PERGAMON

Vision Research 42 (2002) 2493–2498

Vision Research

www.elsevier.com/locate/visres

Short- and long-range effects in line contrast integration

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Received 8 February 2002; received in revised form 29 May 2002

Abstract

Brincat and Westheimer [Journal of Neurophysiology 83 (2000) 1900] have reported facilitating interactions in the discrimination of spatially separated target orientations and co-linear inducing orientations by human observers. With smaller gaps between stimuli (*short-range* effects), facilitating interactions were found to depend on the contrast polarity of the stimuli. With larger gaps (*long-range* effects), only co-linearity of the stimuli seemed necessary to produce facilitation. In our study, the dependency of facilitating interactions on the intensity (luminance) of line stimuli is investigated by measuring detection thresholds for a target line separated from the end of an inducing line by co-axial gaps ranging from 5 to 200 min of visual arc. We find facilitating interactions between target and inducing orientations, producing short-range and long-range effects similar to those reported by Brincat and Westheimer. In addition, detection thresholds as a function of the co-axial separation between target and inducing line reveal an interaction between the spatial regime of facilitating effects and the luminance of the stimuli. Short-range effects are found to be sensitive to changes in local intensity while long-range effects remain unaffected.

Keywords: Line contrast detection; Orientation integration; Co-linearity; Short-range effects; Long-range effects

1. Introduction

The spatial integration of line stimuli involves mechanisms that govern the early cortical stages of orientation and contour processing. Orientation discrimination with co-linear lines (e.g. Brincat & Westheimer, 2000; Westheimer & Ley, 1997) and line contrast detection with co-linear target and inducing lines (e.g. Wehrhahn & Dresp, 1998; Dresp, 2000) are two common psychophysical methods for probing such mechanisms. Experiments by Brincat and Westheimer (2000) have shown that two distinct spatial regimes of orientation integration can be identified on the basis of experiments using orientation discrimination of co-linear lines. A *short-range* regime that is selective to local properties of the stimuli such as their contrast polarity, and a *long-range* regime that operates over a larger spatial scale and is selective to the orientation and co-linearity of the stimuli only. The authors measured orientation discrimination thresholds with various configurations most of which were composed of single pairs of co-linear lines. Two lines of a pair were either identical, or differed along a single dimension such as contrast polarity, for example. The co-axial separation of the lines varied. Orientation discrimination thresholds measured for the target line of a given pair were compared with those of a single line, and it was found that orientation discrimination obtained with closely spaced pairs of lines exhibited a large improvement over those obtained with a single line. This improvement was eliminated when a difference in contrast polarity, binocular disparity, or direction of motion between two lines of a closely spaced pair was introduced. On the other hand, when the stimuli were separated by spatial gaps larger than 15 min of visual arc (arcmin), improvements in performance, by comparison with thresholds for a single line, were found again. Orientation discrimination was then equivalent to that found with more largely separated identical co-linear lines. Brincat and Westheimer concluded that these results represent strong evidence for two distinct spatial domains of orientation integration.

Wehrhahn and Dresp (1998) came to a similar conclusion on the basis of data from line contrast detection

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PII: S0042-6989(02)00198-0

experiments with co-linear target and inducing lines. They measured contrast detection thresholds with single pairs of directly adjacent (abutting), or moderately spaced ($\sim 21'$) co-linear lines, a target and an inducing line. Two lines of a pair were either identical, or differed along a single dimension such as contrast polarity or contrast intensity. Contrast detection thresholds measured for the target line of a given pair were compared with those measured for the target presented without the co-linear inducing line. It was found that thresholds for the detection of the target presented with the co-linear inducing line were often much lower than those for the detection of the target line presented alone. This detection facilitation effect engendered by the co-linear inducing line varied as a function of the contrast intensity of the inducing line, and according to whether target and inducing lines had identical or opposite contrast polarity. When the two lines were directly adjacent and had identical contrast polarity, detection facilitation effects decreased with increasing contrast intensity of the inducing line, when they had opposite polarity, detection facilitation increased with increasing contrast intensity. However, when co-linear target and inducing lines were spatially separated, and the contrast intensity of the inducing line was sufficiently high, the interaction between contrast polarity and contrast intensity disappeared. Then, lines of identical and opposite polarity were found to yield identical detection facilitation effects. This non-selectivity of line contrast detection thresholds to the polarity of inducing lines at a larger spatial separation between stimuli corroborates Brincat and Westheimer's findings with orientation discrimination thresholds. Wehrhahn and Dresp (1998) suggested in the discussion of their work that line contrast integration may follow two distinct spatial regimes, a short-range integration regime and a long-range integration regime. However, their study mainly investigated interactions between contrast intensity and contrast polarity of abutting co-linear lines, and only four thresholds were measured with spatially separated stimuli.

