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Spatial Interactions with Real and Gap-induced Illusory Lines in Vernier Acuity

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Vernier acuity for illusory line targets induced by gaps in a horizontal grating was measured in the presence of real and illusory flanks. In a 500 msec presentation forced choice task, observers judged the position of a comparison illusory line positioned 3 min arc below the target. The results show that illusory lines are capable of interacting with real lines in spatial localization. Thus, they provide psychophysical evidence for a common localization mechanism that supports real and illusory contour definitions. The results further show a sensitivity of the visual system to the contrast polarity of real lines. This sensitivity was absent for illusory lines. The present findings are discussed in terms of their relationship to physiological findings, and in terms of their potential to constrain computational models that account for illusory contour brightness. © 1997 Elsevier Science Ltd. All rights reserved

Illusory lines   Contrast polarity   Vernier acuity   Localization

INTRODUCTION

The lines and boundaries perceived by the visual system are not always physically present in the retinal image. Visual information from the environment contains gaps caused by the blind spot, scotomas, and retinal veins. Despite this, humans do not perceive gaps in their vision because the visual system completes the gaps. Interestingly, humans often cannot distinguish between the completed (illusory) regions of their perception of the scene from the physically present regions (Grossberg & Mingolla, 1985a, b). Illusory lines and boundaries can also be induced between some two-dimensional real contour configurations (Kanizsa, 1955). The processing of these illusory lines and boundaries compared to their real counterparts has theoretical implications in human and computational vision (Grossberg & Mingolla, 1985a, b; Ramachandran, 1992). In this regard, a fundamental question is whether illusory and real lines and boundaries are represented similarly by the visual system. The present experiments explored this question by investigating interactions between real and illusory lines in a localization task (namely vernier acuity).

There is evidence demonstrating that real and illusory lines and boundaries are processed similarly under some conditions, and not in other conditions. Illusory contours have been reported to evoke different responses than real contours in binocular rivalry (Bradley, 1982), the Bourdon illusion (Walker & Shank, 1988) and fragmentation of luminous figures (Halpern & Warm, 1980). Asymmetries have also been reported in the masking of square wave gratings (Weisstein *et al.*, 1974) and in the tilt aftereffect (Paradiso *et al.*, 1989). In contrast, other psychophysical studies suggest a common representation. Symmetric performance has been reported in the Poggendorff illusion (Meyer & Garges, 1979; Beckett, 1989), masking (Smith & Over, 1977), and the tilt aftereffect (Smith & Over, 1975, 1977, 1979; Berkely *et al.*, 1994). Illusory contours appear to be processed in ways similar to real contours in apparent motion (von Grunau, 1979; Ramachandran, 1985, 1986) and motion aftereffects (Weisstein *et al.*, 1977; Smith & Over, 1979). They have also been shown to facilitate amodal completion (Bruno & Gerbino, 1987) and subthreshold line detection (Dresp & Bonnet, 1995). Physiological studies recording from monkey cortical areas known to respond to real contours (e.g. V1 and V2) have revealed neural responses to stimuli perceived as illusory contours by humans (Grosof *et al.*, 1993; von der Heydt *et al.*, 1984; Peterhans & von der Heydt, 1989; von der Heydt & Peterhans, 1989).

Finally, illusory contours have been shown to facilitate reaction time and accuracy in a localization task (Pomerantz *et al.*, 1981). Pomerantz *et al.* (1981) had observers report whether the location of a target (i.e. either a dot or a line segment) was inside or outside the edge of a square. The square was either: (a) a real square made of black lines; (b) an illusory square produced by four filled (e.g. black) pacmen; (c) a control square made of four unfilled pacmen producing a virtual square with no illusory lines present; and, (d) an imagined square.

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Localization performance was facilitated with real and illusory squares. This finding indicates our ability to locate a target is influenced by our perception of nearby edges, whether real or illusory.

