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Detection Facilitation by Collinear Stimuli in Humans: Dependence on Strength and Sign of Contrast

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We measured detection of a thin vertical line (target) in the presence of a slightly thicker collinear, adjacent line (inducer). Sign and strength of contrast of the inducer were varied. Test lines could be either bright or dark. Detection thresholds were obtained through a temporal two-alternative forced-choice (2AFC) procedure with the method of constant stimuli. When target and inducer had equal contrast polarity, low thresholds of target lines were observed for low inducer contrasts and increased with increasing inducer contrast. With opposite contrast polarity of target and inducer, thresholds were high for low inducer contrasts and decreased for increasing contrast thereof. Our results support the hypothesis that cortical mechanisms with different sensitivity to the sign and strength of contrast participate in the detection facilitation of line contours. © 1998 Elsevier Science Ltd. All rights reserved.

Orientation Subthreshold summation Contrast polarity Detection Facilitation Long-range spatial interactions

INTRODUCTION

The contrast detection of luminance targets is facilitated by the presence of oriented inducers that are collinear with the target (Dresp & Bonnet, 1991, 1993; Dresp, 1993; Polat & Sagi, 1993, 1994; Dresp & Bonnet, 1995; Morgan & Dresp, 1995; Kapadia, Ito, Gilbert, & Westheimer, 1995; Dresp & Grossberg, 1997). When the target and the inducer are no longer collinear, or when a stimulus with an orthogonal orientation is inserted between them, detection facilitation usually disappears (Dresp, 1993; Kapadia *et al.*, 1995). The orientation specificity of these facilitation effects indicates that the underlying mechanisms involve cortical interactions and not solely some kind of spatial contrast summation in the retina (Cohn & Lasley, 1975). Strong support for a cortical genesis of these mechanisms comes from extracellular recordings in V1 of awake fixating monkeys showing that orientation-selective neurons display an enhanced response to a line presented in their receptive field when another collinear line is added outside the receptive field. These electrophysiological findings correlate with psychophysically observed detection facilitation in human observers (Kapadia *et al.*, 1995). While it has been shown that collinear targets and inducers of opposite contrast sign produce detection facilitation (e.g. Polat & Sagi, 1994; Dresp & Bonnet, 1995; Dresp & Grossberg, 1997), it is still unclear how the relative contrast polarity and strength of oriented targets and inducers contribute to the facilitatory effects. The results reported here show that detection facilitation of a 20 arcmin long and 1 arcmin wide target line abutting a collinear, 50 arcmin long and 5 arcmin wide inducing line decreases when the strength of contrast of an inducer with equal polarity increases. The reverse effect is observed with an inducer of opposite polarity (see also Wehrhahn & Dresp, 1996). The data will be discussed in relation to pedestal effects (e.g. Foley & Legge, 1981; Morgan & Dresp, 1995; Yang & Makous, 1995), the possible role of long-range cortical interactions (e.g. Gilbert & Wiesel, 1990; Polat & Sagi, 1994; Das & Gilbert, 1995; Kapadia *et al.*, 1995; Zenger & Sagi, 1996) and related assumptions of hierarchically organized cortical mechanisms mediating the detection of contours and boundaries of alternating contrast sign (e.g. Dresp & Grossberg, 1997).

METHODS

Subjects

The two subjects (the authors) were experienced observers in psychophysical experiments with normal or corrected to normal vision.

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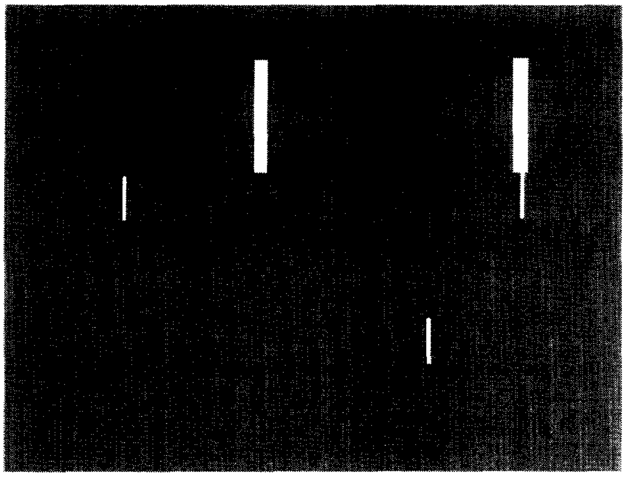

