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Collinear interactions and contour integration

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Abstract—The visibility of a local target is influenced by the global configuration of the stimulus. Collinear configurations are a specific case in which facilitation or suppression of the target has been found to be dependent on the contrast threshold of the target. The role of collinear interactions in perceptual grouping, especially in contour integration, is still controversial. In the current study, the role of collinear interactions in noise was investigated using experimental conditions similar to those utilized in studies of contour integration. The contrast detection paradigm in the presence of similar Gabor elements presented in the background was used. The results show that contrast detection threshold of the target alone is increased (suppression) when it is embedded in randomly oriented background elements. However, when the target is flanked by two collinear Gabor elements, the target is facilitated even at higher target contrast levels. Facilitation is not found for orthogonal configurations. The results suggest that the response to a local element in a contour is modified by lateral facilitative and suppressive inputs from elements comprising the smooth contour and randomly oriented background elements, respectively. Thus, detection of elements along a contour should be considered as integration of global neuronal activity rather than as the output of local and individual neurons.

Keywords: Contour integration; contrast; context; long-range interactions; facilitation; suppression; perceptual grouping; threshold.

1. INTRODUCTION

The global configuration of the stimuli affects the visibility of local elements (Bonneh and Sagi, 1998; Polat and Sagi, 1993, 1994a, b; Polat and Norcia, 1996, 1998; Polat and Tyler, 1998; Kapadia *et al.*, 1995; Sillito *et al.*, 1995; Levitt and Lund, 1997; Polat *et al.*, 1998). This context effect may rely on long-range horizontal connections that tend to interconnect like orientation columns. A special global configuration is formed when the target and flankers are arranged in a collinear configuration. Recent studies indicate that neurons tend to be connected

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along their preferred orientation and are aligned collinearly (Fitzpatrick, 1996; Schmidt *et al.*, 1997).

Several recent experiments have shown that the contrast threshold of a Gabor patch can be either enhanced or suppressed by the lateral placement of other Gabor patches arranged collinearly (Polat and Sagi, 1993, 1994a, b). The collinear facilitation is found for low target contrast (Polat and Norcia, 1996) and near the contrast threshold of individual neurons (Polat *et al.*, 1998). Suppression occurs either locally within a range of about 2 λ (Polat and Sagi, 1993, 1994a, 1994b; Zenger and Sagi, 1996) or from remote regions at the suprathreshold target's contrast (Polat and Norcia, 1996; Polat *et al.*, 1998; Bonneh and Sagi, 1999b).

Our ability to link contour segments together have been studied in a contour detection paradigm (Field *et al.*, 1993; Kovács and Julesz, 1993; Pettet *et al.*, 1998), where observers were required to detect a path of Gabor signals embedded in noise. The experimental conditions in which collinear interactions and contour integration were found to operate optimally are similar to those of the perceptual grouping (Polat, 1999). Thus, it has been suggested that contour integration may rely on long-range interactions (Braun, 1999; Kovács and Julesz, 1993; Kovács *et al.*, 1996; Pettet *et al.*, 1998; Polat and Sagi, 1994a, b; Polat *et al.*, 1995; Polat and Norcia, 1996; Polat, 1999; Yen and Finkel, 1998).

In contrast, a recent study has argued that collinear facilitation does not play a role in contour integration (Hess *et al.*, 1998). Based on the assumption that contrast and the neuronal response are closely related (citation of Tolhurst, 1989), they anticipated that facilitation between contour elements should increase the visibility of the Gabor elements, and they should appear to possess higher contrast relative to non-facilitative conditions. Their results show that observers can detect contour in the presence of very high levels of variability of contrast and that the Gabor patches in the contour do not appear to be of higher contrast. Thus, they concluded that collinear facilitation does not play a role in contour integration.

