Contour Integration Across Polarities and Spatial Gaps: From Local Contrast Filtering to Global Grouping

BIRGITTA DRESP,* STEPHEN GROSSBERG†‡

This article introduces an experimental paradigm to selectively probe the multiple levels of visual processing that influence the formation of object contours, perceptual boundaries, and illusory contours. The experiments test the assumption that, to integrate contour information across space and contrast sign, a spatially short-range filtering process that is sensitive to contrast polarity inputs to a spatially long-range grouping process that pools signals from opposite contrast polarities. The stimuli consisted of thin subthreshold lines, flashed upon gaps between collinear inducers which potentially enable the formation of illusory contours. The subthreshold lines were composed of one or more segments with opposite contrast polarities. The polarity nearest to the inducers was varied to differentially excite the short-range filtering process. The experimental results are consistent with neurophysiological evidence for cortical mechanisms of contour processing and with the Boundary Contour System model, which identifies the short-range filtering process with cortical simple cells, and the long-range grouping process with cortical bipole cells. © 1997 Elsevier Science Ltd. All rights reserved.

Contour   Contrast detection   Bipole operators   Boundary contour system   Illusory contours

INTRODUCTION

Evidence that neurons in the visual cortex of the monkey start firing when a gap between collinear contour elements is presented within their receptive field (Peterhans & Von der Heydt, 1989; Von der Heydt & Peterhans, 1989; Grosof et al., 1993) suggests the existence of cortical mechanisms that "fill in the gaps" between stimulus elements defining the contour of forms and objects. It is likely that the perceptual completion of contours and presumably also the perception of illusory contours are determined by these mechanisms at early stages of visual information processing (Dresp & Bonnet, 1995; Grossberg & Mingolla, 1985a,b; Peterhans & Von der Heydt, 1989; Spillmann & Dresp, 1995). Recently, the role of cortical mechanisms in contour completion has been investigated further (Kapadia et al., 1995) in experiments measuring both the contextual sensitivity of

human contrast thresholds and of superficial layer complex cells in monkey V1. It was found that a human observer's line contrast detection is significantly improved by the presence of collinear, suprathreshold, context lines. The firing rates of complex cortical cells in the monkey showed the same contextual dependency on the relative location and orientation of the lines. The psychophysical findings confirm earlier observations on the effect of context lines on the detectability of a small light target (Dresp, 1993), and are consistent with the fact that collinear stimuli which induce the perception of an illusory contour make thin lines detectable which are not detected when presented out of context (Dresp & Bonnet, 1995).

In this study, we investigate the functional characteristics of the integration of thin line targets presented within or without a visual context consisting of contour segments, the spatial arrangement of which additionally gives rise to the perception of illusory contours. Our experiments address two crucial questions:

*Laboratoire de Psychophysique Sensorielle L.N.2C., URA 1939 C.N.R.S., Université Louis Pasteur, 12, rue Goethe, 67000 Strasbourg, France.
†Department of Cognitive and Neural Systems and Center for Adaptive Systems, Boston University, 677 Beacon Street, Boston, MA 02215, U.S.A.
‡To whom all correspondence should be addressed [Email steve@cns.bn.edu].

1. Does the visual integration of contour elements depend on the relative contrast polarity of the context and the target elements?
2. To what extent do alignment and spatial separation of context and target segments influence this integration?

Contrast detection, contour integration, and illusory contours

Data from psychophysical studies using increment threshold procedures, contrast detection, and subthreshold summation techniques (Dresp, 1993; Dresp & Bonnet, 1991, 1993, 1995; Dresp & Grossberg, 1995; McCourt & Paulsen, 1994; Polat & Sagi, 1993, 1994; Tassi *et al.*, 1995) suggest that facilitatory, or cooperative, neural interactions generate the integration of contour information in the human brain. The general evidence from these studies is described by the fact that the threshold for the detection of a contrast target is lowered when the latter is presented right on the gap which separates aligned stimulus features, some of which additionally induce the perception of an illusory contour. Although spatial interactions that facilitate contrast detection do not require the phenomenal emergence of illusory contours, it can be assumed that their genesis is, at least partly, dependent on the mechanisms probed by these interactions (see Spillmann and Dresp, for a review).

Dresp (1993), Morgan and Dresp (1995), and Kapadia *et al.* (1995) have explained contrast detection facilitation with spatially separated targets and inducers on the basis of coactivation and interaction of multiple cortical detectors tuned to the same orientation. This interpretation is consistent with neurophysiological evidence for long-range interactions between functionally identified neurons in cat visual cortex (Gilbert & Wiesel, 1990; Das & Gilbert, 1995). Evidence for a hierarchical organization in terms of "from-simple-to-complex-cell" processing stages is available (e.g. Gilbert & Wiesel, 1985) and the relevance of these neurophysiological data for the psychophysics of contour integration requires a closer examination of the effects of relative target/inducer polarity.

The role of contrast polarity

Paradoxically, with a tiny circular light probe as target (Dresp, 1993; Morgan & Dresp, 1995), facilitatory effects of collinear context lines do only seem to occur when the target and the inducer(s) have the same contrast polarity. However, when the target is a small line, the facilitatory effect is not specific for a given direction of target/inducer contrast. In other words, an illusory contour induced by stimulus elements of any contrast polarity facilitates the detection of a target line of any contrast polarity (Dresp & Bonnet, 1995; Dresp & Grossberg, 1995). This difference in results suggests that a small, nonoriented probe presumably activates an earlier stage of processing than a line target. Morgan and Dresp (1995) suggested that a first step in contour integration by the human visual system is concerned with the filtering of local contrasts that "belong" to the same contour, or axis of alignment. In fact, when a target and an inducer of the same contrast polarity stimulate the same receptive field, the inducer would act as a luminance "pedestal" that increases the contrast sensitivity of the detector (simple cell), which would explain

why the target is detected at lower intensities when the inducer is present. "Pedestal" effects, or contrast detection facilitation, have been reported earlier for spatially superimposed stimuli. Their implication for models of contrast detection and discrimination are extensively discussed by Foley and Legge (1981).

The extent to which "pedestal" effects matter in contour integration becomes even clearer when detection performances with targets and inducers of the same contrast polarity are compared to performances with targets and inducers of opposite contrast polarity. Facilitation of the detection of a target line has been found to be systematically greater with collinear inducers of the same contrast polarity (Dresp & Bonnet, 1995). When all signs are the same on a given contour axis, simple cells with receptive fields falling on that axis should get more input and may therefore send stronger signals to "collectors" which do not take into account the sign of contrast (complex cells). This interpretation of Dresp and Bonnet's findings (Dresp & Bonnet, 1995) is consistent with neurophysiological data (e.g. Gilbert & Wiesel, 1985) and with current models of contour integration across spatially distributed contrasts of varying polarity (e.g. Grossberg & Mingolla, 1985a,b).