FIGURE 1. All stimuli were displayed on a gray monitor (SONY) with a background luminance of around 5 cd/m^2. Inducing stimuli are above and test stimuli below. Test stimuli are shown brighter than in the experiments where they had contrasts around or below detection threshold. Michelson contrast was varied for both bright and dark inducers. Control stimuli are depicted in the lower panel. The horizontal segments indicate the fixation brackets which were continuously displayed at just detectable contrast. See Method for further details.

Stimuli and procedure

Stimuli were displayed on a color monitor driven by a PC (IBM 486 Clone) with an interface (ELSA). Average brightness of the monitor background was around 5 cd/m^2. Grey levels of the monitor were calibrated (about 120 calibrated values within the linear range) with a device standardized to a Pritchard photometer. The distance between observer and monitor was about 126 cm. The stimuli consisted of a vertical test line, 20 arcmin long and 1 arcmin wide, displayed immediately below a collinear inducing stimulus, 50 arcmins long and 5 arcmin wide (Fig. 1). Target line and inducer were flashed simultaneously on the screen for about 500 msec at a given trial. Small, horizontal fixation brackets (2 arcmin long, 1 arcmin wide) of a just noticeable luminance difference with regard to the background were permanently present on the screen to reduce uncertainty about the spatial location of the target. Contrast strength of the inducer could be set to values of Michelson contrasts from 0.05 to 0.80 for the bright inducer, and to -0.05 to -0.64 for the dark inducer. Contrast thresholds for the test line were determined through a temporal 2AFC procedure, where stimuli were displayed in two successive temporal intervals. By striking a response key, subjects had to decide in which of the two intervals the target line was present. The target lines differed from the background in six equidistant values of luminance (between 0.2 and 1.2 cd/m^2), being either higher or lower than that of the monitor. For each contrast strength and polarity of the inducer, these six target conditions were presented in random order, according to the method of constant stimuli. Each stimulus condition was repeated at least 60 times. Through an interpolation procedure, that target luminance for which subjects correctly identified the presence of the test line in 75% of the cases was determined. These values are plotted as psychophysical thresholds (see Results). Before the experiment, and at regular intervals throughout, control experiments were carried out in which the detection threshold of the test line on the plain screen was measured (Fig. 1, lower panel). Thresholds for this condition were +1.2 cd/m^2 and -1.2 cd/m^2, corresponding to a Michelson contrast of 0.118, from the background for the bright and the dark test lines, respectively, in both subjects and this did not change throughout the experiments.

RESULTS

Equal contrast polarity

Contrast detection thresholds for a white test line were determined for a range of contrasts of a collinear white inducer presented simultaneously. The results are shown in Fig. 2 (upper panel). The standard deviation of the mean was never larger than the symbols used in the plots. In both observers thresholds are low for low inducer contrasts and increase with increasing contrast strength of the inducer. The strongest effect of the inducer on line detectability is observed for low contrasts between 0.05 and 0.2.

When a dark line is presented with a collinear dark inducer thresholds are again low for low contrasts in both observers (Fig. 2, lower panel). Note the inverted sign of the detection thresholds for the dark test line. For increasing contrasts of the inducer, detection thresholds for the test line increase in both observers and the lowest thresholds are observed for the lowest contrast of the inducing line.

Opposite contrast polarity

Thresholds for a dark test line presented simultaneously with a collinear white inducer are shown in Fig. 3 (lower panel). The standard deviation of the mean was never larger than the symbols used in the plots. For low inducer contrast, thresholds are as high as controls, i.e. when no inducer is presented. Thresholds decrease markedly with increasing inducer contrast. Note again the inverted sign of the thresholds for the dark test line. When a white target line is presented with a collinear dark inducer, thresholds are high for small contrasts and decrease with increasing inducer contrast (Fig. 3, upper panel).