Considering the similarities and differences in processing real and illusory contours noted above, and particularly the Pomerantz *et al.* (1981) localization results, the present experiments were aimed at revealing the nature of the interactions between real and illusory lines using a vernier acuity paradigm. We chose a vernier acuity paradigm because it has already been used to study interactions between real contours. For example it has been shown that the localization of a real target line can be influenced by its distance from nearby real lines and the lightness relationships between the target and nearby contours (Badcock & Westheimer, 1985a). It would be important for visual theory to know if similar interactions occur when some of the lines are illusory and some are real or when all of the lines are illusory.

Spatial interactions in localization

While we are extremely adept at localization, our ability to localize contours has been shown to be influenced by the presence of flanking contours nearby (e.g. Westheimer, 1979). It is likely these interactions are occurring at a central level in the visual system considering they are also found under dichoptic presentations (Westheimer & Hauske, 1975; Levi *et al.*, 1985). The influence of nearby contours on localization has been used as a noninvasive probe into the visual system's mechanisms that localize contours. For example, experiments have shown that at small flank-to-target separations (FTTS), lines appear closer than reality (i.e. attraction) when: (i) the flank and target lines have the same contrast polarity (Badcock & Westheimer, 1985a); and (ii) the transient onset of the flank interacts with the target (Hock & Eastman, 1995). At small and large FTTS (up to 9 min arc), repulsion occurs when the flank and target have opposite contrast polarity (Badcock & Westheimer, 1985a), and when the transient offset of the flank interacts with the (same contrast polarity) target (Hock & Eastman, 1995). The implication of these findings is that the localization process is sensitive to the temporal and contrast characteristics of the stimulus. This sensitivity has been explained as the summation of neural activity which forms luminance-based centroids (Badcock & Westheimer, 1985a) or differential activation gradients (Hock & Eastman, 1995).

Recent evidence using edges, not lines, suggests localization occurs via a central mechanism that uses luminance and color information (Greene & Brown, 1995; Rivest & Cavanagh, 1996). Hock and Eastman's (1995) nonluminance-based model fits well with a central mechanism. However, the model cannot give a good predictive account of the luminance-based contrast polarity effect of a flank within 3–4 min arc of a target (Badcock & Westheimer, 1985a). Thus, Badcock and Westheimer's (1985a) account offers a better explanation for luminance lines.

In the present study we contend that if localization does occur via a central mechanism, then real lines and gap-induced illusory lines should interact to produce mislocalizations. Furthermore, the nature of the interaction would determine whether the two are represented similarly by the visual system. It is proposed that if they are indeed represented similarly, then they should interact with each other in a manner similar to that of real lines (Badcock & Westheimer, 1985a). Specifically, a real luminance-defined line next to a gap-induced illusory line should elicit attraction if the perceived lightness is in the same direction, and repulsion if the directions are opposite to each other.

Since the lightness of an illusory line is dependent on the luminance contrast polarity (i.e. direction of lightness) of the inducer, this paradigm allows for a distinction between real line/real inducer interactions compared to real line/illusory line interactions. The goals of the present experiments are to reveal the nature of interactions between real and illusory lines using a localization task, and to determine how these interactions are influenced by the lightness of the real and illusory lines.

METHODS

Stimuli

Figure 1 depicts examples of the experimental displays. In the present set of experiments, the gray background luminance was 2.40 cd/m^2 (black horizontal line displays) and 3.40 cd/m^2 (white horizontal line displays). Light (i.e. positive perceived contrast polarity) illusory lines were induced by black lines (0.7 cd/m^2) [see Fig. 1(a)], and dark (i.e. negative perceived contrast polarity) illusory lines were induced by white lines (9.50 cd/m^2) on these gray backgrounds [see Fig. 1(c)]. Real light and dark luminance-defined flank lines were set at 4.60 cd/m^2 and 2.40 cd/m^2 [white horizontal line displays; see Fig. 1(c)], and 3.40 cd/m^2 and 1.60 cd/m^2 [black horizontal line displays; see Fig. 1(a)], respectively. The displays were created and presented on an NEC RGB monitor using a Data Translation frame grabber (DT2851) interfaced with an Everex PC. The monitor was viewed in the dark at a distance of 7.58 m from a chinrest.