Spatial separation

The spatial limits of contour integration depend on the type of mechanism that is activated by a given configuration of contour elements. Some psychophysical findings indicate that the perceptual grouping of scattered dots into lines is more sensitive to the spatial separation of the individual elements than the grouping of line segments (Dresp *et al.*, 1996). The size of the individual features also seems to matter (Zucker & Davis, 1988). Facilitatory interactions between targets and inducers in contrast detection tasks are found to be sensitive to spatial separation, however, without leading to any general conclusion (Dresp & Bonnet, 1991, 1993, 1995; Morgan & Dresp, 1995). The same holds for the effects of alignment. The findings by Dresp and Bonnet (1995) and Kapadia *et al.* (1995) suggest that the collinearity of targets and inducers is a requirement for detection facilitation, but complex geometrical configurations other than collinear lines or edges have thus far not been tested.

The various effects of spatial separation and spatial arrangement of contour features on their integration by the human visual system has remained one of the challenging problems in visual psychophysics. The Grossberg and Mingolla (1985a,b) and Grossberg (1987) neural model of preattentive form vision was one of the first to deal with the problem of spatial constraints, such as the spacing and perceptual relatedness of features, within a computational approach that simulates interactions between functionally identified cortical detectors. The model proposes that contour integration across space by the visual system is achieved via at least two successive stages of orientation selective processes. The first stage involves a short-range process

that is sensitive to polarity, and the second stage a long-range process that is insensitive to contrast polarity. The latter involves bipole detectors which receive input of either sign from the short-range process. Detectors with the largest amount of input "win" in the final grouping process. Neurophysiological evidence for the existence of these detectors in the visual cortex has been reported by Von der Heydt *et al.* (1984), who found neurons in V2 (monkey) with receptive field properties similar to the functional characteristics of bipole operators.

Two hierarchically dependent stages of contour integration across space?

As already mentioned above, the detectability of targets presented within a contour-context varies as a function of the combination of target/inducer polarity. The fact that like-contrasts, in other words inducers of the same sign as the target, yield stronger facilitatory interactions than inducers of opposite polarity suggests that both types of spatial interaction occur at hierarchically different levels of processing. The first level would be concerned with the filtering of local contrasts of the same sign, the second with the processing of the output signals from the first level, regardless of their sign. In this way, the visual system would be able to "reconstruct" contour information across space and contrast sign. Such a multi-stage processing approach to contour grouping was first introduced by Grossberg (1984), Cohen and Grossberg (1984), and Grossberg and Mingolla (1985a,b).

Recently, Dresp *et al.* (1996) have shown in two separate experiments that response times to virtual contours induced by features of opposite polarity are generally longer than response times to brightness distributions induced by configurations of homogeneous contrast polarity, which supports the idea of two hierarchically different stages of perceptual grouping. The earlier one appears to yield faster decisions than the later one, which is consistent with the idea of short-range and long-range operating principles underlying perceptual grouping. Finally, a two-stage integration hypothesis is plausible with regard to neurophysiological findings showing intrinsic connectivity between contrast selective neurons and contrast insensitive neurons in the visual cortex (e.g. Gilbert & Wiesel, 1985).

The following experiments were designed to disentangle these two stages of contour integration by designing displays in which both stages should be strongly activated, and comparing their perceptual effects with displays in which the second stage, but not the first stage, is strongly activated. This was achieved by measuring thresholds for the detection of a small target line of varying contrast polarity (Experiment 1) presented within a contour context. In one of the conditions, half of the target line (Experiment 2) had the same contrast polarity as the nearest inducer (stage 1 and 2 strongly activated). In another condition it had the opposite contrast polarity compared to that of the nearest inducer (only stage 2 strongly activated). If the second stage of
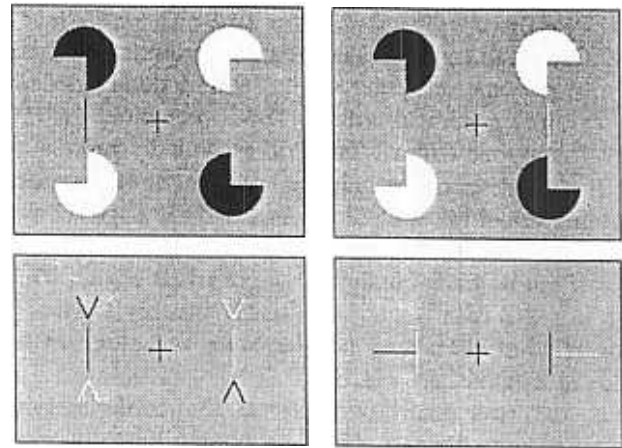

FIGURE 1. The stimuli used in the first experiment. In the test conditions, black and white subthreshold lines were flashed on illusory contours induced by collinear edge fragments of alternating contrast polarity. In the control conditions, the lines were presented either between two collinear "v"-endings of alternating polarity, or at a position adjacent to the end of a perpendicular suprathreshold line of varying contrast polarity.

processing depends directly on input from the first stage, we expect that stronger facilitatory effects on target detection occur in the case of locally grouped like-contrasts. The extent to which these facilitatory effects depend on the alignment of the contextual contour elements (Experiment 3) and their spatial separation (Experiment 4) was also assessed.

EXPERIMENT 1

Dresp and Bonnet (1995), and Dresp and Grossberg (1995) showed that a thin subthreshold line flashed on an illusory contour induced by collinear stimulus fragments makes (1) the illusory contour more discriminable, and (2) the subthreshold line detectable, depending on the instruction given to the observer. The psychometric functions for contour discrimination and line detection were found to be very similar. The facilitation effect is, for discrimination as well as for detection, stronger when the line and the inducers have the same contrast polarity. In the following experiment, a thin subthreshold line of either contrast polarity was flashed on illusory contours induced by collinear stimulus fragments of opposite contrast polarity. The aim of this first experiment was to provide the evidence that the observations made with collinear inducers of a given contrast polarity (Dresp & Bonnet, 1995) also hold in the case of inducers with opposite polarity.

Subjects

Four observers (PA, PT, DP, and BD), including one of us, participated in the experiment. They all had normal or corrected-to-normal vision and were trained in detection tasks. Two of them (PT and DP) were naïve to the purpose of the study.