A conspicuous feature of these results is that—irrespective of the contrast polarity of the test line—equal and opposite contrasts of the inducers influence detection of the test lines rather differently.

DISCUSSION

The results reported here show that inducers with equal contrast polarity, as well as opposite contrast polarity facilitate detection of oriented, collinear, and adjacent targets. The effect of contrast strength, however, is not the same in the two polarity conditions. In view of earlier

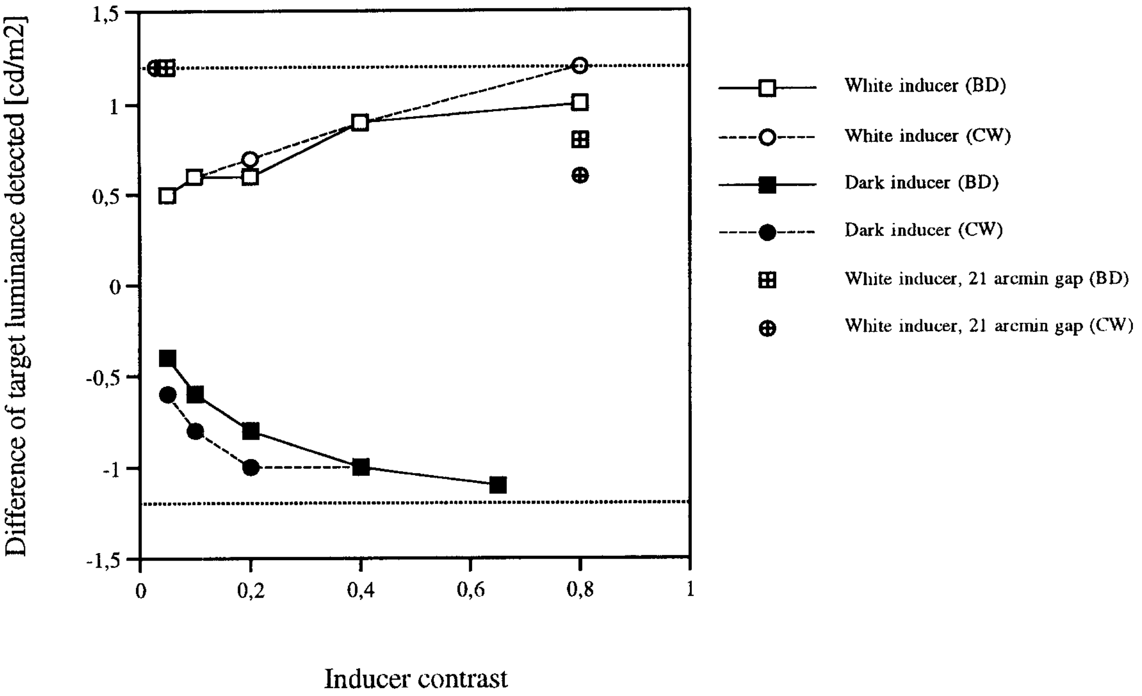

FIGURE 2. Upper graphs: Detection thresholds for a white test line in the presence of a collinear white inducer as a function of the contrast strength of the latter. Stimuli were displayed on a color monitor with a white background of around 5 cd/m^2 and viewed foveally. The vertical test line was 1 arcmin wide and 20 arcmin high. The inducing stimulus was a vertical bar 5 arcmin wide and 50 arcmin long situated directly above the test stimulus. Test and inducing line were presented simultaneously for 500 msec. 60 presentations per data point and per subject. Standard deviation of the mean is in all cases smaller than the symbols used for the mean. Lower graphs: Detection thresholds for a dark test line in the presence of a collinear dark inducer as function of inducer contrast strength. Note that thresholds are plotted with a negative sign for negative luminance values of the test line. The dotted lines at + or -1.2 cd/m^2 represent the light level of the test lines required to be visible for the two subjects in the control experiments, when no inducer was present. The datapoints (+ surrounded by a circle or a square) not linked by a curve indicate the thresholds obtained in the control experiment at a target-inducer gap of 21 arcmin (see Discussion). Apparatus, stimuli, and procedure remained the same.