Procedure

On each trial, the display appeared for 500 msec and the task was to respond by pressing the left or right arrow key on the PC's keyboard to indicate that the comparison line (at the bottom) had been perceived left or right of the target line (above). Each response started another trial 3 sec later. Observers could take a break from the task by withholding their response. Trials were blocked by the separation between the flank and target lines. There were 132 trials per block. The flanks were placed at 1.33, 2.66, 3.69, 5.32, 6.65, 7.98, and 9.31 min arc from the target. There was also a no-flank baseline block. Thus there were seven FTTS, and one baseline configuration. Data were

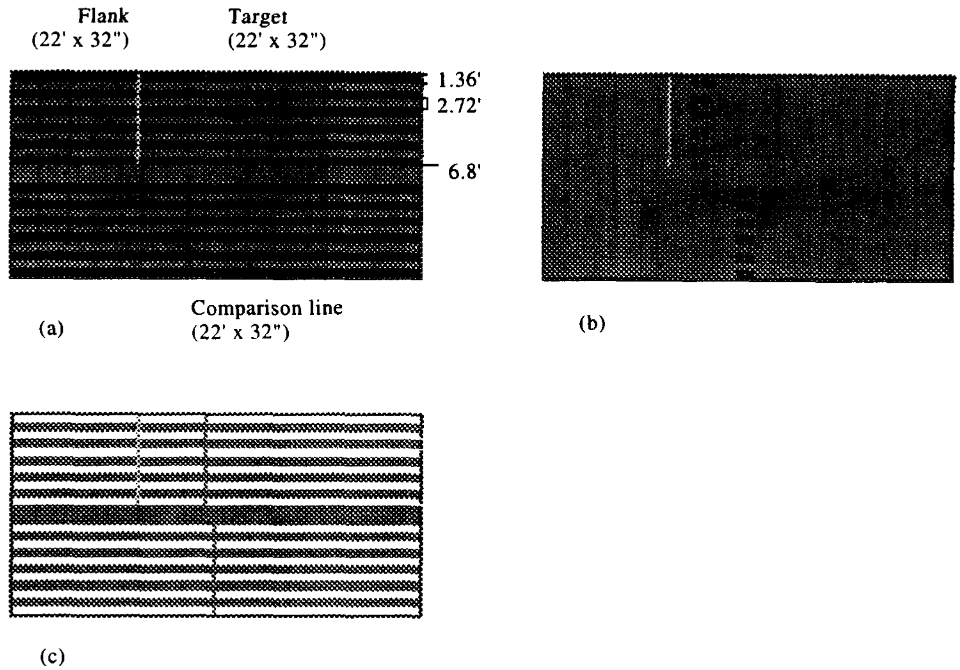

FIGURE 1. Examples of the stimuli used in Experiments 1–3. Vertical lines were 22 min arc × 32 sec arc wide. The height of each horizontal inducing line was 1.36 min arc. The distance between the horizontal lines was 2.72 min arc, and the vertical separation between the top and bottom gratings was 6.8 min arc. The gaps induced a positive perceived contrast polarity (a) or a negative perceived contrast polarity (c) illusory line. In (b), each dot was defined by a 1.36 *min arc* × 1.36 *min arc* square, such that no illusory percept was noticeable by the observers.

collected separately in a within-subjects design for the two (light and dark) real line flank conditions.

Data analysis

Psychometric curves based on the proportion of responses to the right were calculated. Probit analysis (Finney, 1971) was used to obtain the mean value, indicating the vernier offset required to produce 50% responses to the right (i.e. the point of subjective alignment of target and comparison line). Data points in the results section reflect relative performance (from baseline) across sessions. The error bars represent standard errors of the means for relative performance across the sessions (i.e. consistency across sessions).