Stimuli

The stimuli (see Fig. 1) were presented binocularly on a monochrome computer screen (60 Hz, noninterlaced). They were generated with an IBM compatible PC (HP 486), equipped with a VGA Trident graphic card.

The diameter of the inducing elements in the context-contour condition was 30 min arc, and the edges of two collinear inducers were separated by a gap of 1 deg of visual angle. Each configuration consisted of one white inducer $(10 \, cd/m^2)$ and one black inducer $(4 \, cd/m^2)$, presented at alternating positions (top or bottom of the illusory contour, see Fig. 1).

In the two control conditions, the configurational stimuli were either a black or white line presented perpendicularly to the subthreshold line, or two black and white "v" endings presented at the ends of the subthreshold line (see Fig. 1). Dresp and Bonnet (1995) have shown that such controls reduce spatial uncertainty concerning the position of the line target, but in no case make the subthreshold target become detectable. In these previous experiments, the authors used the same kind of stimuli, same luminances, same procedure, same apparatus, and one subject (subject BD) from the present study, and compared performances in a control condition to performances with the subthreshold line presented alone on a blank field. The differences between these two conditions were found to be negligible (see Dresp & Bonnet, 1995).

Luminance values were the same as in the test condition. Subjects PA, PT, and DP were given the first control condition, subject BD did the control with the "v" endings (see also Dresp & Bonnet, 1995). Background luminance was $6.73 \, cd/m^2$. The subthreshold line had the same length as the illusory contour upon which it was added (1 deg of visual angle) and varying luminance, either darker or lighter than the gray background. Effects of black and white subthreshold lines were investigated separately, the corresponding luminance levels being presented in random order (method of constant stimuli) within sessions consisting of 100 trials each. Subjects BD and PA were tested with white lines of 6.85, 6.91, 6.97, 7.03, and $7.09 \, cd/m^2$, and black lines of 6.37, 6.43, 6.49, 6.55, and $6.61 \, cd/m^2$. Subject PT was tested with these same luminance levels plus one more for each polarity (7.15 and $6.31 \, cd/m^2$). Subject DP was tested with white lines of 6.97, 7.03, 7.09, 7.15, and $7.21 \, cd/m^2$, and black lines of 6.25, 6.31, 6.37, 6.43, and $6.49 \, cd/m^2$. Although the range of luminances varied between observers as a function of their individual thresholds for the detection of the lines on a plain background, a black line and a white line always had identical Weber contrast at a given intensity level, for a given observer. In total, 75 linearly increasing/decreasing luminance steps were calibrated with a Minolta photometer, and the values used in the experiments here were chosen from this calibrated set. The illusory contours and the subthreshold line appeared simultaneously on the screen for about 350 msec at each trial and the viewing distance was 75 cm. The inter-stimulus interval was about 800 msec.
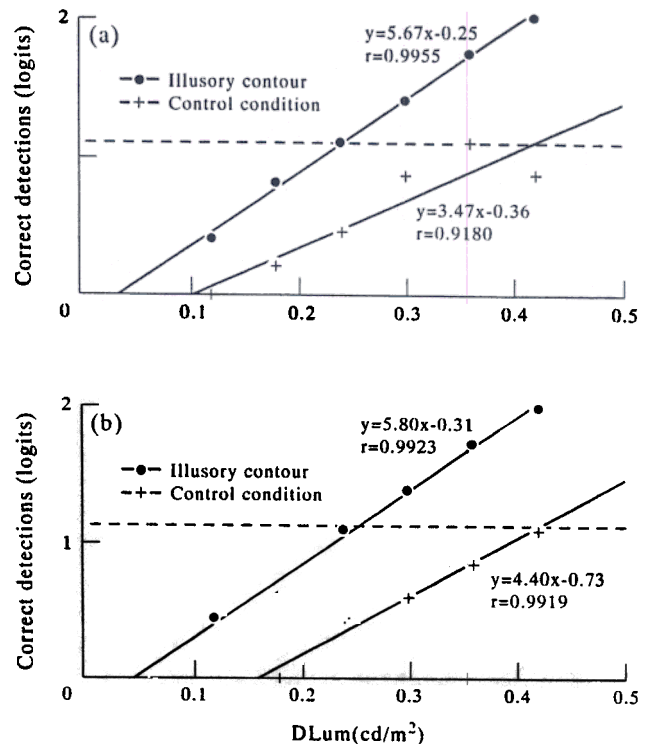

FIGURE 2. (a) Results of one of the four observers from the first experiment with white subthreshold lines (100 measures per datapoint). "DLum" on the abscissa refers to the luminance difference between the target line and the background. Illusory contour discriminability increases with increasing luminance of the line. In the control conditions, the lines were generally not detected at the luminance intensities used in the experiment. The data indicate that performances in the illusory contour discrimination task are facilitated by the presence of a white subthreshold line on one of two contours induced by collinear edge fragments of opposite contrast polarity. (b) Results of one of the four observers with black subthreshold lines (100 measures per datapoint). Again, illusory contour discriminability increases with increasing line luminance, the lines being generally not detected in the control conditions. The data indicate that illusory contour discrimination is facilitated by the presence of a black subthreshold line on one of the contours. A comparison of (a) and (b) indicates that the effects observed with black and white lines, presented at identical Weber contrast for a given luminance difference with regard to the background are, as expected, equivalent.

Procedure

The subthreshold line was added randomly to one of two illusory contours presented simultaneously on the screen (see Fig. 1) and was always aligned with the edges of the inducers. The observers had to press one of two response keys to indicate whether it was the left or the right contour that appeared more visible to them. Each response that corresponded to the perception of a stronger contour on the side where the subthreshold line was added was counted as a "correct detection". In the two control conditions, where no illusory contour was generated, observers had to indicate on which side (left or right of the fixation mark) they suspected the presence of a subthreshold line perpendicular to the suprathreshold line (control 1), or between the two "v"-endings (control 2). The luminance of the subthreshold line varied randomly within a given session consisting of 100 or

120 (observer PT) trials. Each subject was trained in two sessions for each experimental condition and was then run in two (DP), three (BD and PA) or four (PT) test sessions.

Results and discussion

The general results of the first experiment are represented in Fig. 2. The percentage of "correct detections" was calculated for each observer and experimental condition. In the context-contour condition, "correct detection" means that the observer perceived the contour as stronger on the side where the subthreshold line was added. In the control condition, a correct detection means that the observer correctly suspected the presence of a subthreshold line on the side where it was presented. Response probabilities were transformed into logit values and plotted as logistic functions of the difference between the luminance intensity of the subthreshold line and the luminance intensity of the background. For the transformation of the data, the following formula was used: $\text{logit}_{(pi)} = \ln(pi/1 - pi)$, where pi is the probability of correct detection of the subthreshold line for a given observer within a given experimental condition. Each graph shows the data and the psychometric functions with a correlation indice (r) and the parameters (slope and intercept) for the calculation of the theoretical "detection" thresholds. The horizontal lines in the graphs indicate the logit value (1.09) that corresponds to a probability of "correct detection" of 0.75.

