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Spatial facilitation by color and luminance edges: boundary, surface, and attentional factors

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Abstract

The thresholds of human observers detecting line targets improve significantly when the targets are presented in a spatial context of collinear inducing stimuli. This phenomenon is referred to as spatial facilitation, and may reflect the output of long-range interactions between cortical feature detectors. Spatial facilitation has thus far been observed with luminance-defined, achromatic stimuli on achromatic backgrounds. This study compares spatial facilitation with line targets and collinear, edge-like inducers defined by luminance contrast to spatial facilitation with targets and inducers defined by color contrast. The results of a first experiment show that achromatic inducers facilitate the detection of achromatic targets on gray and colored backgrounds, but tend to suppress the detection of chromatic targets. Chromatic inducers facilitate the detection of chromatic targets on gray and colored backgrounds, but tend to suppress the detection of achromatic targets. Chromatic spatial facilitation appears to be strongest when inducers and background are isoluminant. The results of a second experiment show that spatial facilitation with chromatic targets and inducers requires a longer exposure duration of the inducers than spatial facilitation with achromatic targets and inducers, which is already fully effective at an inducer exposure of 30 ms only. The findings point towards two separate mechanisms for spatial facilitation with collinear form stimuli: one that operates in the domain of luminance, and one that operates in the domain of color contrast. These results are consistent with neural models of boundary and surface formation which suggest that achromatic and chromatic visual cues are represented on different cortical surface representations that are capable of selectively attracting attention. Multiple copies of these achromatic and chromatic surface representations exist corresponding to different ranges of perceived depth from an observer, and each can attract attention to itself. Color and contrast differences between inducing and test stimuli, and transient responses to inducing stimuli, can cause attention to shift across these surface representations in ways that sometimes enhance and sometimes interfere with target detection.

Keywords: Spatial facilitation; Boundary completion; Illusory contour; Luminance; Color; Surface perception; Attention; Neural network

1. Introduction

Psychophysical experiments on detection facilitation with collinear targets and inducers, now referred to as spatial facilitation (Yu & Levi, 1997a,b), have generated a coherent body of data and new assumptions on perceptual phenomena such as spatial grouping or contour completion (Dresp & Bonnet, 1991, 1993, 1995; Dresp, 1993; Polat & Sagi, 1993, 1994; Kapadia, Ito, Gilbert & Westheimer, 1995; Dresp & Grossberg, 1997; Yu & Levi, 1997a,b; Wehrhahn & Dresp, 1998). The general conclusion from these studies is that the visual detection of a target object can be facilitated or suppressed by nearby objects, depending on their spatial location, orientation, contrast intensity, or contrast polarity. These facilitatory or suppressive interactions between visual stimuli are supposed to reveal some of the dynamic characteristics of early perceptual grouping, and can be interpreted in terms of short- or long-range

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interactions between feature detectors. Such an interpretation is consistent with neurophysiological data showing that the response characteristics of visual cortical cells change with the context in which a trigger-stimulus is presented (e.g. Gilbert & Wiesel, 1990).

Until now, studies on spatial facilitation were conducted with achromatic stimuli (white or black) presented on achromatic backgrounds (white, black, or gray). The following experiments were designed to compare facilitatory effects obtained in the domain of luminance contrast, to effects produced by color configurations. In a first step, it was determined whether inducers defined by color contrast produce spatial facilitation in the same way as inducers defined by luminance contrast do, and whether stimuli defined by luminance contrast and stimuli defined by color contrast are able to interact in the genesis of spatially induced detection facilitation.

In spatial vision it has, for example, been shown that chromatic and achromatic mechanisms are largely independent at threshold, but appear to interact in suprathreshold processes such as visual masking (see Kulikowski, 1997 for a review). The present experiments were run to test whether spatial facilitation occurs with colored targets and inducers, and whether, and to which extent, chromatic mechanisms can be functionally separated from achromatic mechanisms in the genesis of collinear detection facilitation.

2. Experiment 1

To highlight, and eventually disentangle, mechanisms of form integration across space specifically for color and luminance contours, we presented isoluminant color inducers, color inducers with luminance contrast, and achromatic inducers on gray and red backgrounds. These inducing configurations were combined with the presentation of briefly flashed, red or gray line targets. The presence/absence of spatial detection facilitation/suppression was assessed on the basis of the probability of correct line target detections in a given target-inducer-background configuration.

2.1. Subjects

Two observers (AM and BD), including one of us, participated in the experiment. BD had normal vision, AM's vision was corrected-to-normal. Both observers were psychophysically experienced and well-trained in detection tasks.

2.2. Stimuli

The stimuli (see Fig. 1) were presented binocularly on a high-resolution color screen (Sony, 60 Hz, non-interlaced). They were generated with an IBM compatible PC (HP 486) equipped with a VGA Trident graphic card. The diameter of the inducing elements was about 50 arcmin, and the two collinear edges were separated by a gap of about 100 arcmin of visual angle. The length of the line target, presented right in the middle of that gap and in alignment with the edges of the two inducers, was about 80 arcmin.

The colors of the stimuli were computed by selectively incrementing the R (for red stimuli) or G (for green stimuli) channels of the screen, the other two channels (G and B or R and B, respectively) being kept constantly at zero. Achromatic stimuli were computed by incrementing the three channels (R–G–B) simultaneously. All intensity levels of the R and G channels were carefully calibrated with a Chromaphotometer (Minolta) for luminance and chromaticity. Intensity levels reflecting the combined output of all three channels generating the achromatic stimuli were calibrated with the same device. Only the linear range of screen intensities was used.

Luminance values of the different inducer-background configurations were as follows: Gray background, about 5 cd/m^2, red background about 0.6 cd/m^2 ($x = 0.613$, $y = 0.357$ CIE). Psychophysically isoluminant red and green colors had a luminance of