EXPERIMENT 1: LIGHT ILLUSORY TARGET LINE

Two questions were addressed in this experiment:

1. Do real and illusory lines interact in contour localization?
2. If so, what is the nature of this interaction with respect to the direction of lightness of the real line?

Following the findings of Badcock and Westheimer (1985a), we hypothesized that attraction would occur for the light real line flank and repulsion for the dark real line flank near the light illusory line.

Observers and stimulus

Three trained observers (GJ, BH, HG) participated. HG was aware of the purpose of the experiment. All had normal or corrected-to-normal visual acuity. GJ and BH participated in five sessions per flank lightness condition. HG participated in four sessions per condition. The stimulus was a light illusory line flanked at various separations by a light or a dark real line [Fig. 1(a)].

Results and discussion

The results of the three observers are shown in Fig. 2. The standard error bars reflect the consistency of performance across sessions. At large (4–9 min arc) FTTS there was little difference in performance between the two flank type conditions. The target was either weakly attracted, or repelled from the flank. At small (1–3 min arc) FTTS, the target was attracted towards the light. Trend analyses showed that the light (positive) flank conditions could be fit by U-shaped or negatively sloped linear functions ($P < 0.05$). The results suggest that real and illusory lines can indeed interact in a localization task. Furthermore, the interaction was sensitive to the lightness of the real line flank at small FTTS.

EXPERIMENT 2: BLACK DOTS

It might be argued that the attraction and repulsion found in Experiment 1 was due to an interaction between the real line flanks and the real endpoints of the inducers, and not due to the light illusory line itself. This is unlikely for two reasons. First, the centroid hypothesis predicts a repulsion effect, not attraction if the real line light flank had interacted with the dark inducers. Second, observers

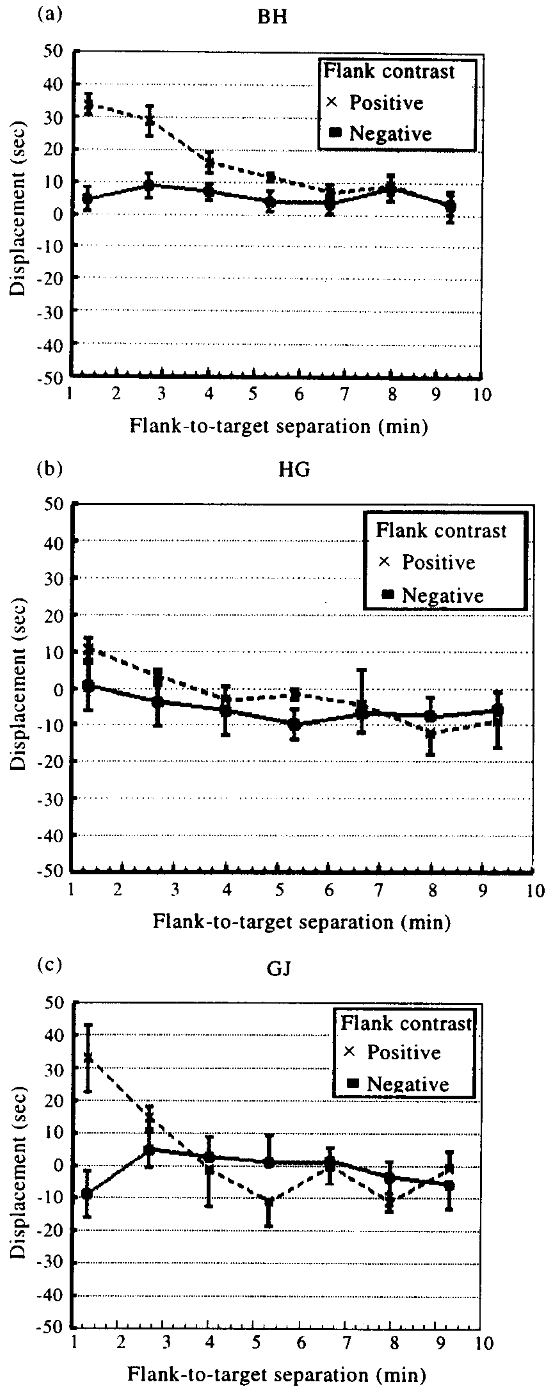

FIGURE 2. Relative displacement of the target from baseline as a function of flank contrast polarity and the separation between the real line flank and the light illusory line target for three observers (a–c). Points above 0 on the y-axis reflect an attraction effect, and points below 0 reflect repulsion.