Performances of illusory contour discrimination with a white subthreshold line are represented in Fig. 2(a). The data of the four observers show that adding a white line to an illusory contour induced by collinear fragments of alternating contrast polarity systematically strengthens that contour and that this effect increases with increasing luminance of the line. In the control conditions where observers had to detect the white line at a position perpendicular to a white or black suprathreshold line (subjects PA, DP, and PT), or in between two "v"-endings of alternating polarity (subject BD), performances are relatively poor. This indicates that the line is indeed presented at subthreshold intensities, which means that it is hardly, if at all, detectable without the illusory contour at the luminance levels used in this experiment. Comparison of the theoretical thresholds (indicated in the graphs) for the "detection" of the line in the two conditions shows that they are systematically lower when the line is presented on an illusory contour. These differences in thresholds between conditions vary slightly with the observers between 0.1 and 0.25 cd/m².

Performances of contour discrimination with a black subthreshold line were basically the same [Fig. 2(b)]. The data show that adding a black line on an illusory contour induced by collinear stimulus fragments of alternating contrast polarity systematically strengthens that contour. As with the white lines, this effect increases with increasing difference between the luminance of the line and that of the background. In the control conditions, the
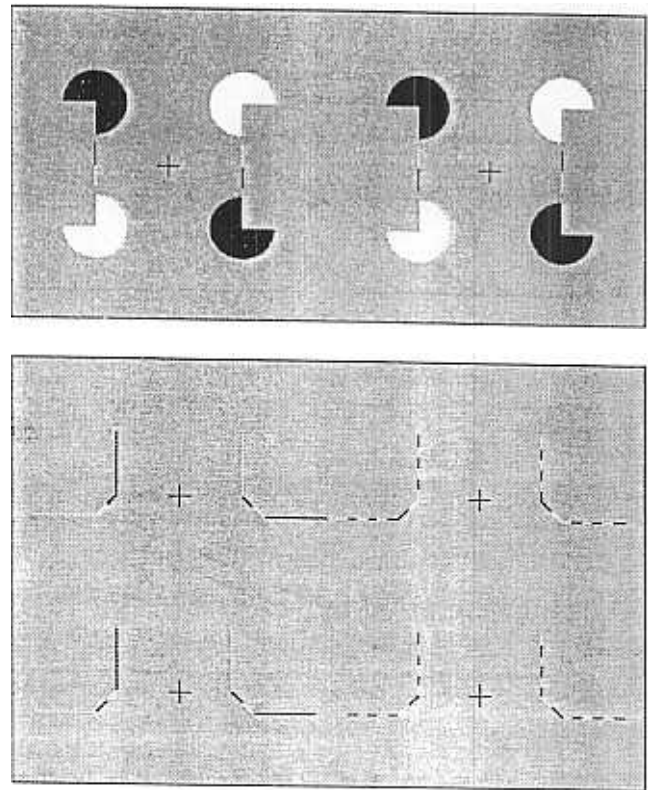

FIGURE 3. The test stimuli used in the second and third experiment. The polarity of half the subthreshold line presented on illusory contours induced by collinear fragments or line-ends of opposite contrast polarity was either the same as the polarity of the nearest inducer or not. In the third experiment, a condition with inducing lines made of line segments with alternating polarity was added. In this case, observers generally do not see illusory contours. Here, the polarity of half the subthreshold line either matched the polarity of the nearest line segment or not. In the control conditions, two very short segments, or two small dots were used as context to reduce spatial uncertainty.

line is not detectable at the luminance levels used in this experiment. Comparison of the theoretical thresholds revealed that they are systematically lower when the line is presented on an illusory contour. The differences in thresholds vary between 0.1 and 0.25 cd/m² as a function of the observer. Generally, performances with the black line were, as expected, equivalent to those observed with the white line, presented at identical Weber contrast. The overall difference between thresholds measured on illusory contours and thresholds measured in the control conditions is, as expected, statistically significant: $F(1,3) = 21.5$; significant at $P < 0.01$.

The results of this first experiment show that a white or a black subthreshold line enhances the discriminability of a virtual contour induced by collinear stimulus fragments of alternating contrast polarity.

EXPERIMENT 2

In the second experiment, the same inducing configurations were used. This time, the contrast polarity of the subthreshold lines was varied to produce situations in which half of the line had the same polarity as the nearest
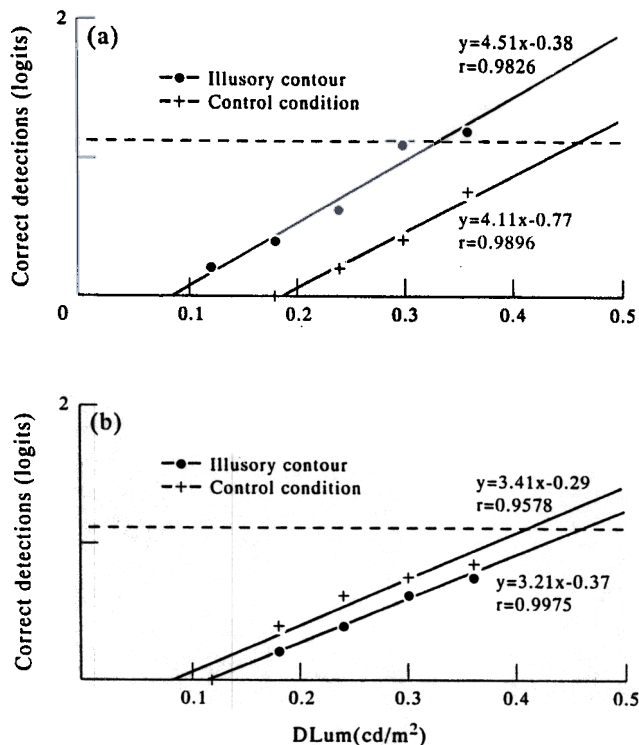
FIGURE 4. The results of one of the four observers from the second experiment in the condition where the polarity of half the subthreshold line matched the polarity of the nearest inducer (a). In this case, illusory contour discrimination is facilitated by the fractioned subthreshold line. In the control conditions, the line is not detected. (b) Results of one of the four observers from the second experiment in the condition where the polarity of half the subthreshold line and the polarity of the nearest inducer were not the same. The data show that the facilitatory effect of the subthreshold line in the discrimination task is destroyed. Observer BD did slightly better in the control condition than in the context-contour discrimination task.

inducers and others where half of the subthreshold line and the nearest inducer had opposite contrast polarity. The aim of this second experiment was to demonstrate the importance of local contrast grouping, which can be supposed to be a first critical step in contour integration across spatial gaps. Only in the case where half of the subthreshold line has the polarity of the nearest inducer is local contrast grouping possible. This should be the condition "*sine qua non*" for all the further steps of processing, namely those involving cooperation of detectors that integrate contour information across polarities.