Brincat and Westheimer's study concludes on the non-selectivity of long-range orientation integration to the contrast polarity of stimuli. The effect of luminance intensity was not investigated. Earlier work on contrast detection thresholds with co-linear stimuli suggests, however, that luminance affects orientation integration (e.g. Morgan & Dresp, 1995; Polat & Sagi, 1993; Wehrhahn & Dresp, 1998; Yu & Levi, 1997; Zenger & Sagi, 1996). The present study extends this work in order to clarify how relative luminance, or local contrast intensity, of co-linear line orientations interacts with the spatial separation of these lines. We investigated the spatial extent of facilitating effects in line contrast detection with co-linear target and inducing lines of varying luminance and polarity. Moreover, we wanted to clarify whether line contrast detection measures would exhibit spatial limits for short-range integration similar to those found by Brincat and Westheimer (2000) with orientation discrimination procedures, and also get some idea of the spatial limits of long-range effects. Brincat and Westheimer did not test for spatial limits of long-range orientation integration. Some results from earlier experiments with edge-like inducers and line targets (Dresp & Grossberg, 1997) would suggest that they might be situated somewhere around 2.5° of visual angle for stimuli of sufficient length. The commonly accepted working hypothesis for long-range orientation integration is that the orientation signals produced by spatially separated co-linear lines of a certain length use the same integration mechanisms as a single, long line.

2. Methods

We measured contrast detection thresholds of a target line presented simultaneously with a co-linear inducing line. The contrast intensity of the inducing line and the contrast polarity of the target line were varied. To get a clear picture of how the possible effects of luminance intensity depend on the spatial separation between orientations, we tested for at least nine different spatial gaps between the target and the inducing line.

2.1. Subjects

Four psychophysically trained observers including one of us, with normal or corrected-to-normal vision, participated in the first series of experimental sessions, which was run with a bright inducing line of relatively low contrast. Three other, also psychophysically trained, observers with normal or corrected-to-normal vision participated in the second set of sessions, which was run with a bright inducing line of high contrast.

2.2. Training

All observers were trained in the experimental conditions and in the control conditions beforehand. 400–600 training trials per observer and condition were run to minimize intra-individual variability in the experimental data.

2.3. Stimuli

Stimuli were presented on a high-resolution monochrome computer screen with a 60 Hz frame rate and a resolution of 640 × 480 pixels. Presentation was generated with an IBM compatible PC (Hewlett Packard 486) equipped with a VGA trident graphic card. The different luminance levels for measuring line contrast detection thresholds were generated by combinations of RGB signals calibrated with an optical photometer. The luminance of the dark background was constant at

2 cd/m^2. The luminance of the bright target line was adjusted individually for each observer as a function of several pre-experimental training sessions. It was set at 2.2, 2.5, 2.8, 3.1, and 3.4 cd/m^2 for observers SD, NL, CG, BD, MT, and YK. Observer DW was run with 2.2, 2.5, 3.1, 3.7 and 4.3 cd/m^2. The luminance of the low-contrast inducing line was 5 cd/m^2, and that of the high-contrast inducing line was 47 cd/m^2. The Michelson contrast $((L_{\max} - L_{\min})/(L_{\max} + L_{\min}))$ of the inducing line with the lower contrast was 0.42, that of the inducing line with the higher contrast was 0.92. Viewing distance was 126 cm to make the angular size of one pixel on the screen equal to 1′. The length of the target line was 15′ and the length of the inducing line 25′. The width of target and inducer was 1′. Co-axial distances between the target and the inducing line varied from 5′ to 200′, and effects for 8–10 different spatial separations were tested with each observer.