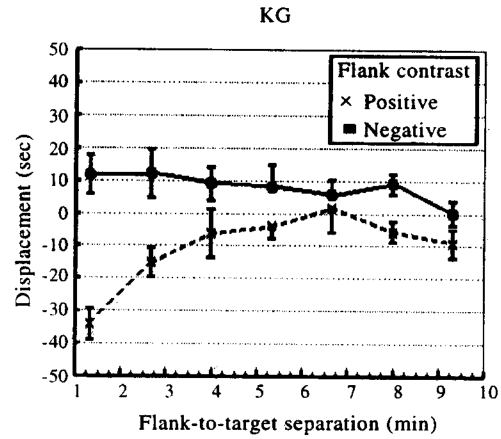

FIGURE 3. Relative displacement from baseline as a function of the distance between the real line flank and the black dot target. The profile of performance was different from when an illusory target was perceived. Points above 0 on the y-axis reflect an attraction effect, and points below 0 reflect repulsion.

clearly perceived the target as an illusory line, not a column of inducers. However, it was necessary to test our argument experimentally. If the interaction in Experiment 1 was between the flanks and the inducers, then the inducers alone should show the same type of performance as that of Experiment 1.

Observers and stimulus

One trained observer (KG) with normal visual acuity participated in this experiment. KG participated in five sessions per flank condition and was unaware of the purpose of the experiment. The illusory line perception was removed by reducing the black lines in Fig. 1 to two columns of 1.36 min arc wide black dots [Fig. 1(b)]. From the observer's viewing distance the target thus appeared as a column of pairs of dots with no perception of an illusory contour. The flanks were real light and dark lines as in Experiment 1.

Results and discussion

The results are presented in Fig. 3. For small (1–3 min arc) FTTS, the patterns of results were different from those in Experiment 1. The light flank repelled, and the dark flank attracted the black dot target. At large (4–9 min arc) FTTS, there was little difference in performance between the flank contrast polarity conditions. Compared to Experiment 1, trend analyses in this experiment showed that the light flank condition could be fit with an inverted U-shaped curve ($P < 0.05$).

To summarize, in Experiments 1 and 2, within a central zone (small FTTS), localization was differentially sensitive to lightness, and outside of this zone, localization was similar irrespective of lightness relationships. However, the difference in performance at small FTTS between Experiments 1 and 2 indicates that performance in Experiment 1 was not based on the endpoints. It was based on an interaction between the visual system's representations of real and illusory contours in the stimulus.

EXPERIMENT 3: DARK ILLUSORY TARGET LINE

At small FTTS, the centroid hypothesis predicts an attraction effect when the flank and target have the same lightness, and a repulsion effect when the flank and target have opposite lightness (Badcock & Westheimer, 1985a). Similar performance (usually repulsion) irrespective of lightness relationships is predicted for large FTTS

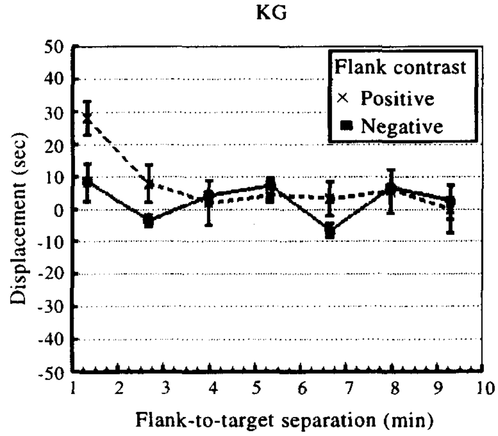

FIGURE 4. Relative displacement from baseline as a function of the distance between the real line flank and the dark illusory target. The profile of performance was similar to that in Experiment 1 when a light illusory target was perceived. Points above 0 on the y-axis reflect an attraction effect, and points below 0 reflect repulsion.