Subjects

The same four observers participated in the second experiment.

Stimuli and procedure

Inducing stimuli and control conditions as well as the luminance values were identical to those in Experiment 1. In this second experiment, the contrast polarity of the subthreshold lines was varied as follows: half of the line was always white, and the other half always black. In one condition, the polarity of half the line was the same as the polarity of the nearest inducer, in the other condition half of the line and the nearest inducer had opposite contrast polarity (see Fig. 3). Instructions and procedures were identical to those described for Experiment 1.

Results and discussion

The results of this second experiment with the same four observers are represented in Fig. 4(a and b). The graphs in Fig. 4(a) show that illusory contour discrimination is facilitated by a subthreshold line when half of the line has the polarity of the nearest inducer. This effect increases with increasing difference in luminance between the line and the background. Results from the control conditions without illusory contours show that the line was not detected by three of the four observers (PT, BD, and DP). Subject PA performed at detection threshold ($pi = 0.75$) when the line was presented at the highest luminance of the individual range of intensities used. The difference between thresholds obtained with locally corresponding polarities and thresholds measured with locally antagonistic polarities is statistically significant: $F(3,9) = 10.3$; significant at $P < 0.01$. However, the slight occasional differences in the slopes of the psychometric functions (illusory contour conditions versus control conditions) are nonsignificant. This is important because it indicates that the superiority of discrimination performances in the illusory contour conditions is criterion-free, in other words, not related to any kind of decision bias or response strategy.

When polarities were not matched, in other words, when half of the subthreshold line and the nearest inducer had opposite contrast sign, performances in contour discrimination were as poor as those in line detection in the control conditions [see the figures in Fig. 4(b)]. The differences between the two experimental conditions were negligible and nonsystematic, indicating that the subthreshold line did not significantly strengthen the illusory contour upon which it was added. However, context-contour discriminability increases with the intensity of the line, but in much the same way as line detectability *per se*. Observers BD and DP even seemed to do better in detecting the line in the control conditions, and the results seem to indicate a slight inhibitory effect of the line on illusory contour discrimination. Interestingly, in some sessions discrimination performances did not exceed 30% of "correct detection" of the illusory contour upon which the line was added, which means that in these cases the illusory contour without the line was perceived as stronger in 70% of trials. Although these partial observations tend to suggest an inhibitory influence of the subthreshold lines when their contrast polarities do not match those of the nearest inducers, it is not possible to draw any further conclusions here, given that such a pattern of results did not occur systematically. Consequently, we decided to repeat these "deviant" sessions and to take into account only those with performances situated around or beyond the "50% correct" barrier for data analysis and curve fitting.

EXPERIMENT 3

Generally, facilitatory interactions observed in different experiments have revealed that an illusory contour is functionally defined by the prolongation of the lines of pixels which constitute the inner borders of two collinear inducing elements in the Kanizsa square (Dresp & Bonnet, 1995), or by the shortest distance between the ends of two inducing lines in other figures. Previous results obtained with a subthreshold method similar to the one used here (Tassi et al., 1995) suggest that early contour information in Ehrenstein figures, for example, induced by lines of varying contrast polarity, is generated by detectors with the operating characteristics of bipole operators as defined by Grossberg and Mingolla (1985a, b) and Grossberg (1994).

In this experiment, the measures were extended to illusory contours arising from line inducers, as those that can be seen in the Ehrenstein illusion, for example. In the latter, the prominent early contour information appears to be provided by operators linking directly the ends of the inducing lines two by two (Tassi et al., 1995) although, phenomenally, the shape of the contour is ambiguous (Day & Jory, 1980; Spillmann & Dresp, 1995).

We flashed subthreshold lines on the gap separating the ends of two line inducers of alternating contrast polarity. Polarity was either homogeneous within a given inducing line, or alternating also within the line. Consequently, local contrast grouping was possible only in the condition where half of the subthreshold line and the nearest inducer had the same contrast sign, and where polarity did not vary within the inducing line itself. Thus, the effect of the subthreshold line on the strength of contour grouping was expected to be strongest in this case. Incidentally, direct estimation experiments have shown that inducing lines made of line segments of alternating polarity like the ones used in one condition of this experiment do not give rise to the perception of illusory contours or brightness enhancement (Dresp et al., 1996).

Subjects

Two of the four observers (PA and BD) from the previous two studies, including one of us, participated in the experiment.