2.4. Procedure

The stimuli were flashed briefly (30 ms) on the dark background of the computer screen. In a two-alternative temporal forced-choice (2AFC) procedure, observers had to press one of two possible keys on the computer keyboard, according to whether they decided that they had seen the target line in the first or the second of two successive temporal intervals. Each experimental session corresponded to a total of 200 successive trials, presenting the five different luminance levels of the target according to the classic method of constant stimuli. In the test sessions, the target was flashed simultaneously with a white, co-linear context line. Each of the sessions (tests and control) was presented thrice to a given observer to produce three threshold measures per target luminance and experimental condition. The co-axial distance separating target and context line varied between sessions. In the control sessions, the target line was presented without the inducing line (see Fig. 1).

3. Results

The percentage, or probability, of correct detection of the target line was calculated for each target luminance, experimental session, and observer. These probabilities were transformed $(\log(p/1-p))$ to yield linear psychometric functions $(y = ax - b)$ of the difference between the luminance of the target line and the luminance of the background (D-lum). Detection thresholds (x) were calculated on the basis of the parameters of the individual psychometric functions obtained in each experimental session $(x = (y + b)/a)$. A threshold is defined here by a probability of correct detection (p) equal to 0.75, which corresponds to a logit of 1.09 on the ordinate (y) of the psychometric function.

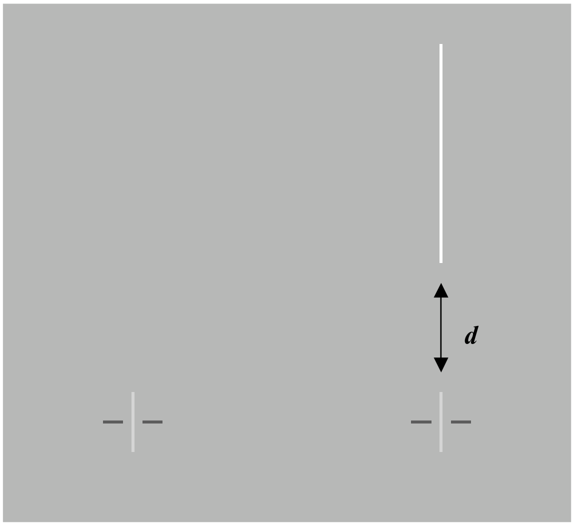

Fig. 1. A light target line was flashed briefly (30 ms) at positions co-linear with a bright inducing line presented upon a uniform, grey background. The co-axial distance (*d*) between target- and inducing line varied. In the control condition, the target was presented alone. Small, dark fixation lines of weak contrast indicated where the observer had to expect the target to appear. An inducing line of weaker contrast intensity and a line of much stronger intensity were presented in separate sessions.

3.1. Low-contrast inducing lines

Detection thresholds of the four observers as a function of the spatial separation between the target line and the inducing line of the lower contrast are shown in Fig. 2. The data of the four subjects are similar in every respect. Intra-individual variability of the thresholds did not exceed 5% of the threshold value in any of the data shown here. The horizontal lines in the graphs indicate the level of the detection threshold in the control condition, where the target line was presented without the co-linear inducing line. The results show that the detection of the target line is more strongly facilitated at the shorter spatial separations. The facilitating effects decrease with increasing spatial separation up to a limit of about 25 min of visual arc. At co-axial separations greater than 25′, facilitating effects of the inducing line are constant up to a spatial separation of about 150′, or 2.5° of visual angle, between the stimuli. This regime of constant detection facilitation describes a long-range integration domain beyond which thresholds rise again to the level of those measured in the control condition without inducing line.

3.2. High-contrast inducing lines

Detection thresholds of the three observers as a function of the spatial separation between the target line and the high-contrast inducing line are shown in Fig. 3.

