

**COLOR FROM MOTION: DICHOPTIC ACTIVATION AND  
A POSSIBLE ROLE IN BREAKING CAMOUFLAGE**

**Carol M. Cicerone<sup>1</sup> and Donald D. Hoffman**

Department of Cognitive Sciences

University of California, Irvine

Irvine, CA 92697

<sup>1</sup> To whom all correspondence should be sent

**Abstract.** "Color from motion" (Cicerone and Hoffman, 1992; Cicerone, Hoffman, Gowdy, and Kim 1995; Miyahara and Cicerone 1996 and this issue) describes the perception of a spread of subjective color over achromatic regions seen as moving. The effect can be produced in a stimulus display of multiple frames shown in quick succession, each frame consisting of a fixed, random placement of colored dots on a high luminance white background with color assignments of some dots, not dot locations, changing from frame to frame. Here we present evidence that the perception of apparent motion and the spread of subjective color can be activated by binocular combination of disjoint signals to each eye: The dichoptic presentation of every odd-numbered frame of the full stimulus sequence presented to one eye and, out of phase, every even-numbered frame to the other eye produces a compelling perception of color from motion equal to that seen with the full sequence presented to each eye alone. This is consistent with the idea that color from motion is regulated in sites at or beyond the convergence of monocular pathways. When the background field in the stimulus display is of low luminance, an amodally complete object, fully colored and matching the dots defining the moving region in hue and saturation, is seen to move behind a partially occluding screen. Observers do not perceive such an object in still view. Hence, color from motion can be used by the visual system to produce amodal completion, suggesting it may play a role in enhancing the visibility of camouflaged objects.

## INTRODUCTION

A number of reports of color phenomena associated with moving or rapidly changing stimulation have been reported since the nineteenth century. The first of these reports is attributed to the French monk Benedict Prevost who, in 1826, observed colors in the vicinity of his fingers when waving his hands about in dim light (Cohen and Gordon 1949; Gregory 1987). This effect was rediscovered at least a dozen times by, among others, Gustav Fechner and Sir David Brewster (Cohen and Gordon 1949). Other related phenomena include Benham's top (1894) in which a rotating disk of black and white patterns produces subjective colors; Bidwell's ghost (1896) describing – under conditions of stimulation by white light, colored light, and darkness – the perception of the complement of the presented color instead of the color itself; Wallach's (1935) observations of enhancement of subjective colors when the pattern is seen in apparent motion; and the recent reports of the perception of motion accompanied by a spread of color over achromatic regions seen as moving (Cicerone and Hoffman, 1992; Shipley and Kellman, 1994; Cicerone, Hoffman, Gowdy, and Kim 1995). In our studies the effect was produced in a stimulus display of multiple frames shown in quick succession, each frame consisting of a fixed, random placement of colored dots on a high luminance white background with color assignments of some dots, not dot locations, changing from frame to frame. Cicerone *et al.* (1995) found that the spread of subjective color into physically achromatic regions is restricted to the part of the display that was seen to be moving. Such spread of subjective color was not seen in still views of single frames. Furthermore, for slow rates of change

in the color assignments of the dots, little or no apparent motion is perceived and the spread of subjective color is not seen. Hence, the effect was called "color from motion."

Miyahara and Cicerone (1996 and this issue) present results showing that in the absence of luminance differences between dots in the test region and those in the surround region, chromaticity difference alone is sufficient to produce color spread from motion. In this case, color spread is perceived despite the absence of a subjective contour. Thus, contour formation appears not to be a prerequisite for color from motion. Miyahara and Cicerone also show that the hue and saturation of the perceived color were governed by the luminance and the chromaticity of the dots in the test region, but not of the dots in the surround region within the luminance range tested. Thus, color from motion may arise in sites different from those responsible for the regulation of color contrast. This study also provides additional evidence for the hypothesis that motion drives the color spread: Under some conditions for which the luminance of the test dots is lower than that of the surround dots, apparent motion can be seen in the absence of color spread.

Presented in this report is evidence that the perception of apparent motion and the spread of subjective color can be activated by binocular combination of disjoint signals to each eye: The dichoptic presentation of every odd-numbered frame of the full stimulus sequence presented to one eye and, out of phase, every

even-numbered frame to the other eye produces a compelling perception of color from motion equal to that seen with the full sequence presented to each eye alone. This is consistent with the idea that color from motion is regulated in sites at or beyond the convergence of monocular pathways. The possible functional role of color from motion is explored in other experiments. If the luminance of the background field is reduced, in the motion mode observers report perceiving an amodally complete object, fully colored and matching the test dots in hue and saturation, moving behind a partially occluding screen, although they do not perceive amodal completion in still view of a single frame. Amodal completion is perceived even when a high proportion of the dots in the surround region are of the same color as in the test region, thus making the test region less visible. Hence, color from motion can be used by the visual system to produce amodal completion, suggesting it may play a role in enhancing the visibility of camouflaged objects.