(Badcock & Westheimer, 1985a). These findings are similar to those in Experiment 1, suggesting that the light illusory line was processed in a manner similar to the processing of real luminance lines. Demonstrations have shown illusory contours can be formed irrespective of the polarity of the inducers (e.g. Shapley & Gordon, 1985). In Experiment 1, the light illusory line appeared to have been treated as though it were a light real luminance line. Does this mean a dark illusory line would be treated as a dark real luminance line? The luminance centroid hypothesis predicts that *if the lightness relationship* between real and illusory lines is the same, a dark real line should attract a dark illusory line at small separations, and a light real line should repel a dark illusory line. Experiment 3 tested this hypothesis.

Observers and stimulus

Observer KG participated in the same manner as before. The dark illusory target was induced by white lines [Fig. 1(c)] and the flanks were real lines as in Experiment 1.

Results and discussion

The pattern of results is depicted in Fig. 4. It shows that the predictions of the centroid hypothesis for a real luminance line-illusory line interaction are not supported. At large FTTS, performance was essentially similar to that in Experiments 1 and 2 (i.e. weak attraction or repulsion) irrespective of lightness relationships. At small FTTS, the target was attracted toward the positive flank, and weakly attracted or repelled from the negative flank. The results are similar to those of Experiment 1 with a light illusory target line. Trend analyses revealed a U-shaped fit for the light flank condition ($P < 0.05$), as was the case in Experiment 1.

One explanation of the results would be that the real line flank interacted with the real line-inducer endpoints. Thus, attraction was elicited for same lightness pairs, and weak attraction or repulsion was elicited for opposite lightness pairs in accordance with the luminance centroid hypothesis. This explanation is unlikely, given the findings of Experiments 1 and 2. In Experiment 1 for example, the light real line flank did not repel the dark inducers, it attracted the light illusory line. A problem in dealing with interactions between real and illusory lines is that of the relative salience of the two (Berkely *et al.*, 1994). We argue that the findings are not hindered by this problem for two reasons. First, we were not concerned with symmetrical effects between real and illusory lines as was the case in previous studies (Berkely *et al.*, 1994). Only the effect of real luminance lines on illusory lines was investigated here. Second, regardless of its direction of lightness (and this was clearly perceived by all observers), the illusory line was strongly attracted by the light real luminance line at small separations.

In summary, the combined findings of Experiments 1–3 are inconsistent with the centroid hypothesis. This hypothesis postulates sensitivity to lightness relationships. At small FTTS attraction should occur for same contrast polarity flank and target, and repulsion should occur for opposite lightness flank and target [Badcock & Westheimer (1985a); Experiment 1, the present study]. In Experiments 1 and 3, the trends of results at small FTTS were the same. Whether the illusory contour target was light or dark, it was attracted by the light flank, and repelled or weakly attracted by the dark flank. These trends are different from those found when the target had no illusory line percept (i.e. Experiment 2 here), indicating that the visual system was using the perceived illusory lines in Experiments 1 and 3. The results of Experiments 1 and 3 also indicate that the lightness of the illusory lines was ignored by the visual system. The difference in the amount of effect found may be due to the relative perceived strength of the flank and target. It is therefore hypothesized that the visual system's representation for the localization of illusory lines is insensitive to their perceived lightness.

EXPERIMENT 4: ILLUSORY FLANKS AND TARGETS

If illusory lines are represented without regard to their perceived lightness, then two opposite lightness illusory lines should attract each other at small FTTS, contrary to the repulsion predictions of the centroid hypothesis suggested by Badcock and Westheimer (1985). The present paradigm is limited in terms of testing such a prediction because we cannot define opposite contrast illusory flank and target lines without introducing a real edge in the inducers between the illusory lines. While a solution to this methodological problem is developed, we can examine the nature of interactions between two illusory lines of the same lightness with the present paradigm. This was the purpose of this last experiment.

