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INFLUENCES OF OCCLUSION, COLOR, AND LUMINANCE ON THE PERCEPTION OF FRAGMENTED PICTURES[1]

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Summary.—The contribution of the magnocellular (M) pathway to perceptual completion and depth processing was examined by comparing performance under black-and-white conditions with isoluminant color and diffuse red background conditions expected to suppress M pathway activity. Participants identified the repeated figure in pictures where only fragments of the figures were visible. The fragments were presented either alone (unoccluded) or with an occluder (occluded) filling the space between them. Identification with an occluder involved amodally completing the fragments behind it, i.e., depth processing. All unoccluded versions were easy to identify indicating perceptual completion of the fragments was not influenced by suppressing M pathway activity. Black-and-white occluded versions were also easy to identify. The significantly longer identification times for occluded versions under isoluminant and diffuse red background conditions indicates amodal completion of the fragments was hindered when M pathway activity was reduced, supporting the importance of M pathway activity for depth processing.

We constantly encounter partially occluded objects in our environment. The speed and ease with which we recognize partially occluded objects is a testament to how fast and efficient the visual system segregates occluding from occluded portions of the visual field. One way researchers have studied this process is using fragmented pictures like those shown in Fig. 1. Recognition is easy with black-and-white stimuli like these whether the fragments are interrupted by blank space, e.g., Fig. 1b, d, f, or perceived amodally complete behind an occluder, e.g., Fig. 1a, c, e) (Brown & Koch, 1993). The fragments are exactly the same in both cases, yet the important and obvious phenomenal difference is the fragments are amodally completed in the occluded versions. Similar processes may be involved in grouping the fragments in both versions, but depth processing associated with amodal completion is only necessary in the occluded versions. The present experiment investigated how the stimulus variables of luminance and wavelength would influence perceptual grouping and amodal completion processes using the stimuli shown in Fig. 1.

Researchers exploring the visual processes underlying perceptual segregation and grouping have manipulated sensory variables known to influence the activity of the parvocellular (P) and the magnocellular (M) visual path-

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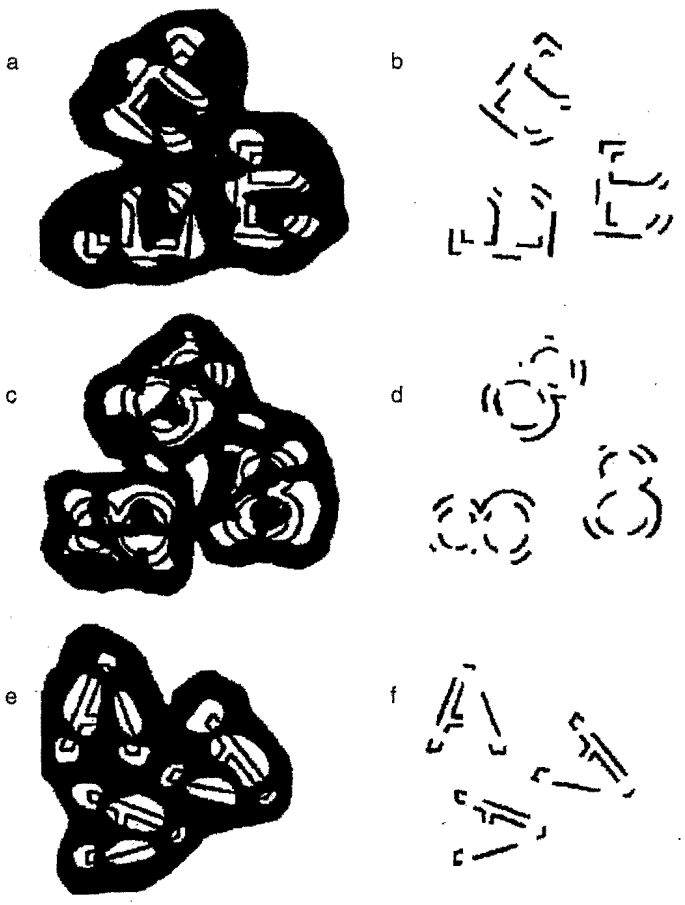