**EXPERIMENT 1: Single eye views can be binocularly combined to produce color from motion**

One frame from the original displays is shown at the left of Figure 1. Each stimulus presentation was comprised of 12 frames. Each frame consisted of a white square filled with a random array of dots. (The figure accurately portrays the dot density but not the actual colors or luminosities.) From frame to frame the location of each dot was held constant, while the assignment of color for each dot was progressively changed according to an algorithm that colored all dots within a

shifting circular area green (test region) and all other dots red (surround region). Thus, dots did not change locations, only color assignments of some of the dots were changed. When such frames are shown in rapid succession, one sees more than just dots changing color; one sees a moving, luminous region, uniformly colored green, that can be bounded by a circular subjective contour, as illustrated at the right of Figure 1. For this stimulus, observers report that the green region appears to be produced by a green spotlight or veil roving over a field of red dots.

*(Figure 1 near here)*

Prior results (Cicerone *et al.*, 1995; Miyahara and Cicerone, 1996 and this issue) suggest that the perception of motion is required for the spread of subjective color into achromatic regions seen as moving. Certainly, unlike neon color spreading in still displays (e. g., Varin, 1971; van Tuijl, 1975), color spread is not seen if single frames of our stimulus are seen in still view. Furthermore, the spread of subjective color is restricted to the area seen as moving. Finally, under some conditions for which the luminance of the test dots is lower than that of the surround dots, Miyahara and Cicerone (1996 and this issue) show that apparent motion can be seen in the absence of color spread. If apparent motion must be perceived in order for the spread of subjective color to be perceived, the locus of the effect can be placed at or beyond the site regulating apparent motion. Apparent motion can be perceived with random texture kinematograms presented dichoptically in spatio-temporal quadrature (e. g., Carney and Shadlen, 1993). Although not without controversy (e. g., Georgeson and Shadlen, 1992), the idea

that apparent motion is achieved at or beyond the site of binocular combination is supported by physiological evidence as well (e. g., Mikami, Newsome, and Wurtz, 1986).

Experiment 1 tests the idea that color from motion occurs beyond the point of binocular combination. The stimuli consisted of twelve frames as before, but the green test dots were missing in every other frame. Observers were asked to judge the spread of subjective color for this reduced stimulus. We then asked whether this reduced set of frames presented separately and out of phase (dichoptically) to each eye could be combined binocularly to produce color from motion as robustly as in the original, full stimulus.

### **Method**

**Observers.** The observers for this experiment were the two authors. Acuity for these two observers were corrected to 20/20. Color vision for each observer was within the normal range as assessed by anomaloscope (Neitz OT, Neitz Instruments Co., Ltd., Tokyo, Japan) matches.

**Stimuli and Apparatus.** The stimuli were generated by an Apple MAC IIfx and displayed on a Raster Ops Color Monitor. CIE 1931 (Wyszecki & Stiles 1982) coordinates and luminosity values for stimuli used in these experiments were measured with a Spectracolorimeter (Photo Research, PR-650). The stimulus we used is shown in Figure 2. (The figure accurately portrays the dot density but not the actual colors or luminosities.) At the left is shown two frames of the sequence seen by the left eye, at the right the corresponding two frames

seen by the right eye. We presented separate views to each eye by means of a simple optical device (Figure 3) which allowed each eye to be stimulated alone (monoptic view) or at the same time with these different stimulus streams (dichoptic view). In the dichoptic view when the observer's right eye saw the first frame of our standard display, the left eye saw an identical array of red dots minus the green dots normally located in the central region. The next frame in the sequence was presented to the left eye while simultaneously a frame without the green dots was presented to the right eye. Thus, the right eye saw every odd-numbered frame of the standard 12-frame display, and the left eye saw every even-numbered frame. Every frame consisted of a white (CIE  $x=0.2756$ ,  $y=0.2907$ ; luminance =  $93.3 \text{ cd/m}^2$ ) square (5 deg of visual angle on each side as viewed from a distance of 44 inches) filled with a random array of 900 dots, each subtending a visual angle of 3 minutes of arc. Within a circular patch subtending 2 degrees of visual angle, the dots were green (CIE  $x=0.2797$ ,  $y=0.6102$ ; luminance= $62.4 \text{ cd/m}^2$ ); all other dots were red (CIE  $x=0.6213$ ,  $y=0.3444$ ; luminance= $20.1 \text{ cd/m}^2$ ). From frame to frame the location of each dot in the surround was held constant, while the assignment of color to dots was progressively changed according to an algorithm (Cicerone et al. 1995) that colored all dots within a shifting circular area green and all other dots red. In the first frame the center of the circular region was 0.75 degree below the center of the display. On each successive frame the center of the circular region was moved up 0.125 degree.