Observers and stimulus

Two trained observers (GJ, JB) participated in the same manner as before. Both had normal or corrected-to-normal visual acuity and were unaware of the purpose of the experiment. GJ had participated in Experiment 1. The stimuli were similar to those used in Experiments 1 and 3, with the exception that the real line flanks were replaced by illusory lines.

Results and discussion

At small FTTS, the illusory target was attracted towards the illusory flank, and at large FTTS repulsion occurred. Trend analyses revealed a negatively sloped linear trend for the light lines condition of GJ ($P < 0.05$), and U-shaped trends for all other conditions for JB and GJ ($P < 0.05$).

Interestingly, a comparison of the light flank and target data for observer GJ in Experiments 1 and 4 reveals a greater attraction effect in Experiment 1 at small FTTS [see dashed data lines in Figs 2(c) and 5(b)]. A plausible explanation for this is the relatively higher contrast of the real line flank in Experiment 1 compared to the illusory line flank in Experiment 4 [see for example Greene & Brown (1995)]. While the findings of this final experiment do not uniquely address centroid-like interactions with two illusory lines, they do suggest that illusory lines are capable of interacting with each other. This supports the idea that the visual system forms internal representations for illusory lines. These representations are somewhat similar to the representations of real lines in that they not only interact with each other, but they also interact with the representations of real lines in a localization task.

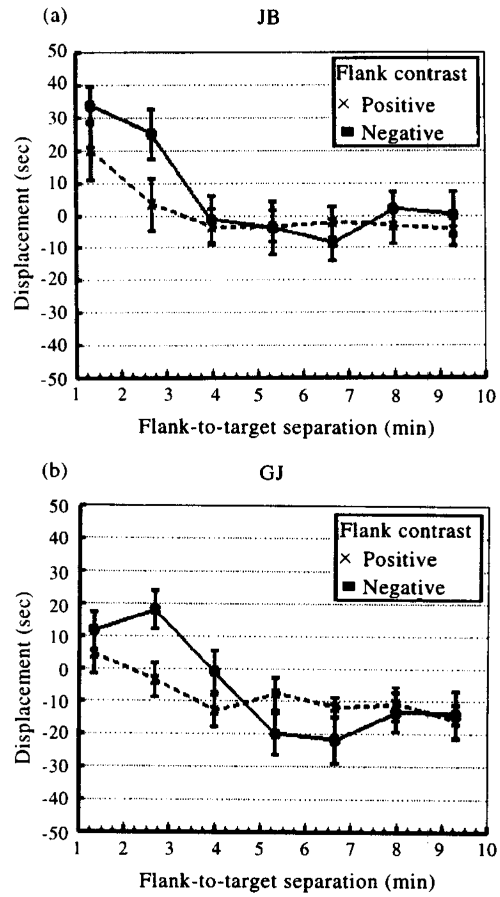

FIGURE 5. Relative displacement from baseline as a function of the distance between the illusory flank and the illusory target. The profile of performance was similar for light and dark illusory stimuli. Points above 0 on the y-axis reflect an attraction effect, and points below 0 reflect repulsion.

GENERAL DISCUSSION

Two main questions were asked in the present study:

1. Can real lines interact with illusory lines to cause displacements in localization?
2. How does the visual system's representation of real lines compare with its representation of illusory lines?

With regard to the first question, Experiments 1, 3, and 4 have shown real line-on-illusory line and illusory line-on-illusory line interactions resulting in localization displacements. A host of theories about line localization have been based on luminance activity (Westheimer & McKee, 1977; Marr, 1982; Badcock & Westheimer, 1985a, b; Watt, 1988). These theories are not sufficient because localization has recently been shown to be interactively sensitive to luminance- and color-defined edges (e.g. Greene & Brown, 1995; Rivest & Cavanagh, 1996). Thus, the localization mechanism is interactively sensitive to different visual attributes. The present study shows that illusory lines (induced by gaps in real lines) may be added to the list of attributes.