Stimuli and procedure

Figure 3 shows the stimuli used in this experiment. The inducing lines had a length of 30 min arc. They were either black and white (condition 1) or made of line segments of alternating contrast polarity (condition 2). In the control conditions, either two small (about 3 min arc) dots of alternating polarity were presented at the ends of the subthreshold line (observer BD), or one of the inducing lines was presented alone (observer PA). The length of the gap between two lines of a given configuration was 30 min arc. In one condition, the polarity of half the subthreshold line had the polarity of the nearest inducer, in the other condition, half of the subthreshold line and the nearest inducer had opposite contrast polarity. All luminance values were identical to
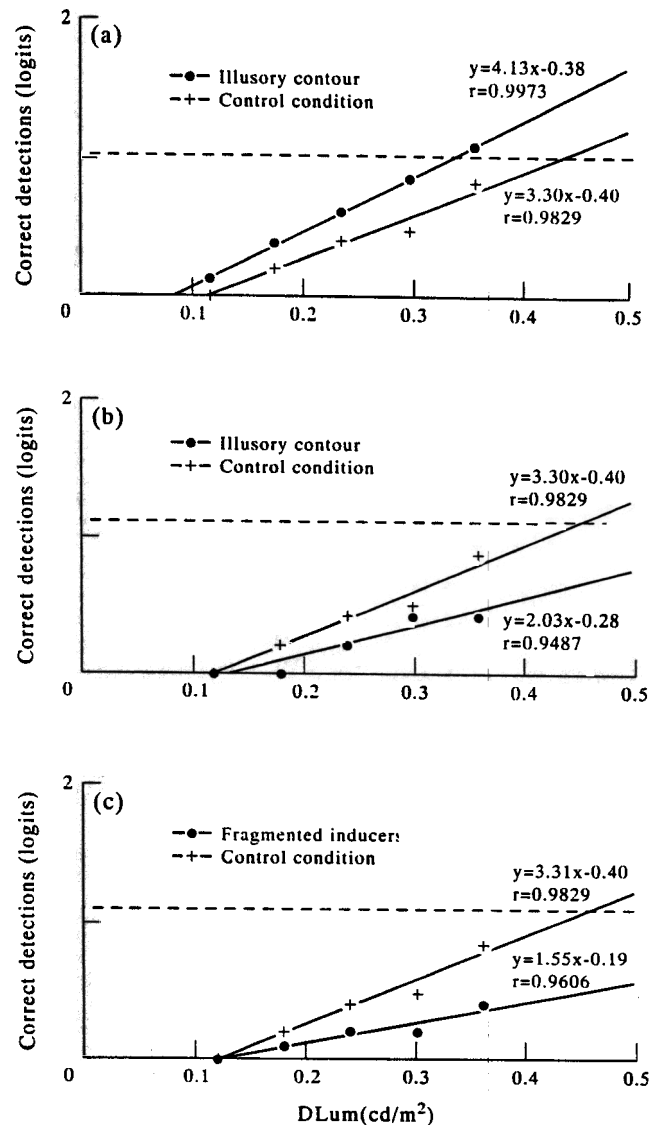

FIGURE 5. The results of one of the two observers from the third experiment with the Ehrenstein contours when the polarity of half the subthreshold line matched the polarity of the nearest inducing line (a). Contour discrimination is found to be facilitated by the line which was not detected in the control conditions, as shown in the graphs. As already seen in the Kanizsa displays, the facilitatory effect of the subthreshold line disappears when its polarities do not match those of the inducing lines (b). The experiment with inducing lines made of small segments with alternating polarity revealed that performances in the contour discrimination task were generally slightly worse compared to those in the control conditions. The data of one of the two observers are shown in (c).

those used in the previous two experiments and so were the instructions and procedures.

Results and discussion

Some of the results of the third experiment are represented in Fig. 5(a and b). When the inducing stimulus is made of two lines with opposite contrast polarity, contour discrimination is found to be facilitated by the presence of a subthreshold line, the polarities of which locally correspond to those of the inducers [Fig. 5(a)]. As in the experiments with collinear inducers
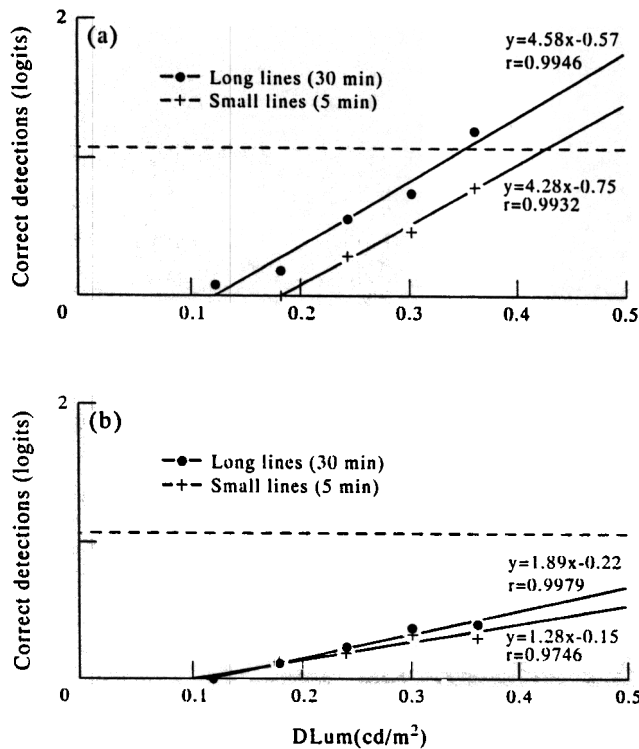
FIGURE 6. In Experiment 4, we varied the length of the inducing lines from Experiment 3, and the size of the gap separating the inducing lines. The data (subject PA shown here as example) in the condition where the polarities of the subthreshold line matched the polarities of the inducers (a) indicate that, at a gap size of 1 deg of visual angle, contour discriminability is better with longer inducing lines (30 min - arc). In the condition where polarities did not match (b), the advantage of the longer lines in contour discrimination is no longer observed.
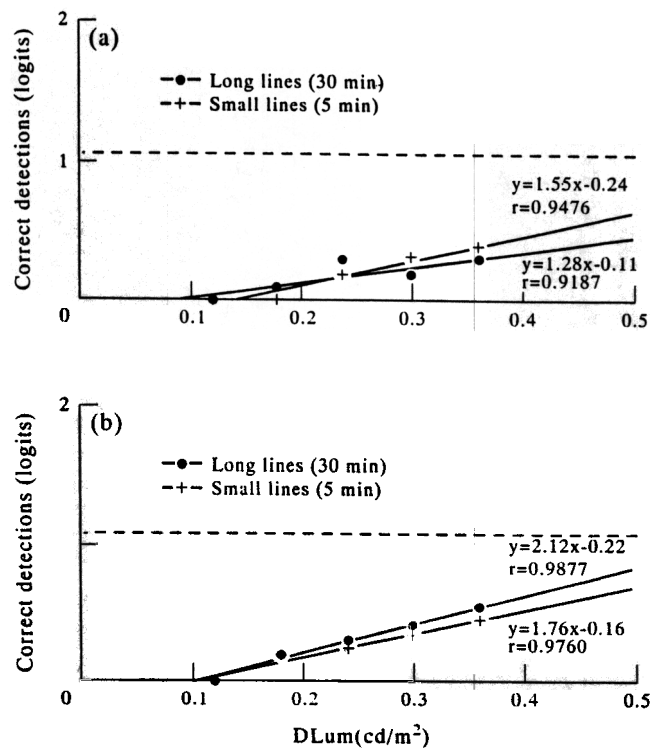
FIGURE 7. Results (subject PA and subject BD) with a spatial separation of 2.5 deg between inducing lines when polarities were locally matched. No facilitatory effect on the discrimination of the context-contours is observed any more.

of the Kanizsa type, illusory contour discriminability increases with the luminance of the subthreshold line. In the control conditions, the line is not detected at the intensities used in the experiment. When the contrast polarities of the lines do not match those of the inducers, this effect is absent [Fig. 5(b)]. The graphs show that in this case illusory contour discriminability is not better than line detectability *per se*. For subject PA (his data not shown in the figures) it was even slightly worse.