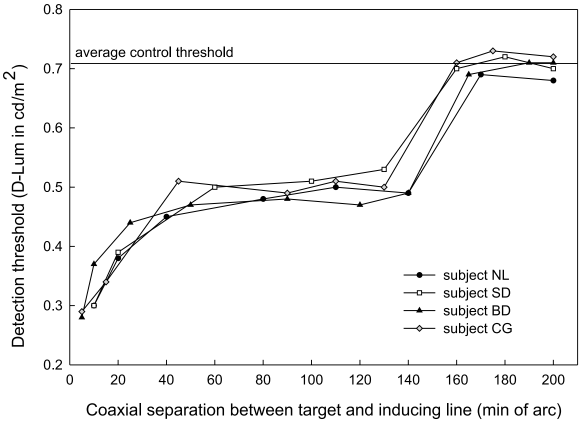

Fig. 2. Line contrast detection thresholds of observers SD, BD, NL, and CG, expressed as differences in luminance (D-lum) between the target and the background, as a function of the co-axial separation between the target- and the low-contrast inducing line. The upper horizontal line in the graph indicates the average detection threshold of the four observers in the control condition where the target line was presented without the co-linear inducing line. Line contrast detection is strongly facilitated up to about 25 min of visual arc (arcmin) of co-axial separation between the lines. Detection thresholds increase with the spatial separation between the stimuli until, at co-axial separations beyond 25′, a constant level of detection facilitation is observed, extending up to a distance of about 150′, or 2.5° of visual angle, between target and inducing line.

Intra-individual variability of the thresholds did not exceed 5% of the threshold value in any of the data shown here. The horizontal lines in the graphs indicate the level of the detection threshold in the control condition where the target line was presented without the co-linear inducing line. The results show that the detection of the target line is not, or only slightly, facilitated at spatial separations of 5′ between the target and the high-contrast inducing line. With subject DW, we observe a considerable masking effect at that separation. Facilitating effects are shown to appear at spatial separations beyond 10′. At co-axial distances longer than 25′, the facilitating effects of the inducing line are maximal and constant up to a spatial separation of about 150′, or 2.5° of visual angle, between the stimuli. This regime of constant detection facilitation describes effects similar to the long-range effects reported with the inducing line of lower contrast. Beyond the long-range regime, thresholds again rise to the level of those measured in the control condition without inducing line.

4. Discussion

The results of this study show that two types of effect can be identified in line contrast detection with co-linear target and inducing lines. Short-range effects, which are observed when the spatial gap between the lines is small

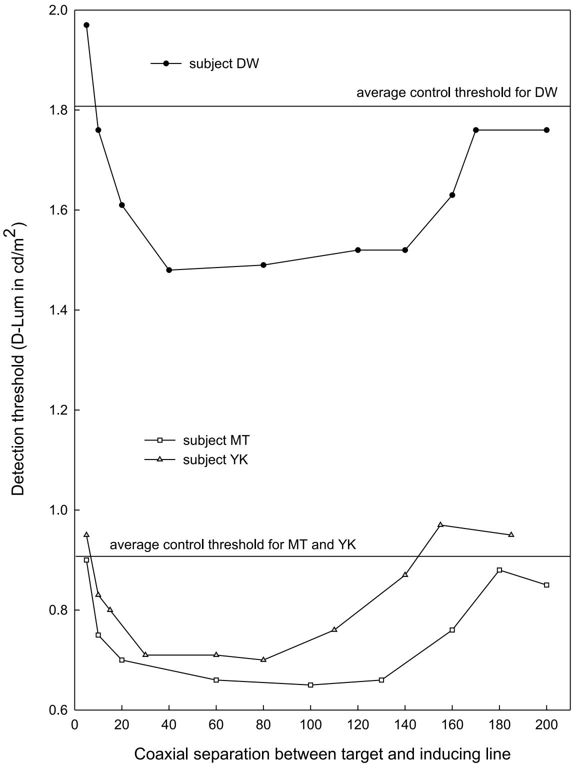

Fig. 3. This figure shows that facilitating effects are suppressed with an inducing line of high contrast up to about 25′ of co-axial separation between the stimuli. At a co-axial separation of 5′, a masking effect is shown in DW's data where thresholds are elevated to a value higher than the average control threshold. The suppressive effects decrease linearly until, at co-axial separations beyond 25′, a constant level of detection facilitation is again observed. As with the low-contrast inducing line, this long-range effect extends to a co-axial distance of about 150′, or 2.5° of visual angle, between target and inducing line.

and long-range effects, which are observed when the spatial separation is larger. The observations are consistent with earlier results by Wehrhahn and Dresp (1998) and with more recent findings by Brincat and Westheimer (2000) established by means of orientation discrimination measures. They corroborate the hypothesis that orientation integration follows two functionally distinct spatial regimes.