FIG. 1. Occluded and unoccluded fragmented figures

ways (Livingstone & Hubel, 1988). Physiological and psychophysical evidence indicates these pathways contribute differently to perception. Originally based on the discover of X and Y ganglion cells in the cat retina (Enroth-Cugell & Robson, 1966), this model is now also grounded on the response properties of P and M ganglion, lateral geniculate nuclei, and cortical cells in primates (Schiller & Malpeli, 1978; Maunsell & Schiller, 1984). The slower responding, more color sensitive P pathway is involved in the resolution of detailed spatial information. The faster responding, lower resolution M pathway is relatively color insensitive (although see Logothetis, Schiller,

Charles, & Hurlbert, 1990, and below) and thought to be vitally involved in the perception of motion, global structure, and depth (Livingstone & Hubel, 1987, 1988). Researchers have explored the contributions of these pathways to perception by manipulating sensory variables known to influence activity in these pathways, e.g., by suppressing it, and observing how perception changes.

Explorations of contributions by the M and P pathways to perception have capitalized on the M pathway's poor sensitivity to color by using isoluminant stimuli. M pathway contributions to perception have been argued to be reduced under isoluminant conditions because it responds poorly to isoluminant edges (Livingstone & Hubel, 1987, 1988). Inferences about M pathway contributions are made by observing how perception is affected at isoluminance. Such an approach has indicated that, among other things, perceived motion (Cavanagh, Tyler, & Favreau, 1984) and the perception of depth from cues such as linear perspective and occlusion, e.g., amodal completion, can be severely impaired under isoluminant conditions (Livingstone & Hubel, 1987, 1988). Integral to the perception of occlusion and depth is the ability to link the edges of an occluded object where they are interrupted by an occluding object (Livingstone & Hubel, 1988; Shipley & Kellman, 1992). Reported difficulties in perceiving depth from occlusion under isoluminant conditions (Livingstone & Hubel, 1988) are particularly relevant to the present study. Thus, luminance differences, which are important for M pathway activity, are also important for depth perception. Reducing M pathway activity at isoluminance can hinder depth perception.

Another manipulation for reducing M pathway activity comes from physiological (Wiesel & Hubel, 1966; Dreher, Fukuda, & Rodieck, 1976; Krueger, 1977; De Monasterio, 1978; Livingstone & Hubel, 1984) and psychophysical (Breitmeyer & Williams, 1990; Breitmeyer, May, & Heller, 1991; Weisstein & Brannan, 1991; Williams, Breitmeyer, Lovegrove, & Gutierrez, 1991; Breitmeyer & Breier, 1994; Edwards, Hogben, Clark, & Pratt, 1996) evidence diffuse red illumination suppresses M pathway activity. Often considered broad-band in its response to wavelength, the M pathway has been found to contain a large proportion of cells with center-surround receptive fields with inhibitory surrounds responsive to long wavelength, red light (De Monasterio, 1978; Livingstone & Hubel, 1984). Thus, diffuse red light creates a tonic suppression of the response of these M cells (Krueger, 1977; Schiller & Malpeli, 1978). The evidence related to isoluminance and diffuse red illumination suppressing M pathway activity was utilized in the present experiment.

If contributions from the M pathway are important for depth perception and linking interrupted edges (Livingstone & Hubel, 1988) and isoluminant conditions, particularly with diffuse red illumination, reduce M path-

way activity, then, in general, the perception of the repeated figure should be worse in the isoluminant color conditions than the black and white condition. The unoccluded conditions allowed us to test whether isoluminance influenced linking the interrupted edges when depth processing was not necessary. If linking interrupted edges is difficult at isoluminance, then the repeated figures should be more difficult to identify in the unoccluded isoluminant than black and white conditions. If depth processing becomes difficult at isoluminance due to reduced M pathway activity, then the repeated figures should be more difficult to identify for isoluminant occluded, e.g., Fig. 1a, c, e, compared to unoccluded, e.g., Fig. 1b, d, f, versions. Both occluded and unoccluded versions should be equally easy when luminance differences are available, as was the case in our earlier experiments using stimuli made from black ink on white paper (Brown & Koch, 1993).