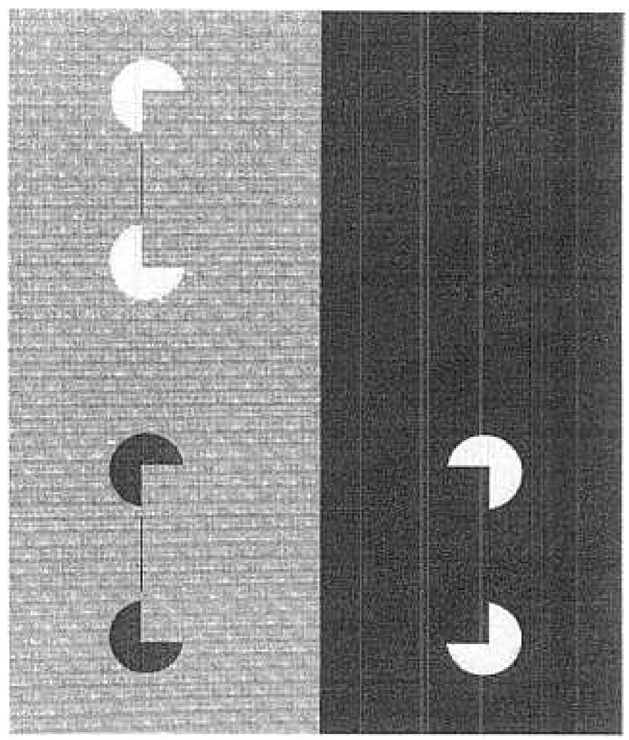

Fig. 1. Colored inducers were presented on a colored and on a gray background, and gray inducers were presented on a gray and on a colored background. The subject had to detect a target line that was flashed briefly on the gap between two inducing edges. The target was either achromatic (gray), or chromatic (red).

about 0.6 cd/m^2 ($x = 0.612$, $y = 0.352$ CIE) for red and about 0.67 cd/m^2 for green ($x = 0.286$, $y = 0.601$ CIE). For both observers, red/green isoluminance corresponded to about the same values, and was assessed by means of a classic flicker test before the experiment. Red and green inducers with additional luminance contrast with regard to either the gray or the red background had a luminance of about 8.2 cd/m^2 for red ($x = 0.612$, $y = 0.354$ CIE) on the gray background, and about 4.8 cd/m^2 ($x = 0.293$, $y = 0.598$) for green on the red background, about 9 cd/m^2 ($x = 0.292$, $y = 0.595$) for green on the gray background. Achromatic inducers on the gray background had a luminance of about 9 cd/m^2, achromatic inducers on the red background had a luminance of about 5.1 cd/m^2. These inducer luminances were chosen to make the luminance contrasts (Weber ratios) of non-isoluminant, colored inducers and achromatic inducers presented on the different backgrounds roughly equivalent.

2.3. Procedure

Two pairs of collinear inducers were presented on either side of a small fixation point located in the centre of the screen. The configuration was constantly displayed during the trials, where a target was briefly flashed, in random order, on one of the two induced contour gaps. The target was announced by a short tone and its exposure duration was about 32 ms (two frames). The observer had to press one of two response keys to indicate whether he/she had seen the target appear on the left or the right contour gap (two-alternative spatial-forced-choice procedure). The five target contrasts (see above) were constant in all conditions (method of constant stimuli), and presented at least 40 times, in random order, within a given experimental condition. Chromatic targets and achromatic targets were presented in separate blocks. The same holds for chromatic and achromatic backgrounds. Target conditions (red or gray target) and background conditions (red or gray background) were crossed. The different inducer conditions were also presented in separate blocks. Control thresholds for the detection of a given target type on a given background type with no inducers (just the central fixation point being displayed) were measured in every experimental session for each observer. The horizontal distance between the left or right target location and the fixation point was about 30 arcmin, and constant in all conditions (with or without inducers). The observers were placed at a distance of about 1.5 m from the screen and performed under free viewing conditions.

2.4. Results

The probability of correct detections was computed for each luminance level of the target, stimulus condition, and observer and then transformed into logit values potted as logistic functions of the difference between the luminance of the target line and the luminance of the background (D-Lum). The graphs represent individual data of the two observers with performance averaged over the number of trials (minimum 80) for a given experimental condition.

2.4.1. Achromatic targets on achromatic backgrounds

The results with gray targets presented on a gray background are represented in the Figs. 2b and 3b. The transformed probability of correct detection is plotted as a function of the luminance contrast of the target as defined above (D-Lum), and the type of inducing configuration. The results of observer AM with gray targets on gray backgrounds are shown in Fig. 2b. The data exhibit roughly equivalent detection performance in the condition with colored inducers and the control condition without inducers with, however, a slightly suppressive tendency with the colored inducers. A strikingly better detection performance is observed with achromatic (gray) inducers. The results of observer BD with gray targets presented on a gray background (Fig. 3b) show the same tendencies as those of AM. Detection performances are roughly equivalent for the condition with colored inducers, again with a slight tendency toward detection suppression in this case, and for the control condition without inducers. Achromatic inducers clearly facilitate the detection of the target. For theoretical thresholds and correlation statistics, see the figure legends.

2.4.2. Achromatic targets on chromatic backgrounds

The data obtained with achromatic (gray) targets presented on a colored (red) background are represented in Figs. 2a and 3a. Here again, the individual psychometric functions are plotted for the different inducer types (green or gray). The results of observer AM with achromatic (gray) targets on a colored (red) background are represented in Fig. 2a. The graphs show that green inducers, whether isoluminant with regard to the background or not, do not facilitate the detection of the target compared to the control condition with no inducers. Achromatic (gray) inducers clearly facilitate detection compared to the control condition. The results of observer BD (Fig. 3a) with achromatic (gray) inducers on a colored (red) background show the same effects as those obtained with observer AM. No detection facilitation is engendered by colored inducers, but a slightly suppressive effect compared to the control condition without inducers. Achromatic inducers clearly facilitate detection.