In this study we used similar experimental conditions to those used in contour integration studies to investigate the role of the collinear interactions in the presence of background noise. The contrast detection of a Gabor target embedded in similar randomly oriented Gabor elements (noise) was measured. Then the same condition was repeated with two Gabor patches flanking the target in a collinear or orthogonal configuration. We found that the contrast threshold of the unflanked target was increased (suppressed) by the presence of the background, but adding two collinear flanks facilitated the target.

2. METHODS

2.1. Stimuli and experimental procedures

Three observers with normal or corrected-to-normal vision in both eyes participated in these experiments. The two-alternative forced-choice paradigm was used in

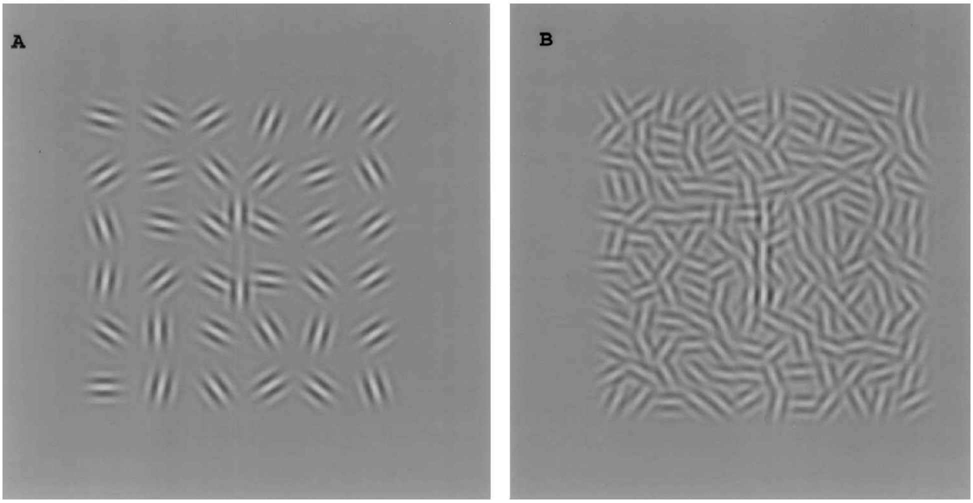

Figure 1. Stimuli. Each noise mask consisted of a set of randomly oriented Gabor patches arranged on a square matrix, with different number and spacing between conditions and 0.2 λ uniform jitter. Four spacing conditions were used 4 λ (A), 3 λ, 2 λ and 1 λ (B) with corresponding number of elements (36, 64, 144, 225) to form a similar noise size of about 2.5 × 2.5 deg. Different amplitudes of the generating Gabor signal were used for the different noise densities to prevent overflow, 70, 40, 40, 20 for the 4, 3, 2, 1 λ spacings respectively. The 'no-noise' condition is the standard lateral interaction experiment (Polat and Sagi, 1993, 1994a, b; Zenger and Sagi, 1996; Ishai and Sagi, 1997). The target-flank separation condition was always 3 λ.

all experiments. Foveally viewed circular Gabor patches ($\sigma = \lambda = 0.12$ deg., 8.33 c/deg. carrier; see Fig. 1) appearing randomly in one of these intervals, served as a target. The observer's task was to detect in which interval the target appeared. When ready, the observer pressed a key activating the trial sequence. In all experiments, the target Gabor patches were presented in the center of a 13 × 10.4 deg. field set to the mean luminance of the patches. Before each trial, a small fixation circle was presented at the center of the monitor. Target threshold contrast was determined by a staircase method, which converged to 79%. Each condition consisted of about 50 trials, in which the spatial frequency and orientation were kept constant. Each threshold was measured at least 4 times.