*(Figure 2 near here)*

*(Figure 3 near here)*

**Procedures.** The observer was instructed to keep gaze centered on the display. (Scanning the display instead does not alter the effect as compared to maintaining fixation anywhere in the display. We instructed the observers to keep gaze centered on the display to standardize the viewing conditions for all observers and to obviate any concerns that tracking eye movements might produce optical blur and, thereby, color spread. Two observations argue against any contamination of the results due to eye movements: First, color spreads uniformly throughout achromatic regions seen as moving. Any optical smearing due to eye movements might be expected to produce nonuniform effects, blur concentrated near the dots or colored streaks originating at the colored dots. Second, if eye movements produce blur in the central test region, then this should also be a factor for the surround dots. There is no color spread in the surround region.) The observer was instructed to rate, on a scale from 0 to 4, the perceived color spread for each stimulus presentation. Zero was to be used if the observer was absolutely certain of the absence of color spread, one if moderately certain of its absence, two if uncertain, three if moderately certain of its presence, and four if absolutely certain of its presence. Thus, the presence of color spread was indicated by ratings greater than 2, its absence by ratings less than 2. In practice each observer used the full range of ratings.

**Design.** We compared three conditions: (1) the right eye only view of the reduced stimulus, (2) the dichoptic view with left and right eyes viewing the

reduced stimulus out of phase, and (3) the monocular or binocular view of the standard stimulus.

The independent variable was the update rate of the 12 frames in each presentation. There were four different update rates (equivalent to speeds of 0.37, 0.92, 1.38, and 2.05 degrees per second). Within a session, either dichoptic or monoptic view and each of the four update rates was presented in pseudorandom order. The results are based on mean values of the ratings over three sessions. The data for the full stimulus was collected in separate sessions from those using the reduced stimulus.

### **Results and Discussion**

Each observer shows an enhancement in perceived color spread with the dichoptic view of the reduced stimulus as compared to the monoptic view of the same stimulus (Figure 4). This shows that the visual system can use the binocular combination of left and right eye views. Furthermore, a comparison of the dichoptic view of the reduced stimulus to the original, full stimulus show that these results are indistinguishable: The dichoptic information is as effective as the information from the full stimulus. Together these comparisons imply that the mechanisms that give rise to color from motion lie central to the point of binocular combination.

*(Figure 4 near here)*

When judgements are based on the right eye only view of the reduced stimulus, color spreading is less than that for the binocular view of the standard stimulus. In this context, we note that the results were identical if the full, standard stimulus was viewed monocularly or binocularly. Thus, it cannot be argued that the difference between the monoptic and dichoptic views of the reduced stimulus is due, at least in part, to binocular combinations of retinal effects. That the dichoptic view produces perception of color spread equal to the full view of the standard stimulus also argues against any significant retinal effects.

These results in combination with previous results discussed above suggest an interaction between the processing of color and motion occurring at a site at or beyond binocular combination. Others have shown that a variety of image cues – not solely luminance contrast – can influence the perception of motion (e.g., Krauskopf and Farell 1990; Nakayama and Shimojo 1990; Kersten, Bulthoff, Schwartz, and Kurtz 1992; Kooi, DeValois, Switkes, and Grosf 1992; Dobkins and Albright 1993; Trueswell and Hayhoe 1993). Our results suggest the reverse: that the perception of motion can influence the perception of color and the spread of subjective color over achromatic regions defined by motion. Furthermore, the finding that color spreads throughout a region defined by motion is consistent with the idea that color information may be retained in the motion pathway. The evidence provided here cannot specify whether the hypothesized interaction between color and motion pathways occurs in early motion systems or at higher levels. The only evidence we offer suggests that the receptive fields subserving the effect may be large: Cicerone et al. (1995) showed that test regions

near one degree of visual angle (as compared to a range of 0.3 to 2.4 degrees) produces optimal color spread from motion.

