions, the lack of facilitation may suggest a different pattern of connectivity at the fovea and periphery. However, this suggestion

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is in conflict with anatomical and physiological findings from the cat and the monkey, since anatomically, the long-range horizontal connections have not been reported to be restricted to those cortical areas that represent the fovea (Gilbert & Wiesel, 1989; Malach, Amir, Harel, & Grinvald, 1993; Ts'o, Gilbert, & Wiesel, 1986). Moreover, physiological recordings taken from the cat and the monkey show extra foveal contextual modulation, up to around 10° eccentricity (Kapadia et al., 1995; Polat et al., 1998). Also, the reports on the existence of lateral facilitation at the near-periphery in some subjects (Levi, Hariharan, & Klein, 2002; Polat & Sagi, 1994b; Zenger-Landolt & Koch, 2001; Williams & Hess, 1998), supports the hypothesis that the fovea–periphery difference is not in the connectivity but rather in its functional expression. It is possible that the pattern of connectivity is the same at the fovea and the periphery, but the interactions are modulated differently in these two regions by some factor. Indeed, contrast summation experiments provide evidence for excitatory lateral interactions in the near-periphery when stimulus contrast is at the detection threshold (Bonneh & Sagi, 1998; Tailby, Cubells, & Metha, 2001). A modulator that may act differently on foveal and peripheral targets is visual attention. Recently, it has been shown that attention modulates lateral interactions in the fovea (Freeman, Sagi, & Driver, 2001). Moreover, the resolution of attention is reduced along eccentricity (He, Cavanagh, & Intriligator, 1996; Intriligator & Cavanagh, 2001). Hence, it is possible that reduced resources of attention at the periphery are responsible for the absence of facilitation around 4°, as measured psychophysically.

In the current study we tried to understand the reasons for the failure to find consistent collinear facilitation at the periphery. Previous studies compared detection thresholds of collinear and no-flank configurations to test for facilitation at the near-periphery (Levi et al., 2002; Williams & Hess, 1998; Zenger-Landolt & Koch, 2001). However, we found it problematic since spatial uncertainty is greater at the periphery, and hence the no-flank condition can suffer from it more than the collinear one. Here we defined collinear facilitation as the advantage of the collinear over the orthogonal configuration at threshold, noting that due to increased spatial uncertainty at the periphery, orthogonal flankers may also facilitate detection relative to detection of a non-flanked target by signaling the target position. We chose the orthogonal configuration as a reference because at the fovea orthogonal flankers were shown not to affect detection thresholds of an unflanked Gabor target (Polat & Sagi, 1993). Nevertheless, if collinear flankers would still facilitate detection relative to orthogonal at the periphery, this facilitation would be orientation-specific and could be attributed to lateral interactions. Therefore, the subjects needed to detect a Gabor target, flanked from above and below by similar, high-contrast Gabor signals, in either collinear or orthogonal configurations. First, we looked for the eccentricity at which collinear facilitation falls off (we tested at 0°, 1°, 2° and 4° eccentricity). Then, several manipulations were carried out in an attempt to find collinear facilitation at 4°: (1) scaling the stimuli by the cortical magnification factor, (2) training on the collinear configuration, and (3) manipulating attention similarly to Freeman et al. (2001) by means of a dual task in order to affect the lateral interactions between the target and the flankers. In the dual task experiment the subjects performed a Vernier acuity task on the flankers concurrent with target detection, presumably better distributing their attention along the stimulus configuration. We found that collinear facilitation diminished with eccentricity. Scaling the stimuli according to the cortical magnification factor did not produce facilitation. Moreover, training also did not generate facilitation. However, for some subjects, collinear facilitation was observed when attention was manipulated. Nevertheless, several subjects showed facilitation under various conditions with no special manipulation. To conclude, we have found evidence for facilitating lateral interactions at the near-periphery. Apparently, the conditions needed to generate the peripheral facilitation are more subject-specific than those for foveal facilitation. The difference between foveal and peripheral lateral interactions can be partially explained by differences in the individual strategy of allocation of attention.

2. General methods

2.1. Apparatus

Stimuli were displayed as a gray-level modulation on a 22″ Mitsubishi Diamond Pro 2060u color monitor using an ATI Radeon Graphic card. The video format was 85 Hz non-interlaced. An 8-bit RGB mode was used and Gamma correction was applied to produce a linear behavior of the displayed luminance. The mean display luminance was 30 cd/m^2 in an otherwise dark environment.

2.2. Subjects

The subjects were 13 paid high-school and undergraduate students with normal or corrected-to-normal vision. Some of them participated in more than one experiment.

2.3. Stimuli

The stimuli were Gabor signals, which are luminance-modulated sinusoidal gratings that were added to a