When the inducing lines are made of line segments with alternating contrast polarity, context-contour discriminability and line detectability (control condition) are equivalent for observer BD when the polarities of the line locally corresponded to the polarities of the nearest line segments, and only in this case. Observer PA had, in both cases, great difficulty in discriminating context-contours and his performances are generally better for line detection in the control conditions. Both observers performed entirely at chance level in the condition where the polarities of the subthreshold line did not locally correspond to the polarities of the nearest line segment. No psychometric function could be fitted to the data in this case. The conclusion here is that the fragmented inducers do not produce groupings or illusory contours in the first place (Dresp *et al.*, 1996) and that, therefore, the

subthreshold line did not produce the effects observed in the previous experiments.

EXPERIMENT 4

In this experiment, we increased the spatial separation of the inducers and the length of the subthreshold line. The inducing lines were either relatively long or very small to test for combined effects of spatial separation and inducer length [see also Lesher & Mingolla (1993) or Dresp *et al.* (1990)]. Previous results suggest that the spatial limits of contour integration across gaps lie beyond 2 deg of visual angle (e.g. Dresp & Bonnet, 1995).

Subjects

The experiment was run with the same observers as Experiment 3 (PA and BD).

Stimuli and procedure

The size of the gap separating a black and a white inducing line was 1 deg of visual angle in one condition and 2.5 deg in the other. The polarity of half the subthreshold line was either the same as the polarity of the nearest inducer or not. The length of the longer inducing lines was 30 min arc, and that of the shorter inducers 5 min arc. Instructions and procedures were identical to those in Experiment 3.

Results and discussion

Some of the results of the fourth experiment are represented in Fig. 6(a and b) and Fig. 7(a and b). When the inducers were longer, and the polarities of the subthreshold line locally corresponded to those of the nearest inducer, context-contour discrimination was more strongly facilitated by the subthreshold line than in the condition where the inducers were shorter [see the figures in Fig. 7(a)]. This difference between conditions was not observed with a gap size of 2.5 deg of visual angle [see Fig. 6(a)]. Furthermore, when the polarity of the subthreshold line did not locally correspond to that of the nearest inducer, performances were identical in the two gap size conditions, regardless of the length of the inducers [compare Fig. 6(b) and Fig. 7(b)]. We feel that the observers could not help doing line detection rather than contour discrimination in these conditions because illusory contour information was no longer available. Generally, the findings tend to indicate that the spatial limit of illusory contour integration with inducers of opposite contrast polarities in Ehrenstein figures is attained at 2.5 deg of visual angle and perhaps even at a smaller gap size. This limit might also slightly depend on the length of the inducing lines (e.g. Shipley & Kellman, 1992), but not necessarily (see Lesher & Mingolla, 1993). It can be assumed that the subthreshold paradigm will allow a very precise test of the spatial limits of contour integration in various figure conditions, including illusory figures, in further experiments.
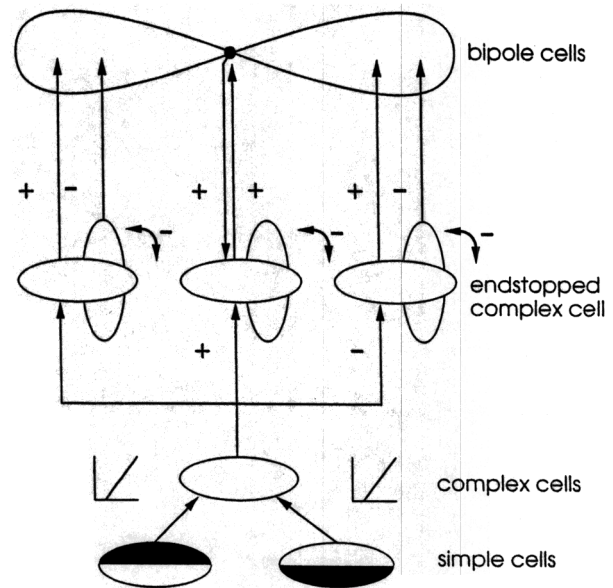

FIGURE 8. Simple cells compute local oriented contrast. They are sensitive to contrast polarity. Their activities are half-wave rectified to generate output signals. Oppositely polarized simple cell outputs activate complex cells. Complex cells activate spatial and orientational competition among endstopped complex (or hypercomplex) cells. Hypercomplex cells excite bipole cells with similar orientational preference and inhibit bipole cells with (nearly) perpendicular orientational preference. Coactivation of of the branches of bipole cell receptive fields generates feedback that initiates the long-range grouping process.

GENERAL DISCUSSION

The present experimental results suggest that contour grouping by the human visual system depends on interactive and presumably hierarchically organized mechanisms. An early stage seems to consist of the filtering of spatially distributed contrast information of the same sign that has to be organized according to certain rules of stimulus geometry. The alignment of lines, edges, or line-ends appears to be of crucial importance, given that stimulus conditions wherein oriented inducers cannot be linked by a straight axis (see the control conditions) do not produce local groupings that find expression in locally lowered thresholds for target detection (Dresp & Bonnet, 1991, 1993; Kapadia *et al.*, 1995). At this stage of processing, detection facilitation (e.g. Foley & Legge, 1981; Dresp, 1993; Kapadia *et al.*, 1995) or masking (Foley & Legge, 1981; McCourt & Paulsen, 1994; Morgan & Dresp, 1995) of spatially coextensive targets may occur, depending on the intensity of the inducer contrast.

At the second stage, contrasts of either sign are grouped and the detection of spatially coextensive targets is facilitated, provided the first mechanism can be activated. The efficiency of a given stimulus configuration in triggering this local-to-global grouping chain depends on spatial separation and relative inducer length. Although further research is clearly necessary to find out whether any general rule for contour integration across

polarity and space, such as a constant inducer-size/gap-size ratio (Grossberg, 1987; Shipley & Kellman, 1992), can be assumed, the present data (Experiment 4) tend to suggest that beyond 2.5 deg of spatial separation, contour information may not be grouped by the visual system, regardless of relative target/inducer polarity and regardless of the length of the inducers.

The present experimental results are consistent with a prediction of the Boundary Contour Systems or BCS model that motivated the experimental design. In the BCS model, a stage of short-range oriented filtering which is sensitive to contrast polarity feeds a stage of long-range oriented grouping which pools inputs from opposite contrast polarities. The short-range stage is identified with simple cells in cortical area V1. The long-range stage is identified with bipole cells in cortical area V2, whose properties were predicted by the model (Cohen & Grossberg, 1984; Grossberg, 1984; Grossberg & Mingolla, 1985a, b) just as they were experimentally reported (Von der Heydt *et al.*, 1984).