2.2. Noise generation

Noise generation was similar to that used by Bonneh and Sagi (1999a). Each noise mask consisted of a set of randomly oriented Gabor patches arranged on a square matrix, with different number and spacing between conditions and 0.2 λ uniform jitter. Four spacing conditions of the noise elements were used (4, 3, 2, 1 λ). Since the area designed for the noise was 2.5 × 2.5 deg. for all conditions, the number of elements increased when the spacing between the noise elements decreased. Thus the number of noise elements was 36, 64, 144 and 225 corresponding to spacing of 4, 3, 2 and 1 λ. Different amplitudes (contrast) of the generating Gabor signal were used for the different noise densities to prevent overflow, 70, 40, 40, 20 for the 4, 3, 2, 1 λ spacing respectively. The 'no-noise' condition is the standard lateral interaction experiment (Polat and Sagi, 1993, 1994a, b; Zenger and Sagi, 1996; Ishai and Sagi, 1997). The target-flank separation condition was always 3 λ in order to capture the maximal facilitation usually found for this separation (Polat and Sagi, 1993, 1994a, b).

Stimulus generation and display were controlled by a SGI Crimson/Reality engine workstation. Stimuli were displayed as grey-level modulation on a Sony color monitor. The video format was 60 Hz non-interlaced with 1280×1024 pixels occupying a 13×10.4 deg. area. An 8-bit RGB mode was used and Gamma correction applied to produce linear behavior of the displayed luminance. The lowest contrast threshold was high enough to be effectively measured with the 8-bit grey level resolution of this set-up. The stimuli were viewed binocularly from a distance of 150 cm and presented for 80 ms. The mean display luminance was 40 cd/m^2 in an otherwise dark environment.

3. RESULTS

The detection of the isolated target (solid lines, open squares) and the flanked target (dashed lines, filled squares) as a function of background density is presented in Fig. 2 for three observers. The x-axis represents the background's element density (1/distance between the Gabor elements in λ units). The y-axis represents the log contrast threshold. The condition of 'no-noise' is presented at background density = 0. The contrast detection threshold of the isolated target (solid line, open squares) increased (suppressed) with increasing background density (decreasing the spacing between the elements). At a background density of 0.25 (distance between the Gabor elements of 4 λ) there was no effect on target detection. However, with increasing background density, i.e. when the distance between the background elements was 3 λ or less, the contrast detection threshold of the target increased by 0.15–0.2 log units at 3 λ and by up to 0.4 log units at the higher densities. Thus, the target's detection was suppressed when the distance between the background elements was smaller than 3 λ.

However, when 2 collinear flanks configured with a target-flank separation of 3 λ were added, the detection of target was facilitated (dashed lines, filled squares). Note that for each noise level, the facilitation was proportional to the isolated target's threshold and that the facilitation was found for high contrast levels (up to 40%). The amount of facilitation for observer YK is smaller (but still significant) than the other two experienced observers. He had no previous experience in any psychophysical tasks, particularly not with collinear experiments that usually improve the facilitation (Polat and Sagi, 1994b, 1995).

To test whether the facilitation is due to a change in uncertainty level caused by the collinear flanks, we repeated the experiment with orthogonal flanks for observers