**EXPERIMENT 2: Background luminance regulates whether color spread is seen as a veiling light or in amodal completion**

In the next two experiments, we consider whether color from motion can provide an effective way to break camouflage, thus making the interpretation of the visual scene more accurate and useful. The idea that motion can break camouflage goes back at least to Wertheimer (1923). His principle of "common fate" is based on the observation that figures that are seen to move together are perceptually grouped, even if they are not grouped when stationary. In still view of our display, the centrally located green dots are grouped, by virtue of their color, from the surrounding red dots. When apparent motion is perceived, the region defined by motion is enveloped in a spread of subjective color into achromatic regions near the green dots. The color spread is uniform and of low saturation (Miyahara and Cicerone, 1996 and this issue). It can be argued that this enhances the perceptual grouping and the visibility of the region defined by motion. We asked whether this could be a mechanism for breaking camouflage. In order to pursue this question, we modified the stimulus to make it more similar to camouflaged views in natural environments. In natural scenes, camouflaged objects often lie behind screening elements. When this type of camouflage is broken, the object is perceived in "whole" or in "amodal completion" (Michotte, Thines, and Crabbe 1964; Kanisza 1979) even if parts of the object lying behind

the screening elements are still occluded. We predicted that we could change the perception from the original veiling spread of color to one in which colored objects are seen in amodal completion by using a stimulus consisting of regions that could more readily be seen as a screen for other regions in the stimulus. For this purpose, we progressively reduced the luminance of the background and measured the effect of such a reduction on the perceived organization of the stimulus and the perceived colors of objects.

### **Method**

**Observers.** The observers for this experiment were the authors and, in addition, three other naive observers who were unaware of the purposes of the experiment. Color vision for each observer was within the normal range as assessed by anomaloscope (Neitz OT, Neitz Instruments Co., Ltd., Tokyo, Japan) matches.

**Stimuli and Apparatus.** The stimuli were generated by a Power MAC 7500 and displayed on a Hitachi Color Monitor. CIE 1931 (Wyszecki & Stiles 1982) coordinates and luminosity values for stimuli used in these experiments were measured with a Spectracolorimeter (Photo Research, PR-650). One of the stimuli we used is shown in Figure 5 (left). (The figure accurately portrays the dot density but not the actual colors or luminosities of the dots or the background.) Twelve such frames were presented in succession at a rate equivalent to 3.07 deg/sec. Every frame consisted of a background (CIE  $x=0.2787$ ,  $y=0.3028$ ; luminance equal to 0.23, 5.93, 22.3, 51.8, or 105  $\text{cd/m}^2$  square (5 degrees of visual angle on each side as viewed from a distance of 44 inches) filled

with a random array of 900 dots, each subtending a visual angle of 3 minutes of arc. Within a circular patch subtending 1 degree of visual angle, the dots were green (CIE  $x=0.2854$ ,  $y=0.5979$ ; luminance= $73.8 \text{ cd/m}^2$ ); all other dots were red (CIE  $x=0.6143$ ,  $y=0.3374$ ; luminance= $19.9 \text{ cd/m}^2$ ). From frame to frame the location of each dot in the surround was held constant, while the assignment of color to dots was progressively changed according to an algorithm (Cicerone et al., 1995) that colored all dots within a shifting circular area green and all other dots red. In the first frame the center of the circular region was 0.75 degree below the center of the display. On each successive frame the center of the circular region was moved up 0.125 degree.

*(Figure 5 near here)*

**Procedures.** In preliminary trials, the observer viewed all stimuli and was asked for a verbal description of what was seen. The observer's verbal reports are detailed below. Briefly, under a range of low luminance backgrounds the observers reported seeing a highly saturated, fully colored green disk moving in front of a red field. Both the red field and the green disk appear to lie behind a dark screen with holes (amodal completion). Depending on the background luminance, this percept could be somewhat ephemeral. Within each trial of 30 sec duration, the observer was instructed to start a stop watch when amodal completion was seen, to stop it when anything other than amodal completion was seen, and to start and stop the watch according to this rule as often as needed during each trial. On each trial we

recorded the number of seconds out of the total 30 sec interval that the observer reported seeing amodal completion of a moving green circle.

**Design.** We varied the luminance of the background over five values, 0.23, 5.93, 22.3, 51.8, 105  $\text{cd/m}^2$ , in pseudorandom order. The results are based on mean values of the trials over three sessions.