Bipole cells have two oriented receptive fields that are (approximately) colinear with their preferred orientational sensitivity. These cells fire when both receptive fields are sufficiently activated (Fig. 8). Bipole cells respond to both contrast polarities because they occur subsequent to the complex cell stage, at which half-wave rectified outputs of oppositely polarized simple cells are added. The net effect is that complex cells perform an oriented full-wave rectification of the image, as in the

texture models of Sutter *et al.* (1989) and Chubb and Sperling (1989). Bipole cells inherit this property.

Some finer properties of the data are also consistent with model properties, but further experiments would be needed to disentangle the several possible contributing factors. A key issue concerns why, as in Experiment 2, there is sometimes a slight inhibitory effect of the line on illusory contour discrimination. In this experiment, the subthreshold line was broken into two or more fragments that were arranged to have like-polarity or opposite-polarity with respect to the nearest illusory contour inducer.

An inhibitory effect could, in principle, be caused by either boundary or surface properties of the image representation. One possible cause of boundary interference could be endcuts at the black–white interface of the subthreshold line. Endcuts are short boundaries that are generated at line ends, or at other sudden changes in oriented contrast. They are caused, in part, by short-range spatial and orientational competition that occurs at, or subsequent to, the complex cell stage (Fig. 8). The spatial competition models the endstopping operation that converts complex cells into complex endstopped, or hypercomplex, cells (Hubel & Wiesel, 1977). Such endcuts should be minimized in the present experimental set-up by the fact that the white and black lines have identical Weber contrast relative to the gray background. If the oppositely polarized simple cells that respond to the black–gray and white–gray line edges deliver approximately equal outputs to their target complex cells, then end cuts should be minimized. On the other hand, activation of simple cells at and near the position of the contrast reversal may be reduced relative to those within the fixed-contrast lines. Due to rectification of simple cell outputs, the target complex cells that pool their signals could also be less active. If this reduction is great enough (only experiments can tell), then endcuts could form.

Why can endcuts interfere with illusory contour formation? Endcuts that are (nearly) perpendicular to a bipole cell's receptive field orientation can inhibit the bipole cell via the competing effects of perpendicular orientations on bipole cell activation (Fig. 8). This property prevents colinear inducers from grouping across arrays of nearly perpendicular obstructions. Illusory contour formation by these bipole cells would hereby be weakened.

Endcuts are not the only way in which bipole cells can be inhibited by the orientational competition. If the lines are thick enough, the black–white edge between the two lines can itself generate activations by simple cells that are oriented perpendicular to the line orientation. These simple cell activations can directly excite like-oriented complex and hypercomplex cells and thereby inhibit the perpendicularly oriented bipole cell receptive field, thereby weakening illusory contour formation.

This possible boundary contribution to the data can be studied in several ways. It may possibly be strengthened by thickening the black and white lines and thereby creating a longer black–white contrast with which to more strongly activate the corresponding simple cells. It may also be strengthened by unbalancing the Weber contrast of the black and white lines, and thereby generating endcuts. It may be weakened by redoing the experiment using, say, equiluminant red and green lines instead of black and white lines. The red–green interface between the line segments should not create significant simple cell activations. Nor should the red–gray or green–gray sides of the lines cause endcuts by generating different levels of simple cell activation, although a reduction of activation near the red–green edge could occur.

Another possible source of illusory contour interference is surface properties of the image representation. The complete model proposes that BCS boundaries regulate the filling-in of surface properties, such as brightness, color, depth, and form, within a feature contour system, or FCS (Arrington, 1994; Cohen & Grossberg, 1984; Grossberg & Todorović, 1988; Paradiso & Nakayama, 1991). The BCS is proposed to occur in the interblob cortical stream and the FCS in the blob stream from LGN to extrastriate area V4 (DeYoe & van Essen, 1988). Both the BCS and the FCS are proposed to interact reciprocally with object recognition and spatial orientation and action systems (Grossberg, 1994) that exist in temporal cortex and parietal cortex (Desimone, 1991, 1992; Desimone & Ungerleider, 1989; Fischer & Breitmeyer, 1987; Gochin, 1990; Gochin *et al.*, 1991; Goodale & Milner, 1992; Harries & Perrett, 1991; Mountcastle *et al.*, 1981; Ungerleider & Mishkin, 1982). These reciprocal interactions can draw attention to prescribed surface regions and boundary segmentations.

In particular, attention can be drawn selectively to multiple targets of the same color (Egeth *et al.*, 1984; Nakayama & Silverman, 1986; Wolfe & Friedman-Hill, 1992). Grossberg *et al.* (1994) have quantitatively modeled how this process may occur. These results suggest that dividing the figure into multiple white and black regions can more easily draw attention to one or the other type of color than the other. Then the figure is regrouped by color-selective attention. Color-specific top-down priming from temporal or parietal areas to extrastriate visual cortex could then break up the illusory contours. In particular, priming could alter the effective Weber contrast of the attended color and thereby create endcuts via feedback pathways that occur from the FCS to the BCS to ensure that a mutually consistent set of boundaries and surfaces is formed (Grossberg, 1994). Elder and Zucker (1993) have reported data that are consistent with this proposal. They have developed a visual search task in which a target outline is identified by virtue of its degree of closure. They showed that closed contours that were built up from oppositely polarized contours produced results nearly equal to those with open figures. They concluded that "contrast reversal eliminates perceptual closure" (p. 986). Elder and Zucker (1993) have, however, erroneously concluded that their results

were incompatible with the BCS/FCS model, because they overlooked polarity-sensitive FCS processing and the influences of polarity-sensitive simple cells on BCS processing.

An analogous interaction between boundary and surface properties may help to account for the relative size of the effects across Experiments 1 and 2. Experiment 2 demonstrated the importance of matching the contrast polarity of the subthreshold line and the nearest inducer by reversing the locations of two short subthreshold lines of opposite polarity. Despite this fact, Experiment 1 reported a significant effect of using a single subthreshold line which always matched one inducer's polarity and mismatched the other. Although Experiment 1 might yield a weaker grouping signal at the mismatched line end, it also provides a more consistent, single-polarity attentive surface signal across the line's full length and that of the matched inducer.

These factors illustrate the subtlety of the interactions that go into such apparently simple percepts as those studied herein. They also clarify why the present experimental paradigm is well-disposed to differentiate some of these factors in a well-controlled way.

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