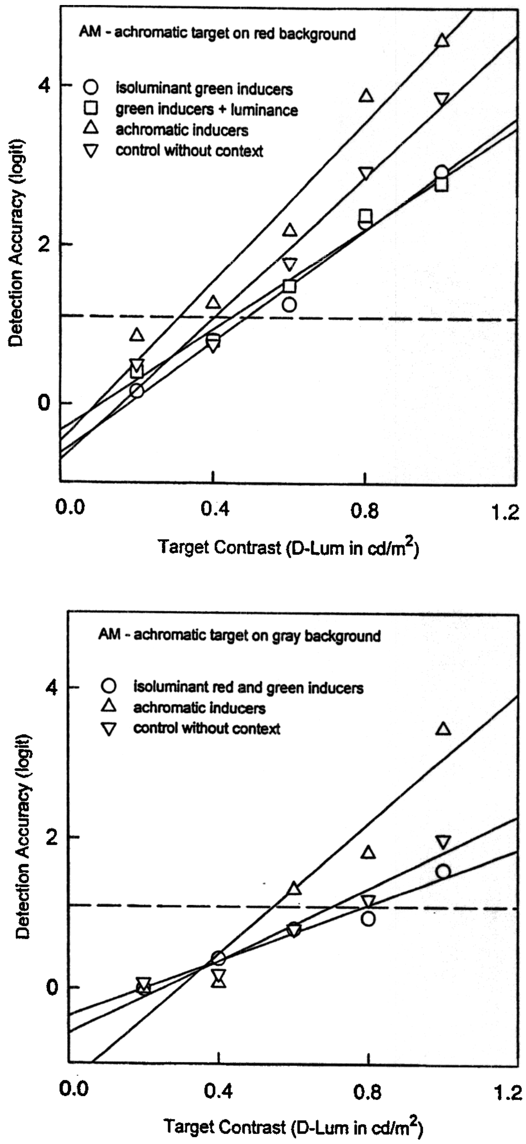

Fig. 2. (a) AM's line target detection performance with achromatic targets on a red background. For a detailed discussion of the effects, see the text. The theoretical contrast thresholds (in D-Lum) in the different conditions (from top to bottom in the legend) are: 0.48, 0.43, 0.44, and 0.79 in the control condition. (b) AM's data with achromatic targets on a gray background. The theoretical contrast thresholds (in D-Lum) in the different conditions are: 0.81, 0.54, and 0.74 in the control condition. Correlation indices (r^2) vary between 0.95 and 0.99.

2.4.3. Chromatic targets on chromatic backgrounds

The results with chromatic (red) targets presented on a colored (red) background are represented in Figs. 4a and 5a. The results of observer AM with red inducers presented on a red background are shown in Fig. 4a. Green inducers, whether isoluminant with regard to the background or not, clearly facilitate the detection of the target compared to the control condition without inducers. Achromatic (gray) inducers, do not facilitate detection of the chromatic target, with a slight tendency towards suppression at the higher target contrasts. The results of observer BD (Fig. 5a) with red targets presented on a red background show the same tendencies as those of AM. Green inducers engender detection facilitation, which is strongest here when the inducers are isoluminant with regard to the background. Achromatic inducers have a clearly suppressive effect on the detection of the chromatic target.

2.4.4. Chromatic targets on achromatic backgrounds

The results with chromatic (red) targets presented on an achromatic (gray) background are represented in Figs. 4b and5b. The results of observer AM with a red

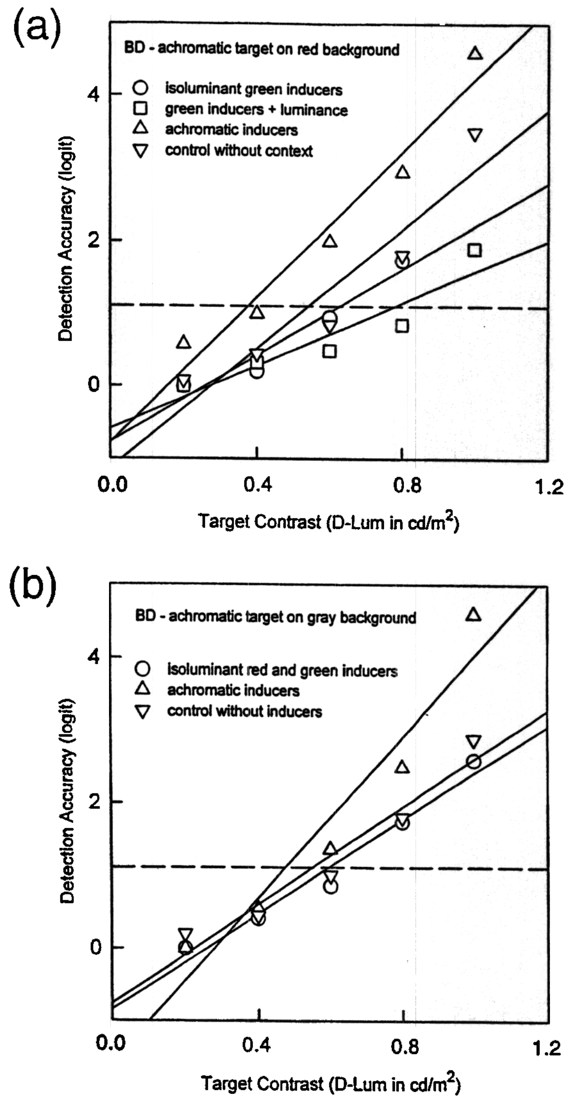

Fig. 3. (a) BD's line target detection performance with achromatic targets on a red background. The theoretical contrast thresholds (in D-Lum) in the different conditions are: 0.62, 0.78, 0.37, and 0.52 in the control condition. (b) BD's data with achromatic targets on a gray background. The theoretical contrast thresholds (in D-Lum) in the different conditions are: 0.61, 0.47, and 0.59 in the control condition. Correlation indices (r^2) vary between 0.95 and 0.99.

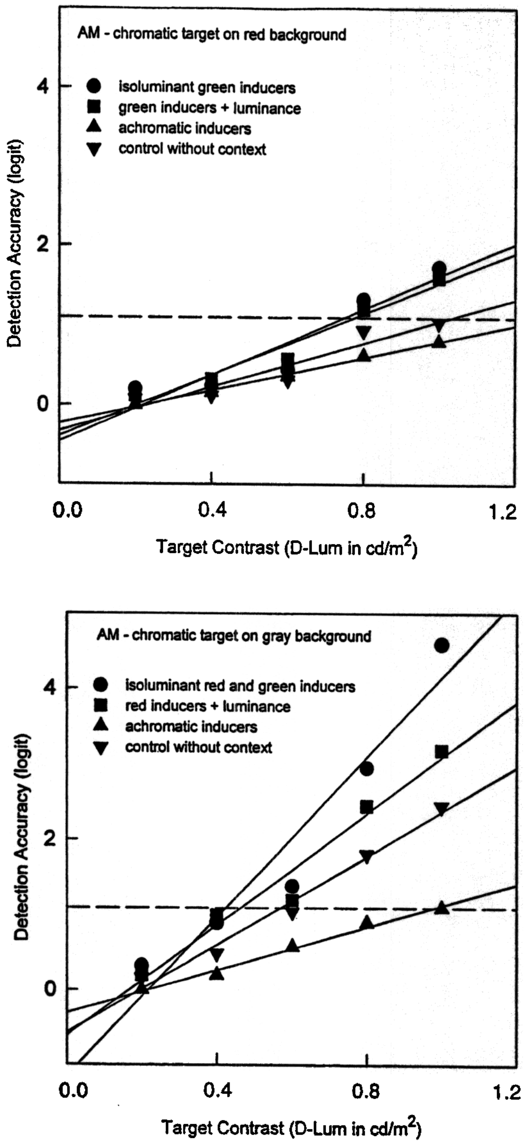

Fig. 4. (a) AM's line target detection performance with chromatic targets on a red background. The theoretical contrast thresholds (in D-Lum) in the different conditions are: 0.74, 0.76, 1.28, and 1.03 in the control condition. (b) AM's data with chromatic targets on a gray background. The theoretical contrast thresholds (in D-Lum) in the different conditions are: 0.42, 0.47, 0.56, and 1.03 in the control condition. Correlation indices (r^2) vary between 0.95 and 0.99.