## **Results and Discussion**

The observers were first asked to verbally describe what was seen under each background condition. In preliminary experiments Observer DH reported seeing amodal completion, but only fleetingly, for all luminances of the background except the dimmest. Because this percept was such a sporadic one for him, we were unable to collect consistent data. The results we show are for the four other observers, three of whom were naive observers. With backgrounds of high luminosity, the observers described a veiling spread of color into achromatic regions near the green dots. The saturation of the veiling color was described to be low, in line with previous measurements under this condition (Miyahara and Cicerone, 1996 and this issue). For backgrounds of low luminance, the observers reported seeing one of two percepts: (1) A dark sheet inscribed with red dots was seen. The sheet had a circular moving hole through which a second dark sheet, this one inscribed with green dots, could be viewed. It should be noted that in this percept, the observer sees a contour but no color spread. (2) A uniformly colored and highly saturated green (matching the green dots) circle was seen to be moving in front of a uniformly colored and highly saturated red field. All was

viewed through a screen seen as a dark sheet with holes punched into it. (This is illustrated at the right of Figure 5.) We designated the latter description as amodal completion. Neither percepts described are seen in still view of single frames of the stimulus, nor are they seen if apparent motion is not perceived.

The results (Figure 6) show that observers see a moving green disk in amodal completion for a large proportion of the viewing time when the background luminance is low (less than 5.93 cd/m<sup>2</sup> for CC; less than 22.3 cd/m<sup>2</sup> for VC; at 5.93 and 22.3 cd/m<sup>2</sup> for PG; and less than 5.93 cd/m<sup>2</sup> for DN). With these dim backgrounds, when amodal completion is not seen, observers report seeing the stimulus as described in verbal report (1) above. It should be emphasized that none of the observers reports seeing amodal completion of a green disk in still view. When the background is of high luminance – 105 cd/m<sup>2</sup> which matches the original conditions – all observers see a low saturation veiling spread of color over the region seen as moving. Amodal completion is never seen.

*(Figure 6 near here)*

These results are consistent with the idea that motion can produce an organization of the visual scene in which objects seen to lie behind a partially occluding screen are perceived as fully colored. In order for this perception to occur, color must spread throughout regions defined by motion, even into those regions which are occluded from view. In this sense, the amodal completion of the green disk is a percept mediated by motion and color. As compared to color from

motion seen with the original stimulus (Cicerone et al. 1995; Miyahara and Cicerone 1996 and this issue), the perceived color spread in this case is markedly higher in saturation and the organization of the scene is different. Nonetheless, in both cases, the perception of motion appears to be essential in producing a spread of color over the region defined by motion. Hence, in this respect, the mechanisms driving the color spread, whether seen as a desaturated veiling color or as a highly saturated disk, are likely to be the same.

### **EXPERIMENT 3: Color from motion breaks camouflage for objects hidden by color camouflage**

Although motion and amodal completion enhance the visibility of a green disk seen as lying behind a partially occluding screen in Experiment 2, the clear segregation of red dots in the surround and green dots in the central test regions allows an obvious grouping according to color even without motion. We reasoned that a robust camouflage-breaking motion mechanism should be able to render the green disk visible even under conditions for which color is not a reliable cue in still view. We devised a stimulus in which a proportion of the dots in the surround were also green. When half or more of the dots in the surround region were green, the green test region was not easily seen in still view (Figure 7). Observers could not reliably point out the test region and amodal completion was never seen in still view. The effects on visibility of amodal completion were measured as a function of the proportion of surround dots painted green.

*(Figure 7 near here)*

## **Method**

**Observers.** Four observers, three naive, from the previous experiment served in this experiment. VC, PG, and DN were unaware of the purposes of the experiment. CC was one of the authors. Color vision for each observer was within the normal range as assessed by anomaloscope (Neitz OT, Neitz Instruments Co., Ltd., Tokyo, Japan) matches.

**Stimuli and Apparatus.** The stimuli and apparatus were identical to those of Experiment 2 with the following exceptions: The background was fixed at 5.93 cd/m<sup>2</sup> and the surround dots were varied in chromaticity such that all, three-quarters, one-half, or one-quarter of the total number were red. All other dots, including dots in the test region, were green.

**Procedures.** The general procedures of Experiment 2 were followed. Within each trial of 30 sec duration, the observer was instructed to start a stop watch when amodal completion was seen, to stop it when anything other than amodal completion was seen, and to start and stop the watch according to this rule as often as needed during each trial. We recorded the number of seconds out of the total 30 sec interval that the observer reported seeing amodal completion of a moving green circle.

**Design.** We varied the color composition of the background dots over five values – one-fourth red and three-fourths green; one-half red and one-half green; three-fourths red and one-fourth green; all red – in pseudorandom order. The results are based on mean values of the trials over three sessions.

