Effect of spatial frequency on collinear facilitation

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Abstract—Contrast sensitivity for a Gabor target can be increased by a factor of two when identical patches are separated by about three wavelengths ($\lambda$) and positioned collinearly (Polat and Sagi, 1993, 1994a, 1994b). The facilitation effect was found for a wide range of spatial frequencies but was tested with well-experienced observers. Since practice modifies the range of lateral interactions, in this study naive observers were tested in order to document the initial stage of collinear facilitation. Surprisingly, we found that facilitation is maximal for the high spatial frequencies and minimal for the low spatial frequencies. We also found that when experienced observers were tested, facilitation at the low spatial frequencies was evident, suggesting that the initially reduced facilitation was due to inefficient lateral interactions. We suggest that the absence of facilitation for low spatial frequencies is due to the slow propagation velocity of the remote input, resulting in a mismatch between the flanker’s input and the target’s integration time.

Keywords: Contrast sensitivity; facilitation; collinear; spatial interactions; temporal processing; propagation time.

INTRODUCTION

Contrast is one of the most important attributes of the visual stimulus that determines visual neuronal response. The visual system can detect small, local luminance differences (contrast) and group them into behaviorally relevant objects, a process that is context-dependent and requires integration between remote image parts. Contrast sensitivity function (CSF) describes the contrast sensitivity (the reciprocal of threshold contrast) against spatial frequency and usually peaks at 3–6 cycles per degree (cpd) when measured with extended gratings. Contrast sensitivity measured with Gabor patches (GPs) is facilitated when the target is flanked by 2 identical GPs positioned at a separation of about $3\lambda$ or more from the target and arranged in a collinear configuration (Adini and Sagi, 2001; Adini et al., 1997;

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Bonneh and Sagi, 1998; Polat and Sagi, 1993, 1994a, 1994b; Solomon and Morgan, 2000; Woods et al., 2002). The facilitation reached was up to a factor of two (0.3 log units) in many cases and was found for a wide range of spatial frequencies (Polat et al., 2005; Polat and Sagi, 1993). Thus, facilitation is expected to shift the CSF upward by about a factor of two.

The lateral interactions, as implied by Polat and Sagi (1993), showing spatial scaling of the facilitation with spatial frequency, would predict a general principle of operation within the visual system that could be applied across all spatial frequencies. Such generality may be very appealing but anatomical support has not yet been found in the visual cortex to support this prediction. A recent study has shown that the size of both the carrier and the envelope of the Gabor affects lateral interactions at short distances (Woods et al., 2002). However, this study also shows that at larger target–flanker distances there is spatial scaling.

A key argument against the spatial scaling of the lateral interactions is that the size of long-range connections in area V1 is almost fixed, about 1–2 mm, which is far too short to account for the effects seen psychophysically from the lateral interactions, especially with the lower spatial frequencies (for a review, see Angelucci and Bressloff, 2006).

Another argument against the spatial scaling is based on the fact that the propagation time of the lateral interactions is slow. Since excitatory effects from outside the receptive field propagate to the target’s location through the lateral connections, lateral interactions are slow, relative to the direct input received by the receptive field (less than 2λ). The estimated propagation speed of lateral excitation derived from psychophysical studies is about 3°/s (Cass and Spehar, 2005; Tanaka and Sagi, 1998), in agreement with the estimates from intracellular and optical imaging studies (Bringuier et al., 1999; Series et al., 2003). Therefore, facilitation is possible only if the propagation of the excitatory input from the mask to the target is not delayed by a longer period than the integration time of the feedforward input. An estimate of the integration time of the target response taken from physiological experiments (Albrecht, 1995; Mizobe et al., 2001; Polat et al., 1998) provides an upper limit of 200 ms. This estimate is consistent with psychophysical results showing that the integration time for contrast detection at threshold is 160–200 ms (Watson et al., 1983). Our results are consistent with this estimate, and we found that the saturation level of integration time is reached after 100 ms for targets of 6 cpd (Polat et al., 2007). Thus, a stimulus that arrived beyond a time window of 100–200 ms will fail to facilitate the target’s response. Support for the importance of the relationships between propagation time and integration time was found in the study of Cass and Spehar (2005). They found that the facilitation increased with increasing presentation time of the target, reaching an optimal time of facilitation at 3λ at 80 ms.

Taken together, spatial scaling of the facilitation effect may pose a considerable challenge for our understanding of visual processing: (a) how the facilitation is mediated for the lower spatial frequencies, and (b) since the retinotopic distance