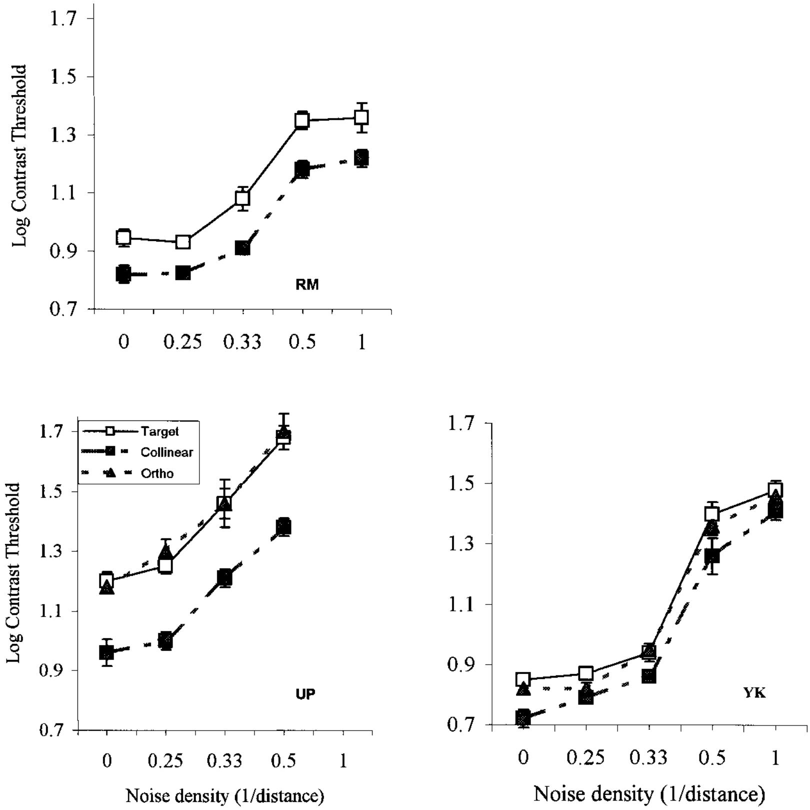

Figure 2. Log target contrast threshold as a function of density of background noise elements with (dashed lines, filled squares) and without (solid lines, open squares) a pair of flanks collinear to the target. Two observers (UP and YK) was also tested with a pair of orthogonal flanks. Observer YK had no previous experience in psychophysical experiments.

LM and UP. The results show (dashed line, solid triangles) that the orthogonal flanks did not facilitated the target at any of the background densities.

4. DISCUSSION

The main effect that we have presented in this study is that the response to a target element is determined by pooled facilitative and suppressive inputs from the elements comprising the collinear flanks and the background elements, respectively. We have demonstrated that the detection contrast threshold of the target alone was increased (suppression) when it was embedded in randomly oriented background elements and that the target is facilitated by collinear flanks even at the higher contrast levels. Our result is consistent with the finding of direct relationships between the background noise density and the contour detection thresholds (Kovács *et al.*, 1996; Braun, 1999). Thus, detection of elements along a contour should be considered as integration of global neuronal activity rather than as an output of local and individual neurons.

The suppression of the target detection by the background noise is reminiscent of the crowding effect (Flom *et al.*, 1963; Leat *et al.*, 1999). Visual acuity for letters surround by other letters or contours is usually reduced compared with that of single letter presented alone.

Our results, in addition to those found previously (Bonneh and Sagi, 1998, 1999b; Polat and Sagi, 1993, 1994a, b; Polat and Norcia, 1996, 1998; Polat *et al.*, 1998; Polat and Tyler, 1998; Kapadia *et al.*, 1995; Sillito *et al.*, 1995; Levitt and Lund, 1997), clearly show that regulation of contrast occurs in a spatially distributed fashion. It has been suggested that long and short-range lateral interactions that occur between local mechanisms create a second stage of spatial integration that is made up of antagonistic weighting functions (Polat, 1996, 1998; Polat, 1999). These studies considered a model of lateral interactions assuming that excitation and inhibition produce a network of neuronal connectivity that modifies the neuronal response. The balance of the network may control the output of the individual filter. A neural network concept has been suggested in several theoretical models (Adini *et al.*, 1997; Somers *et al.*, 1998; Stemmler *et al.*, 1995; Yen and Finkel, 1998; Wilson and Cowan, 1973; Usher *et al.*, 1998).

A recent study (Hess *et al.*, 1998) has argued that mean response and contrast are intimately related, i.e. that the response should increase with increasing contrast. Even though this assumption is based on neurophysiological data (Tolhurst, 1989), they did not considered other neurophysiological studies showing that the firing rate of an individual neuron is modulated by other neurons responding to surround stimuli (Levitt and Lund, 1997; Sillito *et al.*, 1995; Polat *et al.*, 1998; Sengpiel *et al.*, 1998).