The nature of attribute interaction is not a simple one. For edge contours defined by luminance and color, attraction towards the luminance-defined flank was found without regard for the flank's direction of lightness (Greene & Brown, 1995; Rivest & Cavanagh, 1996). For luminance-defined lines, on the other hand, attraction or repulsion have been shown to be influenced by the flank's lightness (Badcock & Westheimer, 1985a), configuration (Badcock & Westheimer, 1985b), and temporal characteristics (Hock & Eastman, 1995). In the present study, the lightness of real flanks also affected the nature of the illusory line-on-real line interaction. However, the perceived lightness of the illusory lines did not seem to be an influencing factor. Light and dark illusory target lines showed similar patterns of interactions with real flank lines.

With regard to the second question addressed in this study, these findings indicate that while the visual system's representation of real luminance lines is contrast polarity sensitive, its representation of gap-induced illusory lines is not. This conclusion is supported by the subthreshold summation findings of Dresp and Bonnet (1995). These authors report facilitation in the detection of real subthreshold lines superimposed on illusory contours irrespective of perceived contrast polarity.

The present results indicate that direction of lightness is not retained for illusory line processing in a localization task. These results might seem at odds with some physiological reports related to lightness and illusory lines (e.g. Peterhans & von der Heydt, 1989; von der Heydt & Peterhans, 1989). For example, V2 cells that preferred dark real lines have been found to respond well to dark illusory lines (of the sort used in the present study) (von der Heydt & Peterhans, 1989). V2 cells that had no real line lightness preference, also responded well to dark illusory lines. Similarly, V2 cells that selectively responded to the dark side of a real dark-to-light edge, also showed selective response for the dark side of an illusory dark-to-light edge (Peterhans & von der Heydt, 1989). Control observations indicated that the cells were not indiscriminately responding to darkness in the stimulus. From these physiological observations, it has been suggested that lightness is coded in order that we may distinguish light from dark illusory figures (Peterhans & von der Heydt, 1989). While this may be the case for the perception of real lines and figures, our psychophysical evidence found no selectivity for lightness direction when illusory lines were used for localization.

The findings of the present study also provide constraints for models of illusory contour formation. One such model that addresses the issue of contrast polarity is the form-and-color-and-depth (FACADE) neural network model (Grossberg & Mingolla, 1985a, b; Grossberg, 1987, 1994). Of present concern are two modules in FACADE, called the static boundary contour system (BCS), and the feature contour system (FCS). The BCS forms an illusory boundary irrespective of the polarity of the inducers, and the FCS spreads illusory brightness until the boundaries are encountered. According to FACADE, in the present study, vertically oriented hypercomplex cells at the line ends of the horizontal inducing lines activated bipole cells, which in turn activated other vertically oriented hypercomplex cells to complete the illusory boundaries (see Grossberg, 1994). Visibility of the illusory line was due to filling-in signals by the FCS. The question of representation of real luminance lines and illusory lines now becomes one of deciding whether the filling-in signals for real lines are the same as those for illusory lines. If they are the same, then their contrast relationships should be similar in psychophysical performance. The present set of experiments suggest that lightness relationships are not represented in the filling-in of illusory lines. An interpretation of the present results within FACADE's structure suggests that illusory and real lines share the same boundary formation mechanism (i.e. BCS), but use different filling-in (FCS) signals.

In conclusion, the present findings are important for theories of real and illusory line formation and processing. The logic of our paradigm shows great potential for exploring interactions between real and illusory lines, as well as between illusory lines themselves. Gap-induced illusory lines appear to be like real luminance-defined lines in the fact that they interact with real and illusory lines, influencing our ability to localize them in space. However, they are different from real luminance-defined lines in the way these interactions occur as a function of perceived direction of lightness.

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