findings on detection facilitation in similar situations, we will discuss our results in relation to two complementary, explanatory axes: short-range spatial facilitation (e.g. Dresp, 1993; Yu & Levi, 1997) or "pedestal effects" (e.g. Foley & Legge, 1981), and long-range spatial interactions identified with cortical mechanisms that may account for visual grouping of spatially separated contour fragments of any contrast sign (e.g. Polat & Sagi, 1994; Kapadia *et al.*, 1995; Dresp & Grossberg, 1997).

SHORT-RANGE SPATIAL FACILITATION AND "PEDESTAL EFFECTS"

Considering the condition where the target and the inducer have the same polarity, our data are consistent with earlier observations, frequently conceptualized in terms of "pedestal effects" (e.g. Foley & Legge, 1981; Morgan & Dresp, 1995; Yang & Makous, 1995). In these conditions, detection facilitation is found to be strongest for low inducer contrasts, and it is shown that the facilitatory effect decreases when the contrast of the inducer increases. This result is consistent with the classic pedestal effect, where low contrast inducers enhance the perceived contrast of the target via subthreshold summation and high contrast inducers suppress the contrast of the target via masking, two predictions which can be derived from Weber's law. Spatial frequency channel models have been proposed to account for pedestal effects (e.g. Foley, 1994; Yang & Makous, 1995). However, the spatial separation of targets and inducers has been shown to be a critical parameter in detection facilitation. For example, (Polat & Sagi, 1994), using a target Gabor patch flanked by two collinear suprathreshold Gabor patches, found that high contrast inducers mask a target of the same polarity when the spatial separation is small, but begin to facilitate target detection at larger spatial gaps. Zenger & Sagi (1996) have shown that, with an optimal spatial gap, high contrast inducers may facilitate the detection of a target of any contrast polarity. The complexity of the effects of the spatial separation of targets and inducers and their contrast polarity on detection facilitation has been revealed further in recent experiments by Yu & Levi (1997). The authors show that the detection of a very short target of both contrast polarities is either facilitated or masked within a range of target-inducer gaps up to about 20 arcmin, depending on the location of the target. This spatial facilitation is explained by functional properties of cortical simple cells with end-stopped receptive field structure. In the experiments described