target presented on a gray background are shown in Fig. 4b. Red, as well as red and green inducers together, produce detection facilitation compared to the condition with no inducers. Achromatic inducers have a clearly suppressive effect on the detection of the chromatic target. The results of observer BD (Fig. 5b) with red targets presented on a gray background show that red inducers produce the strongest detection facilitation. Red and green inducers also facilitate detection, but not as strongly as when red inducers only are presented. Achromatic inducers, as expected from AM's data, suppress the detection of the chromatic target. For the theoretical thresholds in the different conditions and for correlation statistics, please see the figure legends.

2.5. Conclusions

The results of Experiment 1 show that collinear, chromatic inducers facilitate the detection of collinear, chromatic line targets with varying luminance, whether the background is colored or achromatic; they do not facilitate the detection of achromatic targets with varying luminance in any case shown here, but rather tend to suppress target detectability. Achromatic inducers

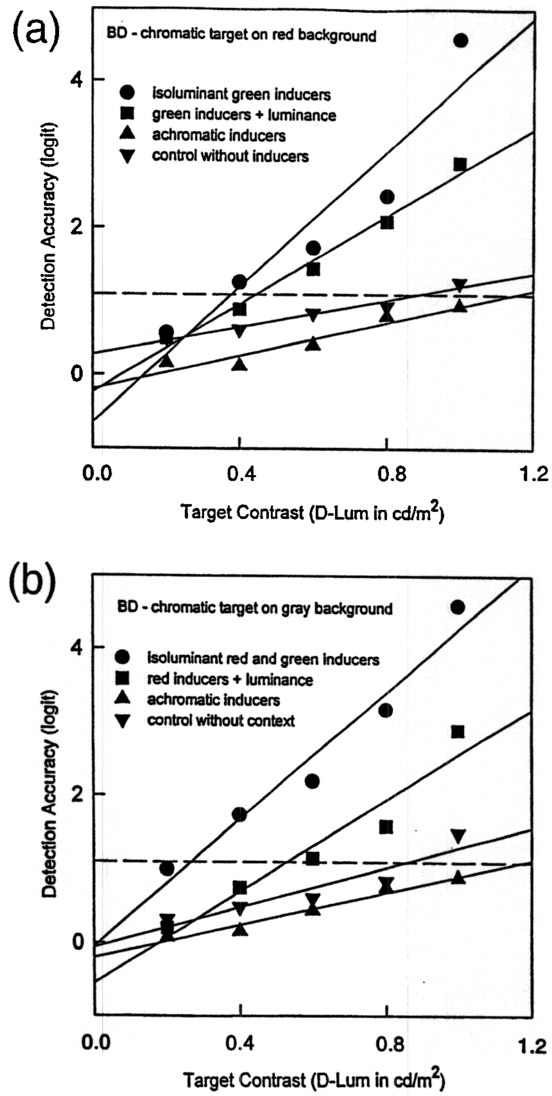

Fig. 5. (a) BD's line target detection performance with chromatic targets on a red background. The theoretical contrast thresholds (in D-Lum) in the different conditions are: 0.37, 0.41, 0.89, and 1.03 in the control condition. (b) BD's data with chromatic targets on a gray background. The theoretical contrast thresholds (in D-Lum) in the different conditions are: 0.25, 0.55, 1.16, and 0.88 in the control condition. Correlation indices (r^2) vary between 0.95 and 0.99.

facilitate the detection of achromatic targets with varying luminance, whether the background is achromatic or colored. They clearly suppress the detection of the chromatic targets.

3. Experiment 2

Given the length of the targets and inducers used in Experiment 1, we expect the facilitatory effects we report to be situated within the spatial scale of long-range interactions shown by Dresp and Grossberg (1997) and by Wehrhahn and Dresp (1998) in previous spatial facilitation experiments with long stimuli. Wehrhahn and Dresp's data in particular show that facilitatory interactions between long line targets and inducers extend over spatial gaps that lie beyond the limits of the short-range interactions shown by Yu and Levi (1997a). The conceptual distinction between short- and long-range effects we suggest here is based on the sizes of psychophysically assessed perceptive fields (Jung & Spillmann, 1970; Yu & Levi, 1997b). Perceptive fields within the shorter range of spatial effects integrate targets and inducer not longer than 10 arcmin, over spatial gaps not larger than 20 arcmin (e.g. Dresp, 1993; Levi & Waugh, 1996; Yu & Levi, 1997a). They are selective to the contrast polarity of targets and inducers (e.g. Wehrhahn & Dresp, 1998). Perceptive fields within the longer range of spatial effects integrate, or group, targets and inducers that are considerably longer than 10 arcmin, over spatial gaps well beyond 20 arcmin, but not larger than 2.5° of visual angle (Dresp & Grossberg, 1997).

To clarify the spatial extent of the facilitatory interactions observed in Experiment 1, we varied the spatial separation between the target line and a single inducer, choosing values within and well beyond the short-range spatial scale of perceptive fields that give rise to facilitatory spatial interactions in line contrast detection. The spatial separation between targets and inducers in both the condition where chromatic inducers facilitate luminance detection of a chromatic target, and the condition where achromatic inducers facilitate luminance detection of an achromatic target, was tested. Here, we present context conditions with one inducer only on top of the target at different spatial separations (0, 20, 30 arcmin, and 2° of visual angle). Apart from these newly introduced variations, the general design and apparatus, stimuli, procedure, and conditions of presentation were exactly the same as in Experiment 1.

3.1. Results

The effect of spatial separation of the target from a single inducer on the luminance detection of the targets are represented in Fig. 6a, b (BD) and Fig. 7a, b (AM).