Recently, Polat (1999) has suggested that excitation and inhibition produce a network of neuronal connectivity that modifies the neuronal response. In this model, each filter receives three types of visual input: direct thalamic-cortical excitatory input, lateral excitation and lateral inhibition. The excitation is organized along the filter's optimal orientation and is superimposed on a suppressive area surrounding the filter. The balance of the network may control the contrast response function of the individual filter. Thus, since the output of an individual neuron is determined by a combination of thalamic-cortical input and lateral modulation, the output of a neuron cannot be predicted solely from the stimulus parameters. For example, in a recent study, Polat *et al.* (1998) have shown that collinear interactions modified the firing rate of individual neurons relative to their contrast threshold; facilitation near contrast threshold and suppression at supra-threshold contrasts. Some neurons with high contrast thresholds (above 30%) were facilitated at this high contrast level. Thus, the collinear flanks increased the firing rate near contrast threshold and decreased the firing rate at supra-threshold contrasts. Therefore, response of an individual neuron to increasing contrast, under certain conditions, may result in reduction rather than increase of the firing rate.

In the current study, when the contrast threshold of the target was increased (suppressed) by the background noise (about 30%), the contrast threshold with the collinear flanks became significantly lower (facilitation). Note that the assumption that there is a close relationship between contrast and response (or visibility), leading to the prediction that facilitation should increase the visibility of the target (e.g. Hess *et al.*, 1998), also leads to the prediction that suppression should decrease the visibility. However, note that the visibility was the same, at threshold, regardless of whether it was facilitated or suppressed, and regardless of the target contrast.

However, considering the neural network approach (Polat, 1999), it is more likely that the effect of collinear facilitation was to reduce the suppressive effect introduced by the background. In other words, the excitation from the collinear flanks balanced the inhibitory inputs from the background, thus reducing the suppression effect. A similar effect was demonstrated using single unit recordings from the visual cortex of alert monkeys (Kapadia *et al.*, 1995). The response of individual neurons decreased when line elements surrounded the receptive field. However, adding lines in a collinear configuration reduced the suppression caused by the background noise (facilitation).

Perception of global objects may be mediated by the mutual activity of many neurons, each responding to local features of the image but modulated by the other neurons responding to remote parts of the image. Such second-stage processes act to correlate and to equate the responses of neurons belonging to the same global pattern (see Polat, 1999). This idea is supported by recent studies (Polat *et al.*, 1998; Sengpiel *et al.*, 1998) showing that an individual neuron's range of responses to a large change of contrast was dramatically decreased when the neuron was activated with collinear flanks presented outside its receptive field. In other words, an individual neuron may change its firing rate only slightly to large contrast changes under collinear interactions (see Polat, 1999). Indeed, the finding that contours can be detected despite large contrast differences between the elements comprising the contour (Hess *et al.*, 1998) further supports our proposal.

It is possible that attention may modulate contextual effects in a selective way. Observers may be able to judge saliency preattentively whereas contrast judgement may require attention. Thus, contour integration may lead to increasing firing rate (presumably mediated by collinear interactions) under preattentive conditions without involvement of contrast judgement. However, when contrast judgement is required, the involvement of attention may not contribute to collinear facilitation. Such possibility is supported by a recent study which showed that varying the attentional state may have a differential effect on the response of the receptive field and the contextual effect (Ito and Gilbert, 1999). Furthermore, collinear interactions were found in the primary visual cortex under anaesthetized conditions in which attention was not involved (Polat *et al.*, 1998) supporting the idea that attention is not critical factor for collinear facilitation.

We suggest that contour integration may be attributed to global effects formed by the local elements comprising the contour such as response saliency, response synchronization or a combination of the two (Yen and Finkel, 1998; Li, 1998). Moreover, smoothness of the elements comprising the contour, which is a critical feature for contour detection (Field *et al*., 1998; Kovács and Julesz, 1993; Pettet *et al*., 1998; Bonneh and Sagi, 1998), may be achieved by the elongated collinear filters (Polat and Norcia, 1998; Polat and Tyler, 1998) that group the elements into a smooth contour (Polat, 1999). Elongated collinear filters are less sensitive to local contrast variability along the contour (see Polat, 1999).

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