An alternative hypothesis is identification of the repeated figures should be the same whether an occluder is present under all luminance and color conditions. This hypothesis is based on the finding that identification of two-dimensional letters and the perception of depth from occlusion relations was just as good when the stimuli were defined by luminance edges or isoluminant color edges (Treisman, Cavanagh, Fischer, Ramachandran, & von der Heydt, 1990). Based on these results we should find no differences in performance for occluded and unoccluded stimuli under any color or luminance combination.

Method

Participants

Subjects were undergraduate introductory psychology students receiving course credit for their participation. All had normal or corrected to normal vision, and normal color vision. Color vision was tested using the AO H-R-R Pseudoisochromatic Plates of the American Optical Company under appropriate lighting. A total of 320 students participated, with 16 participants in each condition.

Stimuli and Apparatus

Stimuli were created and presented with a computer-controlled Data Translation 2862 Frame Grabber output to an NEC DM-2000P high-resolution color monitor (P-22 phosphors; CIE coordinates of the red, green, and blue phosphors, respectively, are $x = .625$, $y = .318$; $x = .277$, $y = .587$; $x = .148$, $y = .069$, according to manufacturer's specifications). The monitor was positioned 1.22 m from the subject with the entire screen subtending 14.4° (high) × 18.8° (wide). Viewing was binocular from a chin-rest. Without an occluder the sizes of the stimuli were 12.0° (high) × 10.0° (wide) for Fig. 1d, 11.6° (high) × 9.8° (wide) for Fig. 1b, and 10.7° (high) × 9.3° (wide) for Fig. 1f. With the occluder added, the total sizes were 13.8° (high) × 10.9° (wide) for Fig. 1e, 14.3° (high) × 12.9° (wide) for Fig. 1c, and 14.3° (high) × 13.4° (wide) for Fig. 1a. The individual lines making up the fragments were 3-4 mm thick, i.e., subtending 8.4–11.4'.

Design

A 10 (color combination) × 2 (occluded/unoccluded) between-subjects design was used, with participants randomly assigned to one of the 20 experimental groups. Stimuli varied according to the color combination (green-on-red, blue-on-red, gray-on-red, white-on-red, red-on-green, red-on-gray, blue-on-gray, green-on-gray, gray-on-green, and black-on-white) and occlusion (occluder present or absent). Participants saw either three occluded or three unoccluded stimuli under one of the color combinations. The stimuli were presented in pseudorandom order with half the participants seeing the *B*s first followed by the *8*s, then the *A*s, and half seeing the reverse order.

Procedure

Flicker photometry.—A heterochromatic flicker photometry procedure was followed for isoluminant conditions. Two different colored squares subtending 5° alternated at the center of the screen at 12 Hz. The faster responding M pathway is isolated by the fast flicker rate while its poor wavelength sensitivity means the perception of flicker due to the alternating squares is due to luminance differences between them. As the luminance differences between the two squares reaches isoluminance, the M pathway response is reduced and minimal flicker is perceived.[2]

For the red-on-gray, gray-on-red, green-on-gray, and gray-on-green conditions a gray square of a fixed luminance (54.47 cd/m^2) alternated with a variable luminance red or green square. The luminance of the variable colored square was adjusted until minimal flicker was perceived. Five minimal

[2]The term isoluminance as used here is a psychophysically determined stimulus category wherein the perceived brightness/luminance of the different colors used to create the stimuli were first matched using flicker photometry. The purpose of creating our stimuli this way was to examine how performance at (or near) isoluminance would be affected relative to high contrast, e.g., black-on-white, conditions. We consider our stimuli as near isoluminant given the fact that a "true" isoluminant stimulus is difficult to attain and that even at "true" isoluminance, M pathway activity is expected to be reduced, not eliminated (Logothetis, *et al.*, & Hurlbert, 1990; Schiller, Logothetis, & Charles, 1990; and cf. Breitmeyer, 1992, for a review). The following factors could have contributed to less than perfect, i.e., near, isoluminant stimuli. (a) Without an appropriate lens (Powell, 1981), artificial pupil, or blurred edges, chromatic aberrations of the various wavelengths would have produced slight differences in luminance. (b) Although in the real world occlusion relations are available and perceived across the visual field, unless stimuli were restricted to the central 1-2° of vision, retinal inhomogeneities would have likely led to small luminance differences. (c) Even if these factors were controlled for, it would only allow us to imply that the M cell response might be reduced slightly more, i.e., M cell activity would never be eliminated, compared to the present near-isoluminant conditions. Thus, our isoluminant conditions should be considered at or near isoluminance and be expected to produce relatively less M cell activity compared to the high-contrast conditions.

flicker settings were made with the average of the last four settings used as the isoluminant point. For these conditions the gray stimulus regions were always 54.47 cd/m^2, and the red or green stimulus regions were the individual's isoluminant value.