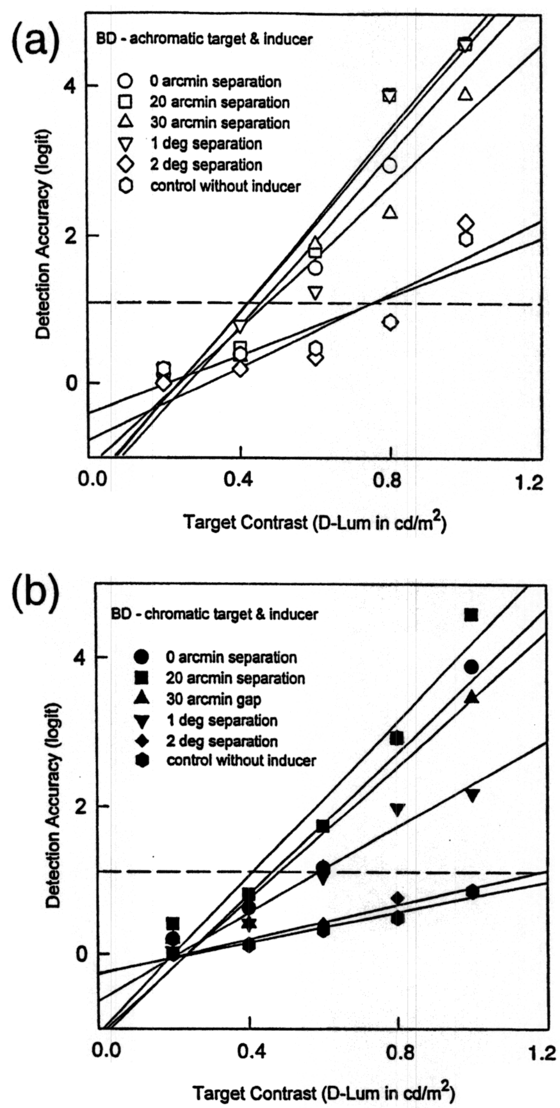

Fig. 6. (a) BD's data with achromatic targets and one achromatic inducer with varying spatial separation, on a gray background. The theoretical contrast thresholds (in D-Lum) in the different conditions (from top to bottom) are: 0.45, 0.41, 0.47, 0.42, 0.75 and again 0.75 in the control condition. (b) BD's data with chromatic stimuli. The theoretical contrast thresholds (in D-Lum) here are: 0.46, 0.41, 0.48, 0.58, 1.30, and 1.18 in the control condition. Correlation indices (r^2) vary between 0.95 and 0.99.

The graphs show that for both chromatic luminance targets presented near chromatic inducers on isoluminant background and for achromatic luminance targets presented near achromatic inducers on achromatic background, detection is strongly facilitated for spatial gaps of 0, 20 (BD only was run with these two gaps), and 30 arcmin. At a spatial separation of 1° of visual angle, facilitation is shown to be diminished, especially in the chromatic case, and for a separation of 2° of visual angle, detection performances in the achromatic and the chromatic condition are no longer different from those observed in the control conditions.

3.2. Conclusions

The detection facilitation effects reported here are situated within the scale of long-range spatial effects reported previously by Dresp and Grossberg (1997) and Wehrhahn and Dresp (1998) with achromatic targets and inducers. Chromatic target-inducer combinations apparently do not produce effects of spatial separation that would be drastically different from the effects reported for spatial facilitation with achromatic stimuli.

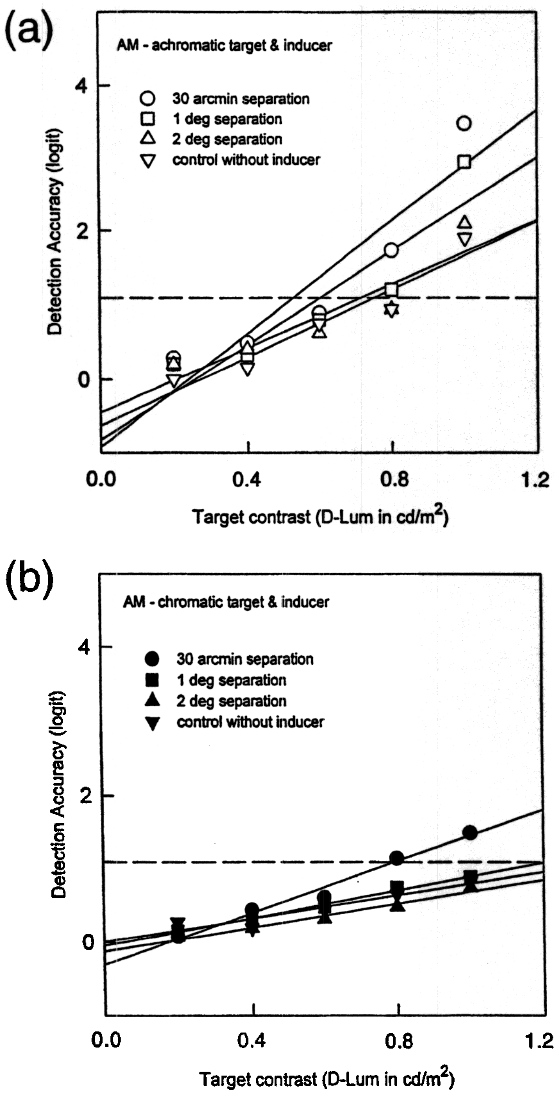

Fig. 7. (a) AM's data with achromatic targets and one achromatic inducer with varying spatial separation, on a gray background. The theoretical contrast thresholds (in D-Lum) in the different conditions (from top to bottom) are: 0.52, 0.60, 0.75, and 0.71 in the control condition. (b) AM's data with chromatic stimuli. The theoretical contrast thresholds (in D-Lum) here are: 0.80, 1.20, 1.49, and 1.37 in the control condition. Correlation indices (r^2) vary between 0.97 and 0.99.

4. Experiment 3

The results of the first and the second experiment point towards two separate mechanisms for spatial facilitation with, however, an apparently similar sensitivity to spatial separation. One mechanism appears to selectively group colored luminance targets and inducers whereas the other one selectively groups luminance defined, achromatic targets and inducers. Interestingly, both mechanisms disregard background color. This is to some extent consistent with the fact that in spatial facilitation with achromatic targets and inducers, the contrast polarity of the background has no influence. In other words, spatial facilitation is observed with white inducers on a dark background (Dresp & Bonnet, 1991; Dresp, 1993; Dresp & Bonnet, 1993) as well as with dark inducers on a light background (e.g. Dresp & Grossberg, 1997).

Leonards and Singer (1998) have reported psychophysical evidence for two separate mechanisms underlying figure-ground segmentation in stimuli defined by color contrast and stimuli defined by luminance contrast. Their results show that temporally defined figures; i.e. a situation where figure-ground segregation is achieved by introducing a temporal gap between the presentation of the figure and the presentation of the background, need offset intervals longer than 50 ms to be perceived in isoluminant color stimuli. In luminance defined stimuli, figures with temporal offsets shorter than 50 ms are clearly perceived. The authors conclude that their data are consistent with some of the functional properties of magno- (M) and parvocellular (P) processing streams in the visual system. The M-system defines a subclass of visual neurons with brisk, and transient response properties, and is particularly sensitive to luminance contrast and briefly flashed stimuli. Neurons of the P-system have more sustained response properties, are far less sensitive to luminance contrast, but respond well to isoluminant stimuli that differ from the background only in their color.