## Results and discussion

As the proportion of red dots in the surround decreases, the region of the test is less clearly segregated from the surround by color alone. Consider a condition like the one shown in Figure 7 with half the dots in the surround colored green and half red. As can be seen at the left of Figure 7, the test region (marked in the right figure), filled with green dots is more difficult to pick out. We asked observers to pick out the centrally located green test dots in randomly selected still frames. Observers were unable to consistently distinguish this region when the surround green dots composed more than half of the surround dots. Thus, in these conditions, the test dots themselves were effectively camouflaged in still view. Nonetheless, when apparent motion is perceived, a green disk is seen in amodal completion under these conditions. As shown in the data plots of Figure 8, the green disk is seen in amodal completion by all observers in all conditions with up to half the surround dots painted green. One naive observer, DN, sees amodal completion even with 75 % of the surround dots painted green. In this case, he reports that the object seen in amodal completion and apparent motion is not roughly circular in shape but roughly rectangular. These results provide evidence that objects, not visible in still view because of color camouflage, can be seen in amodal completion when they are seen in apparent motion. This suggests that motion can overcome camouflage by inducing a spread of color throughout regions defined by motion, even those occluded from view. This grouping by

color helps organize a scene into objects, foreground, and background and thus enhances the visibility of camouflaged objects.

*(Figure 8 near here)*

## GENERAL DISCUSSION

"Color from motion" (Cicerone, Hoffman, Gowdy, and Kim 1995; Miyahara and Cicerone 1996 and this issue) describes the perception of a spread of subjective color over achromatic regions seen as moving. In the absence of luminance differences between the motion-defined, central region and surround regions, chromaticity differences alone are sufficient to produce color spread from motion (Miyahara and Cicerone 1996 and this issue). In this case, a subjective contour is not seen. Thus, the spread of subjective color in achromatic regions defined by motion does not appear to require the formation of a subjective contour in order to define the extent of spread. These observations suggest that the regulation of color from motion is separate from the formation of subjective contours. Experiments also indicate that the hue and saturation of the subjective color depend on the chromaticity and luminance of the central test dots – those defining the region seen in apparent motion – not those of the surround dots (Cicerone and Miyahara 1996 and this issue). Thus, for the range of chromaticities and luminances explored, the mechanisms regulating color from motion are likely to be distinct from those regulating color contrast. These findings imply that the perception of motion itself, not contour formation or color contrast between the motion-defined region and the surround, is fundamental to the perception of color from motion.

In this work, Experiment 1 provides evidence that the locus of the mechanisms regulating the perception of color from motion is at or beyond

binocular combination. Monocular and binocular views of the original full stimulus produce identical results: A desaturated but distinct subjective color is seen to spread over regions defined by apparent motion. Observers describe the effect by saying that a green spotlight is seen to move over a fixed array of red dots. As compared to the original stimulus, a reduced stimulus, consisting of a set in which the central green dots were removed in every other frame of the stimulus, was created. The perception of color spread was diminished for the reduced stimulus as compared to that with the original full stimulus. However, when the reduced stimulus was presented out of phase to the two eyes separately, color from motion was judged to be as compelling as with the original stimulus. Observers show an enhancement in perceived color spread with the dichoptic view of the reduced stimulus as compared to the monoptic view of the same stimulus (Figure 4). This shows that the visual system can use the binocular combination of left and right eye views. Furthermore, a comparison of the dichoptic view of the reduced stimulus to the original, full stimulus show that these results are indistinguishable: The dichoptic information is as effective as the information from the full stimulus. That the dichoptic view produces perception of color spread equal to the full view of the standard stimulus also argues against a retinal locus for the subjective spread of color. These results in combination with previous results discussed above suggest an interaction between the processing of color and motion occurring at a site at or beyond binocular combination.

Challenges to the notion of strict segregation of pathways for the perception of properties such as motion or color have recently gained ground (e.g.,

Merigan and Maunsell 1993; Stoner and Albright 1993). Contrary to earlier ideas about motion processing, it is clear that the perception of motion is not based solely on luminance variations in the image. There is now ample evidence, as noted above, that the motion system can use a variety of image segmentation cues such as color, depth, and transparency, previously thought to be processed independently of motion. Our results suggest the reverse: that the perception of motion can influence the perception of color and the spread of subjective color over achromatic regions defined by motion. Furthermore, the finding that color spreads throughout a region defined by motion is consistent with the idea that color information may be retained in the motion pathway. The evidence provided here cannot specify whether the hypothesized interaction between color and motion pathways occurs in early motion systems or at higher levels. The only evidence we offer suggests that the receptive fields subserving the effect may be large: Cicerone et al. (1995) showed that test regions near one degree of visual angle (as compared to a range of 0.3 to 2.4 degrees) produce optimal color spread from motion.