For conditions not containing gray or including blue, e.g., red-on-green, green-on-red, blue-on-gray, and blue-on-red, a slightly different procedure was followed. For the red-on-green and green-on-red conditions, green was first set isoluminant to gray (as described above). The luminance of the green square was then fixed at that setting while it was alternated with a variable luminance red square. The luminance of the red square was then adjusted to obtain minimal flicker. For the blue-on-red and blue-on-gray conditions, blue was used as the standard (71.26 cd/m^2), and either red or gray was adjusted to it. Blue was set as the standard because it was the least visible and had the fewest addressable luminance levels after linearization. For the white-on-red and black-on-white nonisoluminant conditions, the white regions had a luminance of 78.79 cd/m^2. For the white-on-red condition we used an average isoluminant setting from a pilot study wherein participants set red isoluminant to gray (45.56 cd/m^2). The luminance of the black regions was 8.9 cd/m^2.

Experimental trials.—A picture containing a different repeated figure was presented each trial. Participants verbally identified the repeated figure as quickly as possible. The dependent measure was time elapsed between stimulus presentation and correct identification of the repeated figure with a 60-sec. limit. After incorrect responses participants were told to continue. Participants responded until either the repeated figure was identified or the 60-sec. trial had elapsed. If participants were unable to identify the repeated figure by the end of a trial, they were given an identification time of 60 sec.[3]

Results and Discussion

The dependent measure was each participant's mean identification time. The results are shown in Fig. 2. A 10 (color combination) × 2 (occlusion) between-subjects analysis of variance yielded significant main effects of color combination ($F_{9,135}=5.99$, $p<.0001$) and occlusion condition ($F_{1,15}=91.05$, $p<.0001$) and a significant interaction for color combination × occlusion ($F_{9,135}=5.18$, $p<.0001$). Overall, identification times were longer for the occluded compared to the unoccluded condition. *Post hoc* analyses (Newman-Keuls) indicated ($p \leq .05$) identification times were significantly longer for occluded than unoccluded versions for each color combination except black-on-white and red-on-gray. Identification times for unoccluded versions were not significantly different from each other. When comparing within occluded conditions, black-on-white and red-on-gray had shorter identification times than all other color combinations. These differences were significant when compared with gray-on-green and the four combinations with a red background, i.e., blue-on-red, green-on-red, gray-on-red, and white-on-red but not significant when compared with the blue-on-gray, green-on-gray, and red-on-green combinations. Performance in the black-on-white conditions replicates previous findings with black ink on white paper stimuli of comparable size (Brown & Koch, 1993). This is important because it demonstrates the replicability of the effect and the generalizability of the effect across stimulus-presentation modes.

[3]This method was used in our previous study which allowed for direct comparison between studies. This decision was also based on a pilot study using a 3-min. trial limit wherein identification usually occurred within 1 min. Beyond 60 sec., occasionally participants eventually identified the repeated figure, but more often they became frustrated and stopped guessing. Assigning 60 sec. for trials when identification did not occur imposed a ceiling on identification times, but this really only affected the occluded color conditions already indicating they were different with a 1-min. limit.