To highlight the possible segregation between mechanisms grouping colored forms and those grouping forms defined by luminance in the genesis of spatial facilitation, we have run a second experiment where the exposure duration of the inducers was varied. In one condition, colored inducers, isoluminant with regard to the background and coupled with a chromatic (red) target were presented (chromatic facilitation). In the other condition, we presented gray inducers on a gray background, coupled with an achromatic (gray) target (achromatic facilitation). In both cases, the exposure duration of the inducers was varied, the target being always presented during the last 32 ms of the inducer presentation. On the basis of Leonards and Singer's data on figure-ground segmentation, assuming that they reflect some mechanisms of visual grouping that also underlie spatial facilitation, we expect achromatic spatial facilitation to occur with inducer exposures as short as 30 ms. Chromatic spatial facilitation, on the other hand, should require an exposure duration that is longer than 30 ms.

4.1. Subjects

The same observers as in Experiments 1 and 2.

4.2. Stimuli

The same material, design, and stimuli as in Experiment 1 with the exception that here, only the achromatic inducers (light gray) presented on the achromatic background (a darker gray) and coupled with the achromatic target were taken in one condition. In the other condition, chromatic inducers (green), were presented on the isoluminant, red background and coupled with the chromatic (red) target. For size, luminance, and all the other details, see the description given for Experiment 1.

4.3. Procedure

The procedure was essentially the same as in Experiment 1, with the exception that here, the duration of the inducer exposure was varied. In both experimental conditions (chromatic spatial facilitation vs. achromatic spatial facilitation), the inducers were presented for about 32 (two frames), 64 (four frames), and 192 (eight frames) ms in separate sessions. The exposure duration of the target was always roughly 32 ms, and it was always flashed during the last 32 ms of the inducer presentation.

4.4. Results

The results of the second experiment are represented in Figs. 8a,b and 9a,b. The graphs represent individual data, with performances averaged over the number of trials (minimum 80) for a given target contrast, stimulus condition, and observer. Psychometric functions are plotted for each observer, inducer condition, and exposure duration.

4.4.1. Achromatic configurations on gray backgrounds

The results of observer AM with gray targets and inducers presented on a gray background are shown in Fig. 8a. Strong detection facilitation is observed with the achromatic stimulus configuration for any of the exposure durations of the inducers. Exposure duration of the target was constant (30 ms in all the conditions). The results of observer BD (Fig. 9a) with gray targets and inducers presented on a gray background show the same tendencies as the results of AM. The achromatic

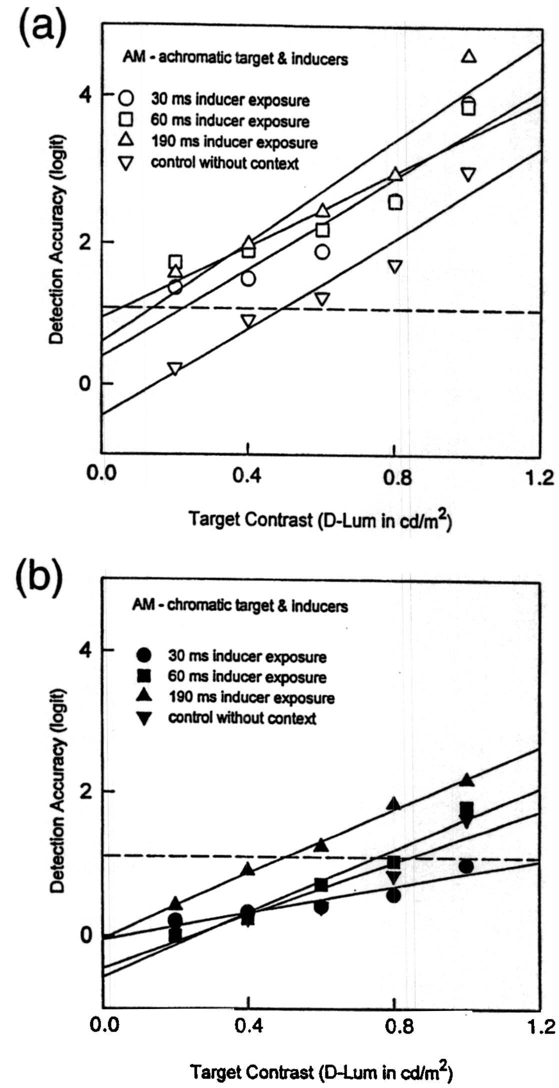

Fig. 8. (a) AM's data with achromatic targets and achromatic inducers with varying exposure duration, on a gray background. Exposure duration of the target is always 30 ms. The theoretical contrast thresholds (in D-Lum) in the different conditions (from top to bottom) are: 0.22, 0.10, 0.13, and 0.43 in the control condition. (b) AM's data with chromatic stimuli. The theoretical contrast thresholds (in D-Lum) here are: 1.25, 0.75, 0.61, and 0.84 in the control condition. Correlation indices (r^2) vary between 0.98 and 0.99.

stimulus configuration produces detection facilitation for all exposure durations of the inducers. Exposure duration of the target was constant (30 ms). For the theoretical thresholds in the different conditions and for correlation statistics, see the figure legends.

4.4.2. Chromatic configurations on red backgrounds

The results of observer AM with red targets and green inducers presented on a red background, isoluminant with regard to the inducers, are shown in Fig. 8b. The exposure duration of the inducing configuration was varied, target exposure was constant (30 ms). Short exposure duration (30 ms) of the chromatic configuration slightly suppresses target detection compared to the control condition without inducers. Only exposure durations of 60 ms and longer induce detection facilitation. The results of observer BD (Fig. 9b) with red targets and green inducers presented on a red background, isoluminant with regard to the inducers, show the same tendencies as AM's data. The shortest exposure duration (30 ms) of the inducers suppresses target detection. Only the longer exposure durations induce detection facilitation. Exposure duration of the target was constant (30 ms).