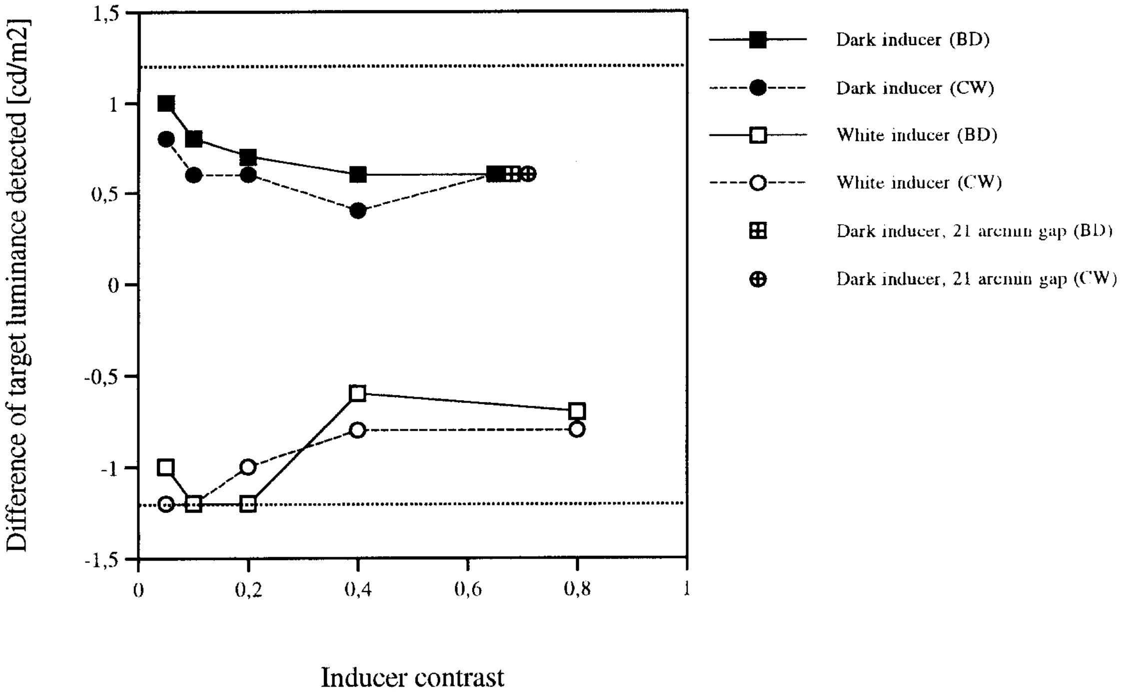

FIGURE 3. Upper graphs: Detection thresholds for a white line in the presence of a dark inducer plotted as a function of contrast strength of the latter. Other conditions as in Fig. 2. Lower graphs: Detection thresholds for a dark line in the presence of a white inducer plotted as a function of contrast strength. Note that (as in the lower panel of Fig. 2) contrast thresholds are plotted with a negative sign. The dotted lines at + or -1.2 cd/m^2 represent the light level of the test lines required to be visible for the two subjects in the control experiments, when no inducer was present. The datapoints (+ surrounded by a circle or a square) not linked by a curve indicate the thresholds obtained in the control experiment at a target-inducer gap of 21 arcmin (see Discussion). Apparatus, stimuli, and procedure remained the same.

here, we have used inducers that are more than 10-times longer and target lines that are 4-times longer than those in Yu & Levi's study. With our stimuli, facilitation with abutting targets and inducers of opposite polarity is observed within a different spatial scale, and only occurs at high inducer contrasts. All these results together suggest that short- and long-range mechanisms participate in the genesis of spatial facilitation.

From-short-to-long-range spatial interactions and the perceptual grouping of contour fragments

Dresp & Grossberg (1997) have proposed an explanation of detection facilitation with line targets and edge- and line-inducers of varying or alternating contrast polarity in terms of cortical short- and long-range interactions that involve a from-simple-to-complex-cells processing hierarchy (see also Gilbert & Wiesel, 1985). Kapadia *et al.* (1995) relate the detection performances of human observers to neural reponses in V1 of the awake monkey. Their interpretation of spatial facilitation by oriented inducers and targets is that they are processed by detectors with overlapping receptive fields. This had been suggested earlier by Dresp (1993) and might have as a consequence that the firing level of neurons, or detectors, is raised when the receptive fields coincide with like-oriented stimuli, but suppressed when they overlap with stimuli of orthogonal orientations (Kapadia *et al.*, 1995). Such an interpretation is consistent with neurophysiological evidence for long-range interactions in the visual cortex of the cat (e.g. Gilbert & Wiesel, 1990; Das & Gilbert, 1995). From-short-to-long-range cortical interactions could account for our observations as follows. Let us consider that the assumption of detectors with overlapping receptive fields (Dresp, 1993; Kapadia *et al.*, 1995) holds:

1. In the case where collinear targets and inducers have the same contrast sign, the critical level of processing would be that of neurons with the classic antagonistic receptive field structure (simple cells, see Fig. 4, first picture), and higher cortical levels do not have to be taken into account to explain spatial facilitation. It has often been shown that neurons with simple cell receptive field profiles are highly sensitive to stimuli in the low contrast range (e.g. Hubel & Livingstone, 1990). Therefore, critical interactions between them may essentially be triggered by stimuli with low contrast intensity. In fact, the responses of cortical neurons in V1 that correlate with detection facilitation (Kapadia *et al.*, 1995) were mainly activated by stimuli of 0.1–0.22 contrast. This may explain why short-range detection facilitation by inducers and targets of the same contrast polarity is strong with low inducer contrast and disappears at higher contrasts.
2. In the opposite contrast case, in order to achieve facilitation, the local input to detectors with simple cell receptive field structure has to be integrated by