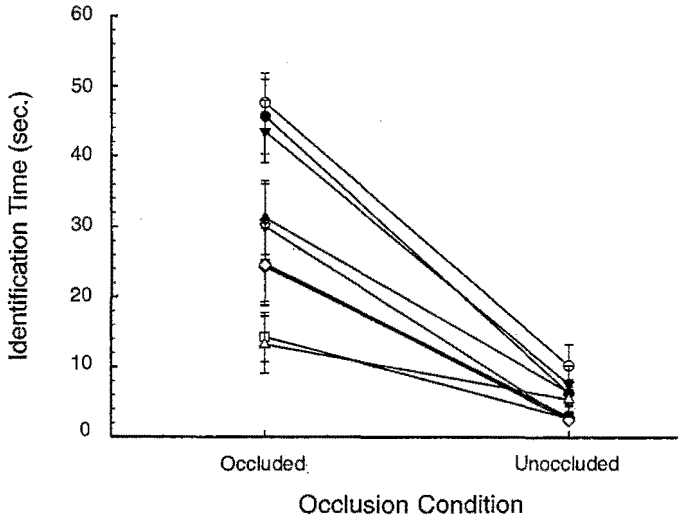

FIG. 2. Mean identification time for 10 stimulus-on-background color combinations as a function of occlusion (Blue-on-red, ○; Green-on-red, ●; Gray-on-red, ▼; Gray-on-green, ▲; White-on-red, ▽; Red-on-green, ■; Blue-on-gray, ◆; Green-on-gray, ◇; Red-on-gray, □; Black-on-white, △)

The similar performance in the unoccluded conditions indicates it did not matter whether the fragments were isoluminant or seen on a diffuse red background. Irrespective of the luminance or the color of the stimuli, it was easy to interpolate the fragments across the blank space and recognize the

repeated figures. These findings are consistent with Treisman, *et al.* (1990) and contrary to suggestions that linking by collinearity is more difficult at isoluminance (Livingstone & Hubel, 1988).

Identification times were significantly longer for occluded compared to unoccluded versions in seven of the eight isoluminant conditions. The difficulty with the conditions requiring amodal completion of the fragments suggests depth processing was more difficult under isoluminant conditions, a finding consistent with previous research (Livingstone & Hubel, 1988). The difficulty with the occluded versions was not due to problems seeing the fragments, as evidenced by the good performance with the unoccluded versions. The difficulty identifying the fragmented figures in the majority of the occluded isoluminant conditions, particularly those with a diffuse red background, suggests reducing the luminance contrast between the stimuli, i.e., the fragments and the occluder, and the background made it more difficult amodally to complete the fragments behind the occluder, i.e., segregate the fragments and occluder in depth. These results support the position M pathway activity is important for depth processing and reducing its activity using isoluminant and diffuse red background conditions hinders depth processing.

Although our interpretation of the results in terms of M pathway activity is supported by the majority of results, this interpretation must be qualified somewhat considering the results from the occluded red-on-gray condition, wherein identification was as fast as the black-on-white condition. At present it is not clear why this particular isoluminant condition differs from the others. It should be noted, however, that, although the occluded red-on-gray condition was the only isoluminant condition where identification times did not differ from its unoccluded counterpart, the occluded red-on-gray condition was not significantly different from the occluded blue-on-gray, green-on-gray, and red-on-green conditions. Isoluminant conditions, then, may negatively affect identification of the occluded fragmented figures, but influence was greatest with a diffuse red background.

The effect of a diffuse red background is highlighted by the difficulty in the occluded white-on-red condition. Despite the presence of luminance differences between the white stimuli and the red background, the inhibitory effect of the diffuse red background on M pathway activity appears to have been enough to interfere with amodal completion, and therefore, depth processing. Again, this was not due to some inability to perceive the fragments as evidenced by the white-on-red unoccluded results. Thus, the inhibitory effect of a diffuse red background on M pathway activity was surprisingly capable of influencing identification even when luminance differences were present.

General Discussion

The present study examined how the sensory variables of color and luminance influence perceptual completion and depth processing using occluded and unoccluded fragmented figures. Identification in the unoccluded conditions required grouping the fragments into separate figures and perceptually completing them. Identification in the occluded conditions would have required the additional processes of segregating the fragments as distinct from the occluder and amodally completing them behind it. Considering the occluder is phenomenally seen in front of the fragmented figures, the results indicate that, for the most part, depth segregation and amodal completion were hindered when the stimuli were at or near isoluminance with the background, particularly when the background was red. When the occluder was absent eliminating the need for depth processing, completion and recognition of the fragmented figures was unaffected by the color or luminance conditions. These findings support the hypothesis that depth processing should be hindered under isoluminant conditions due to reduced M pathway activity making it more difficult to identify the repeated figures in the occluded compared to unoccluded versions. The ability to complete amodally the fragments behind the occluder was more difficult when M pathway activity was reduced. When luminance differences were available, however, both occluded and unoccluded conditions were equally easy, as was the case in our earlier experiments using stimuli made from black ink on white paper (Brown & Koch, 1993).