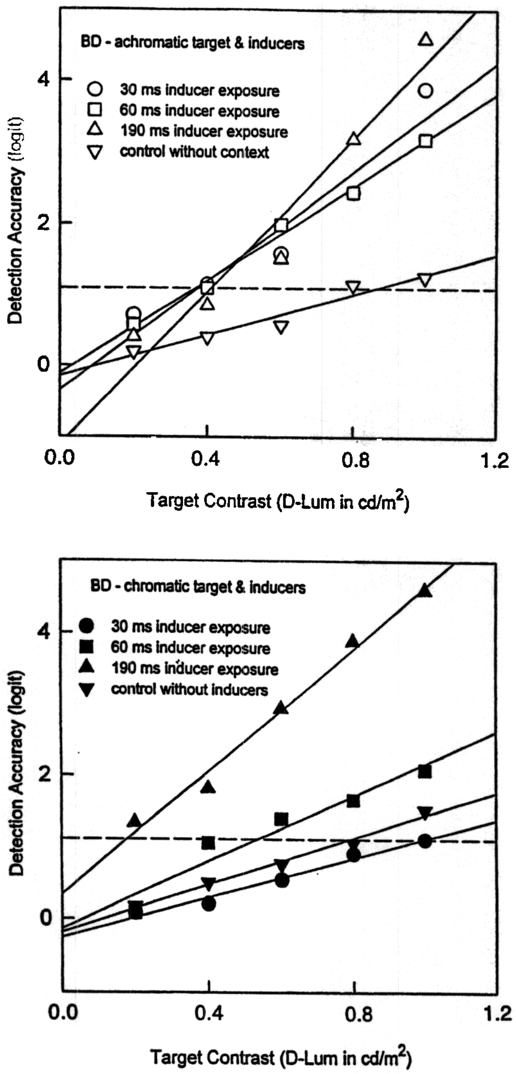

Fig. 9. (a) BD's data with achromatic targets and achromatic inducers with varying exposure duration, on a gray background. Exposure duration of the target is always 30 ms. The theoretical contrast thresholds (in D-Lum) in the different conditions (from top to bottom) are: 0.37, 0.37, 0.41, and 0.86 in the control condition. (b) BD's data with chromatic stimuli. The theoretical contrast thresholds (in D-Lum) here are: 0.99, 0.53, 0.18, and 0.78 in the control condition. Correlation indices (r^2) vary between 0.98 and 0.99.

4.5. Conclusions

Spatial facilitation with achromatic targets and inducers is fully effective with inducer exposures as short as 32 ms. Spatial facilitation with chromatic inducers, presented on an isoluminant background, and chromatic targets requires an inducer exposure longer than 32 ms, but seems to become effective at exposure durations of about 60 ms.

5. General discussion

The results of Experiment 1 gave a first indication that colored stimuli and stimuli defined by luminance only are likely to be grouped by different mechanisms in the genesis of spatial facilitation with collinear stimuli. Experiment 3 provided further evidence for such a functional segregation, and the data are consistent with Leonards and Singer's (1998) observations on texture segmentation. In particular, the M-pathway may help to explain why spatial facilitation occurs selectively with targets and inducers that are solely defined by luminance contrast, whereas the P-pathway may help to explain why spatial facilitation occurs selectively with targets and inducers that are both defined by color and luminance contrast. On the other hand, M- and P-pathway properties are not as separable as originally thought. For example, some P cells can respond to high rates of flicker, up to 30 Hz (Merigan & Eskin, 1986); and many M neurons show some color selectivity (Wiesel & Hubel, 1966; Schiller & Malpeli, 1978; Livingstone & Hubel, 1988; Schiller, Logothetis & Charles, 1990).

Granted that there may be differences in processing speed within the M- and P-pathways, it still remains to explain the pattern of results that has been disclosed in Experiments 1–3. It is suggested below how all the main effects may be qualitatively explained by existent neural models that, in fact, suggested some of the experimental manipulations. These are models of how the brain builds up boundary and surface representations of the visual world, and of how sustained and transient properties of these surface representations may selectively attract attention and thereby alter detection accuracy.

The data are consistent with the following hypotheses, each of which is discussed, modelled, and supported by several different types of data in Grossberg (1994) (see also Grossberg, Mingolla & Ross, 1994; Baloch & Grossberg, 1997; Chey, Grossberg & Mingolla, 1997; Grossberg, 1997; Grossberg & McLoughlin, 1997; Grossberg & Pessoa, 1998): The visual cortex contains separate achromatic and chromatic surface representations; each of these surface representations is organized in an opponent fashion (e.g. red–green, blue–yellow, white–black); there are multiple copies of each achromatic or chromatic surface representation to represent objects at different relative depths from the observer; a change in stimulus contrast can cause a change in perceived surface depth that corresponds to activation of a different depth-selective surface representation; the surface representations can compete with each other for attention; and transients due to stimulus onset can automatically attract attention to themselves on these surface representations.

The surface representations are formed as a result of interactions with boundary representations. Unlike surface representations, the boundary representations do not segregate achromatic and chromatic signals into different representations. Rather, they pool signals from all achromatic and chromatic sources in order to generate the most accurate boundaries possible in response to any given stimulus array. Because of this property, boundaries also pool signals from opposite contrast polarities. As a result of this pooling process, the cells that represent boundaries do not carry a visible perceptual quality, such as brightness or color. Visible percepts are a property of the surface representations.

Why does the brain bother to create boundaries, given that they are perceptually invisible within the boundary system? The theory suggests that the surface system discounts the illuminant at an early processing stage. The discounting process suppresses brightness and color signals in regions where these signals change slowly across space. Subsequent processing levels use the surviving signals to fill-in surface representations wherein the effects of illuminant variations are much reduced. The filling-in process behaves like a diffusion of activity between neighboring cells. Signals from the boundary system form barriers to diffusion within the surface representations, and thereby help to segment a scene into the objects and events that are ultimately perceived.

The model predictions that the brain possesses a sign-invariant boundary system and a sign-variant surface system have been subsequently supported by many experiments, most recently those of Elder and Zucker (1998) and Rogers-Ramachandran and Ramachandran (1998). The latter experiments provide evidence for 'a fast, sign-invariant system concerned with extracting contours and a slower, sign-sensitive system concerned with assigning surface color' (p. 71). In some of these experiments, the surface color in the experiment is achromatic. Despite this fact, a boundary percept emerges under conditions which are too fast for a clear surface percept to be visible. Thus, even if one assumes that achromatic processing is faster than chromatic processing, that distinction, on its own, cannot explain the full pattern of results that is reported herein.

Why are boundaries processed faster than surfaces, even in the achromatic domain? The model suggests that this is true because boundaries must be formed before they can be used to control the filling-in of surfaces. In particular, Grossberg (1994) described how boundaries regulate the process of surface capture, whereby brightness and color signals selectively fill-in only those surface representations whose depth-selective boundaries are spatially in-phase with the surface signals that survive discounting of the illuminant. In this way, brightnesses and colors fill-in their surfaces at the correct depths.