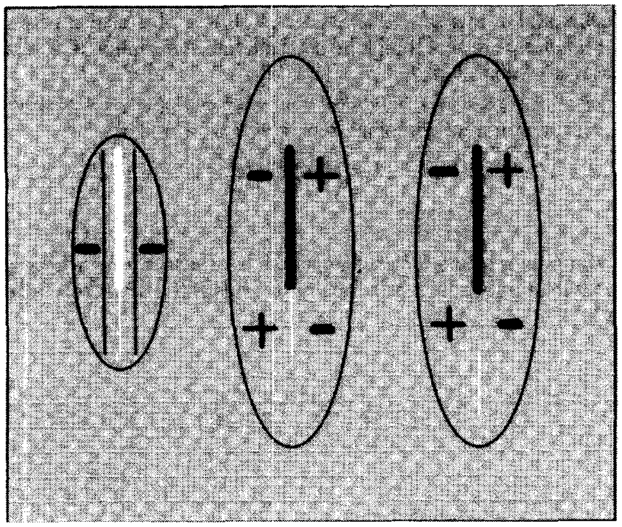

FIGURE 4. A schematic representation of the receptive field profiles of the mechanisms underlying short- and long-range spatial facilitation. The short-range mechanism presumably operates on the basis of functional properties of cortical simple cells, possibly exhibiting end-stopping (not shown here; but see Yu & Levi, 1997). The long-range mechanism requires a larger receptive field with functional characteristics identified with those of complex cortical cells.

higher-order detectors sensitive to the strength of contrast only, but not to its sign (see Fig. 4, second picture). This could happen via complex detectors with elongated receptive fields, referred to as eclectic collector units by some authors (e.g. Morgan & Hotopf, 1988), and as bipole operators by others (Grossberg, 1994). However, the important point is that the mechanisms underlying detection facilitation would in this case occur at a higher cortical level and would most likely operate over a larger spatial scale. In fact, the findings by Dresp & Grossberg (1997) imply that line targets and line inducers of opposite contrast polarity produce detection facilitation when a larger receptive field is covered, compared with line targets and inducers of the same polarity. They imply further that the underlying mechanism has a higher tolerance for spatial separation. Such a mechanism would, for example, explain perceptual grouping of spatially discontinuous stimulus fragments of any contrast sign that have a certain probability to "belong" to the same contour. Increasing contrast strength may compensate for decreasing spatial proximity within the same receptive field (see also the psychophysical evidence from Zucker *et al.*, 1983; Zucker & Davis, 1988). To test the effect of the contrast strength of the inducers at a larger spatial gap than the one used here, we have run a control experiment. We measured detection thresholds with the same stimuli at a target-inducer gap of 21 arcmin, i.e., beyond the critical gap zone for short-range integration reported by Yu & Levi (1997). At this larger gap, facilitation is observed with high contrast inducers only and regardless of the polarity of the target (see the datapoints marked with an asterisk in the Figs 2 and 3). Facilitation disappears completely with low-contrast inducers, which give rise to detection facilitation of abutting targets of the same polarity. These results strongly suggest that spatial facilitation with targets and inducers of any contrast sign occurs at larger spatial gaps (Fig. 4, third picture). This seems to be achieved by way of a mechanism which compensates for a decrease in stimulus proximity by a higher sensitivity to an increase in contrast strength within the receptive field. This interpreation is consistent with psychophysical evidence for perceptual grouping of collinear dots as a function of their luminance and their spatial separation (Zucker *et al.*, 1983; Zucker & Davis, 1988).

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