In part, our results could be interpreted as support for Livingstone and Hubel's (1987, 1988) assertions M pathway activity is predominant in depth processing and is suppressed at isoluminance (Livingstone & Hubel, 1987, 1988). However, our different results with different color combinations suggests all isoluminant conditions are not equally effective at reducing M pathway activity and, therefore, M pathway contributions to depth processing. This interpretation is supported by physiological evidence showing considerable variation across M cells in the luminance ratios that are effective at minimizing their activity (Logothetis, *et al.*, 1990). Thus, using isoluminance only may not be the most effective way of attempting to reduce M relative to P pathway activity because some M cell activity is likely and P cell activity may also be reduced at isoluminance (Logothetis, *et al.*, 1990).

We discuss the results from the perspective of Breitmeyer's work (1992; Breitmeyer & Breier, 1994) related to the suppressive effects of diffuse red illumination on M pathway activity and Weisstein's work related to spatiotemporal vision and figure-ground perception (Klymenko & Weisstein, 1986; Brown & Weisstein, 1988; Weisstein & Brannan, 1991; Weisstein, Maguire, & Brannan, 1992). By focusing on the tendency of diffuse red illumination to selectively suppress M cell activity, Breitmeyer has shown the temporal as-

pect of transient M pathway activity can be disrupted (Breitmeyer & Williams, 1990; Breitmeyer, *et al.*, 1991; Williams, *et al.*, 1991; Breitmeyer & Breier, 1994). Applying the same logic to spatial aspects of vision, Weisstein, *et al.* (1992) have proposed that whether a region in the field is seen as figure or ground is related to the relative activity of the P and M pathways within the region. Thus, any stimulus variable that increases P pathway activity or suppresses M pathway activity within a region increases the likelihood of that region being processed and perceived as figure. For example, the P pathway is more sensitive to higher spatial frequencies relative to the M pathway. Previous research using figure-ground ambiguous stimuli filled with sine-wave gratings has shown that the regions containing the relatively higher spatial frequency gratings were predominantly seen as figure (Klymenko & Weisstein, 1986; Brown & Weisstein, 1988). Consistent with these results, Weisstein and Brannan (1991) found the relatively higher spatial frequency half of a bipartite field filled with two slightly different low spatial frequency sine-waves (1.0 and 1.4 cpd) was seen predominantly as figure under achromatic conditions. However, when red light was superimposed on one side and green light matched for luminance superimposed on the other side, the red side consistently appeared as figure to the green side regardless of spatial frequency. Their interpretation was the red illuminated region was predominantly seen as figure because P pathway activity was relatively greater in those regions due to the suppressive effect of the red light on M pathway activity. From this perspective, the red backgrounds of our stimuli would have led to greater suppression of M pathway activity than any of the other isoluminant conditions. This would have produced a relatively greater "figure" response from the red background regions interfering with the interpretation of the fragments as the visible portions of white figures behind a white occluder. This interference could have produced the observed increased identification times.

In conclusion, our results are accounted for well by Breitmeyer's (1992) model of the perceptual consequences of decreased M pathway activity in the presence of diffuse red illumination. Our results indicate that the contribution of M pathway activity to perceptual grouping and depth segregation is not a simple function of whether or not luminance information is present. The idea that M pathway activity is vital for depth segregation and is reduced or eliminated under isoluminant conditions is partially supported by our results, although alternative explanations exist (i.e., see Grossberg, 1994). The difficulty identifying the repeated figure in the isoluminant occluded conditions with red backgrounds supports the idea M pathway contributions are important for depth perception and M pathway activity is reduced under diffuse red illumination. As Breitmeyer (1992) has noted, "it is likely that further exploration of the suppressive effects of diffuse red light on M neurons will reveal additional properties of the M and P pathways and their respective contributions to spatial and temporal aspects of human vision" (p. 57). Our results provide additional evidence of the suppressive effects of diffuse red light on M pathway contributions to spatial aspects of human vision.

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