In Dresp and Grossberg (1997), it was suggested how the boundary system could be used to explain the relative amounts of facilitation that occur when the relative contrasts of achromatic inducers and test stimuli were manipulated with respect to the background. This explanation used the hypothesis that short-range oriented simple cell detectors, which are polarity-specific and color-specific, filter visual inputs before they output to longer-range complex cells that group signals from opposite contrast polarities and all colors (Thorell, DeValois & Albrecht, 1984; Grossberg & Mingolla, 1985). In these experiments, the test stimuli were directly contiguous to the inducers, so that the short-range filters could respond in a polarity-specific way to contiguous test-and-inducer combinations. In the present experiments, however, the same pattern of results is obtained when the gap between test and inducer is 10 arcmin (data of Experiments 1 and 3), or 0 or 20 arcmin (data of Experiment 2).

It therefore seems unlikely that spatially short-range, polarity-specific simple cells are sufficient to explain the pattern of results. In addition, the responses of the longer-range grouping cells should be, by and large, insensitive to changing the achromatic and chromatic combinations in the displays. On the other hand, the surface representations are highly sensitive to changes in these displays. Some of these surface properties were used to explain the data of Dresp and Grossberg (1997). The present experiments bring them to the fore.

The main effects in Experiments 1 and 2 can be qualitatively explained as follows. In the data of Figs. 2b and 3b, the surface system is activated by the inducers and is directly involved in facilitating or suppressing targets that are aligned with the edges of the surface that is being represented. The red inducers would be processed on a different surface representation than are the gray target and background. Attention could thus be selectively drawn to this red surface representation, and away from the achromatic surface representation, much as subjects can restrict visual search to just red targets and distractor regions (Egeth, Virzi & Garbart, 1984; Wolfe & Friedman-

Hill, 1992), or as conjunctions of color-and-depth can pop-out during visual search (Nakayama & Silverman, 1986). This surface competition effect can interfere with, and neutralize, some of the boundary effects when colored (here red) inducers are used. In principle, the detection of a gray target can get facilitated within the boundary system by either achromatic or red collinear inducers, because this system pools signals from both achromatic and chromatic inputs before the processing stage at which boundary completion occurs. The model suggests how this pooling process occurs no later than the complex cells of cortical area V1, as reported neurophysiologically (e.g. Thorell et al., 1984). However, if a conflicting surface representation interferes with the boundary signals, then the effect might be destroyed.

In the data of Figs. 2a and 3a, the gray target on a red background with achromatic inducers generates a higher percentage of detections at a low luminance difference than does the gray target on a gray backgound with achromatic inducers in response to the same luminance difference in Figs. 2b and 3b. This result is consistent with the fact that the gray target and inducers have better figure-ground separation in the former case. The greater facilitation by achromatic than chromatic inducers of gray target detection in Figs. 2a and 3a has the same explanation as in Figs. 2b and 3b. The suppressive effect of green inducers with additional luminance contrast in Fig. 3a could be partly attributed to a greater attentional shift away from the achromatic target towards the green inducers as their contrast is increased. In fact, increasing the contrast of the green inducers can cause a shift in perceived depth, which was noticeable to observers of the displays. Such interactions between contrast and perceived depth have been reported in various other paradigms (e.g. Kanizsa, 1974; Egusa, 1983; Bradley & Dumais, 1984; Dosher, Sperling & Wurst, 1986; Purghe & Coren, 1992). Surface representations that are separated by greater depths are structurally more separated from each other in the model. As a result, attention that is focused upon inducers represented on one of them (as in the case of the contrastive green inducers) will interfere more with detection of targets on the other (as in the case of the gray target).

In the data of Figs. 4a and 5a, achromatic inducers interfere with the detection of red targets, just as red inducers interfered with the detection of achromatic targets in Figs. 2 and 3. The fact that green inducers can facilitate red targets is consistent with the hypothesis that surface representations have an opponent organization, and that red and green surfaces are close to one another, but not identical, in this organization. Fig. 5a also shows that green inducers with luminance contrast gave less facilitation than isoluminant green inducers. This difference is consistent with the greater depth difference that is perceived using green inducers with luminance contrast than with isoluminant green inducers, given that the amount of contrast of the green inducers is greater than that between target and background in this experimental series. Thus the target is closer to the isoluminant green inducers than to the green inducers with contrast. In addition, any secondary activation of the achromatic surface representation by the contrast manipulation would also tend to shift attention away from the red target.

Figs. 4b and 5b show the same trends with a red target and red inducers, or red and green inducers, that were shown in Figs. 4a and 5a. Fig. 5b is of particular interest, because it shows that using exclusively red inducers facilitates more than using a combination of red and green inducers. This property is consistent with the hypothesis that red and green surface representations are close, but not identical, due to the opponent surface organization. This opponent property can also be seen by comparing Fig. 4a with Fig. 5a, and Fig. 4b with Fig. 5b. In both cases, red inducers cause more facilitation of a red target than do green inducers.

In summary, an explanation of the total pattern of these facilitation and interference effects cannot merely invoke achromatic vs. chromatic effects. Rather, one may need to also consider the relative separation of surface representations—whether due to differences of color, depth, or opponent organization—and how attention to one such surface representation may facilitate or interfere with attention to another, depending upon how close these surface representations are to each other.

Figs. 8 and 9 probe how long it takes for the facilitation effects to occur in the achromatic and chromatic cases, with achromatic facilitation being faster. Our present interpretation is that this difference is partly due to the different times taken to activate achromatic versus chromatic surface representations due to the different processing speeds of the M-cell and P-cell pathways, respectively. The difference of processing speeds in M and P pathways might not be big enough, however, to account for the current results (Lennie, 1993). The types of surface processes that have been mentioned above seem also to play a role. In particular, we use these factors to explain the paradoxical finding that a 30 ms chromatic inducer exposure tends to elicit lower detection probabilities than the no inducer case, even though 60 and 190 ms chromatic inducer exposures elicit monotonically increasing detection probabilities (Figs. 8b and 9b), and all achromatic inducer durations (30, 60, 190 msec.) yield facilitation of target detection (Figs. 8a and 9a). This is attributed to the slower processing of the chromatic system, including its processing of transient responses. It is suggested that the effects of these transient responses have not yet settled down in response to the 30 ms inducer exposure and, as in many other situations, that these transients attract attention to themselves and thus away from the target stimulus (Yantis & Jones, 1991).

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