When apparent motion is perceived in our original display, the central dots are enveloped by the spread of a desaturated subjective color throughout achromatic regions defined by motion. Sometimes described as a moving spotlight, this suggests that the perceptual grouping produced by apparent motion is enhanced by the spread of subjective color within the area seen as moving. We link the perception of color from motion to mechanisms for breaking camouflage in Experiments 2 and 3. Reducing the luminance of the background while keeping all

else the same markedly changes the perception of color spread. Now a green disk is seen in amodal completion: Against a highly saturated and uniformly colored red background, a highly saturated and uniformly colored green disk is seen to be moving behind a dark screen filled with holes. One explanation of the change in perception is as follows: In natural scenes, camouflaged objects often lie behind screening elements. When this type of camouflage is broken, the entire object is perceived even if parts of the object are still occluded because they lie behind the screening elements. As predicted, by darkening the background so that it could more readily be seen as a screen, the original perception of a veiling spread of desaturated color was changed to a disk, highly saturated in color, seen in amodal completion. Although motion enhances the visibility of a partially-occluded green disk under the conditions of Experiment 2, the clear segregation of red dots in the surround and green dots in the central test regions allows an obvious grouping according to color even without motion. We reasoned that a robust camouflage-breaking motion mechanism should be able to render the green disk visible under conditions for which color is not a reliable cue in still view. When half or more of the dots in the surround region were green instead of red, the grouping of green dots in the test region was not easily seen in still view (Figure 7). Nonetheless, when apparent motion is perceived, the full green disk is seen in amodal completion. Thus, we conclude that color from motion may be a mechanism for breaking camouflage.

The perception of motion itself can break camouflage (Wertheimer 1923).  
Occlusions of one part of a scene by another part when portions of the scene

move, called "kinetic occlusion," is also an effective way to break camouflage (e.g., Gibson 1979; Kaplan 1969; Andersen and Braunstein 1983; Yonas, Craton, and Thompson 1987; Andersen and Cortese 1989; Stappers 1989; Shipley and Kellman 1993; Shipley and Kellman 1994). Amodal completion and the idea that amodal completion of objects and forms is related to the organization of the visual scene also has a distinguished history (e.g., Michotte, Thines, and Crabbe 1964; Kanizsa 1979; Nakayama and Shimojo 1990; Nakayama, Shimojo, and Ramachandran 1990; Nakayama and Shimojo 1992; Yamada, Fujita, and Masuda, 1993; Grossberg 1994). Here we propose that , in addition to kinetic occlusion and amodal completion of objects and forms, color from motion, arising at a central site, can be used by the visual system to produce amodal completion and thereby break camouflage.

**Acknowledgements.** This work was supported by grant EY11132 (PHS-NIH National Eye Institute) to CMC.

**REFERENCES**

Andersen G J and Braunstein M L, 1983 "Dynamic occlusion in the perception of rotation in depth" *Perception & Psychophysics* **34** 356-362

Andersen, G J and Cortese J M, 1989 "2-D contour perception resulting from kinetic occlusion" *Perception & Psychophysics* **46** 49-55

Benham C E , 1894 "The artificial spectrum top" *Nature* **51** 200

Bidwell S, 1896 "On subjective colour phenomena attending sudden changes in illumination" *Proceedings of the Royal Society* **60** 368-377

Carney, T and Shadlen, M N, 1993 "Dichoptic activation of the early motion system" *Vision Research* **33** 1977-1995

Cicerone C M and Hoffman D D, 1992 "Dynamic neon colors: Perceptual evidence for parallel visual pathways" *Advances in Color Vision Technical Digest* **4** (Washington, D. C. : Optical Society of America) 66-68

Cicerone C M, Hoffman D D, Gowdy P D, and Kim J S, 1995 "The perception of color from motion" *Perception & Psychophysics* **57** 761-777

Cohen J and Gordon D A, 1949 "The Prévost-Fechner-Benham subjective colors"  
*Psychological Bulletin* **46** 97-136

Dobkins K R and Albright T D, 1993 "What happens if it changes color when it moves?: I. Psychophysical experiments on the nature of chromatic input to motion detectors" *Vision Research* **33** 1019-1036

Georgeson M A and Shackleton T M 1992 "No evidence for dichoptic motion sensing: A reply to Carney and Shadlen" *Vision Research* **32** 193-198

Gibson J J, 1979 *The Ecological Approach to Visual Perception* (Boston: Houghton Mifflin)

Gregory R L, 1987 *Oxford Companion to the Mind* (Oxford: Oxford University Press) pp 78-79

Grossberg S, 1994 "3-D vision and figure-ground separation by visual cortex" *Perception & Psychophysics* **55** 48-120.