Brincat and Westheimer reported a spatial limit of roughly 15′ for short-range effects in orientation discrimination. Our data on line contrast detection suggest a limit of roughly 25′. This slight difference in results could be due to an effect of stimulus length on spatial interactions between co-linear lines. Brincat and Westheimer used lines that were 10′ long, our lines were 30′ (inducing line) and 15′ (target line) long. This could mean that, within some dynamic range of values that remains to be determined, longer lines would yield more extended short-range effects than shorter lines. Another possibility would be that line length per se has no effect and that orientation discrimination measures simply yield less extended short-range interactions than line contrast detection measures. Concerning long-range effects, our findings suggest a spatial limit of roughly 150′. The spatial limits of long-range interactions between co-linear orientations have thus far not been investigated systematically and conclusive data are therefore not available. However, some earlier findings with longer, edge-like inducers and longer target lines (Dresp & Grossberg, 1997) suggest that long-range interactions between co-linear orientations would be limited to roughly 150′, or 2.5° of visual angle, which is consistent with what we find here with noticeably shorter stimuli. How long spatially separated orientations would have to be to optimally probe long-range integration mechanisms is not known and remains to be investigated.

Our data clarify the effects of relative stimulus intensity as a function of the spatial separation between co-linear orientations. When target and inducing lines are separated by gaps smaller than 25′, target detection is most strongly facilitated by inducing lines of comparatively weak contrast, and tends to be suppressed by high-contrast inducing lines. This finding is consistent with observations reported by Polat and Sagi (1993) and Zenger and Sagi (1996), who used Gabor patches as stimuli. It also corroborates findings by Morgan and Dresp (1995) and Yu and Levi (1997), who used much shorter, co-linear lines and squares, or those by Wehrhahn and Dresp (1998), who used long, thick inducing bars and thinner, abutting target lines.

When target and inducing lines are separated by gaps larger than 25′, we find that detection facilitation is independent of the luminance intensity of the inducing line, showing that long-range interactions between co-linear orientations are insensitive to the contrast intensity of the stimuli. These findings, once again, bring to the fore that the, sometimes dramatic, effects found at smaller separations between orientations are cancelled out in the long-range spatial regime. Indeed, long-range effects always find expression in constant detection facilitation of similar amplitude independent of local attributes of the stimuli other than their co-linearity.

It is widely assumed that the physiological substrate of orientation integration across spatial gaps is identified in lateral interactions between neural ensembles in V1 (e.g. Brincat & Westheimer, 2000; Gilbert, 1998; Kapadia, Ito, Gilbert, & Westheimer, 1995; Polat, 1999). Assuming that both short-range and long-range orientation integration use such interactions seems plausible. We furthermore suggest that these interactions involve quantitatively and qualitatively different degrees and types of neural connectivity as the spatial separation between stimuli increases. Such a view is consistent with neuroanatomical data by Bosking, Zhang, Schofield, and Fitzpatrick (1997). Their study combined optical images of intrinsic signals with extra-cellular injections to quantitatively assess the specificity of horizontal connections with respect to both the map of orientation preference and the map of visual space in tree shrew striate cortex (Bosking et al., 1997). The findings distinguish local connections from their long-distance counterparts. The local connections appear to be less orientation specific than long-distance connections, which preferentially link larger numbers of neurons with co-oriented and co-axially aligned receptive fields or, in other words, exhibit a higher degree of iso-orientation connectivity. This difference in specificity of local and long-distance horizontal connections could reflect, as suggested by other neurophysiological studies (e.g. Albus & Whale, 1994), a difference in the relative contribution of excitatory and inhibitory neurons resulting in a larger contribution of inhibitory activity to the local connections (Bosking et al., 1997). Such a difference in the relative weight of inhibitory and excitatory connections may be the key to understanding why short-range interactions between co-linear orientations produce sometimes facilitating, sometimes suppressive effects, whereas long-range interactions exclusively produce facilitating effects. At shorter separations, co-linear orientations may selectively tap excitatory or inhibitory connections as a function of changes in local stimulus parameters, at larger separations between orientations such selectivity may no longer occur because the stimuli then tap a much wider network of mainly excitatory connections.

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