Kanizsa G, 1979 *Organization in Vision* (New York: Praeger) p.195

Kaplan G A, 1969 "Kinetic disruption of optical texture: The perception of depth at an edge" *Perception & Psychophysics* **6** 193-198

Kersten D J, Bühlhoff H H, Schwartz B L, and Kurtz K J, 1992 "Interaction between transparency and structure from motion" *Neural Computation* **4** 573-589

Kooi F L, De Valois K K, Switkes E, and Grosf D H, 1992 "Higher order factors influencing the perception of sliding and coherence of a plaid" *Perception* **21** 583-598

Krauskopf J and Farell B, 1990 "Influence of color on the perception of coherent motion" *Nature* **348** 328-331

Merigan W H and Maunsell J H R, 1993 "How parallel are the primate visual pathways?" *Annual Review of Neuroscience* **16** 369-402

Michotte A, Thines G, and Crabbe G, 1964 *Les complements amodaux des structures perceptives* (Louvain: Publications Universitaires de Louvain)

Mikami A, Newsome W T, and Wurtz R H 1986 "Motion selectivity in macaque visual cortex: II. Spatio-temporal range of directional interactions in MT and V1" *Journal of Neurophysiology* **55** 1328-1339

Miyahara E and Cicerone C M (1996) "Chromaticity and luminance contribute to the perception of color from motion" *Investigative Ophthalmology and Visual Science* **37** S4

Miyahara E and Cicerone C M (this issue) "Color from motion without contour formation or color contrast" *Perception*

Nakayama K and Shimojo S, 1990 "Toward a neural understanding of visual surface representation" *Cold Spring Harbor Symposia on Quantitative Biology* **55** 911-924

Nakayama K and Shimojo S, 1992 "Experiencing and perceiving visual surfaces" *Science* **257** 1357-1363

Nakayama K, Shimojo S, and Ramachandran V S, 1990 "Transparency: relation to depth, subjective contours, luminance and neon color spreading" *Perception* **19** 497-513

Shipley T F and Kellman P J, 1993 "Optical tearing in spatiotemporal boundary formation: When do local element motions produce boundaries, form, and global motion?" *Spatial Vision* **7** 323-339

Shipley T F and Kellman P J, 1994 "Spatiotemporal boundary formation: Boundary, form, and motion perception from transformations of surface elements" *Journal of Experimental Psychology: General* **123** 3-20

Stappers P J, 1989 "Forms can be recognized from dynamic occlusion alone"  
*Perceptual Motor Skills* **68** 243-251

Stoner G R and Albright T D, 1993 "Image segmentation cues in motion processing: Implications for modularity in vision" *Journal of Cognitive Neuroscience* **5** 129-149

Trueswell J C and Hayhoe M M, 1993 "Surface segmentation mechanisms and motion perception" *Vision Research* **33** 313-328

Van Tuijl H F J M, 1975 "A new visual illusion: Neonlike color spreading and complementary color induction between subjective contours" *Acta Psychologica* **39** 441-445

Varin D, 1971 "Fenomeni di contrasto e diffusione cromatica nell'organizzazione spaziale del campo percettivo" *Rivista di Psicologia* **65** 101-128

Wyszecki G and Stiles W S, 1982 *Color Science* (New York: John Wiley & Sons)

Wallach H, 1935 "Über visuell wahrgenommene Bewegungsrichtung"  
*Psychologische Forschung* **5** 325-380

Wertheimer M, 1923 "Untersuchungen zur Lehre von der Gestalt"

*Psychologische Forschung* **4** 301-350

Yamada W, Fujita, N, and Masuda N, "Amodal completion as another perception of color-spreading stimuli" *Perceptual and Motor Skills* **76** 1027-1033

Yonas A, Craton L G and Thompson W B, 1987 "Relative motion: Kinetic information for the order of depth at an edge" *Perception & Psychophysics* **41** 53-59

**FIGURE CAPTIONS**

Figure 1. One of the twelve frames from the original display is shown (left). Each frame consisted of a white square filled with a random array of dots as shown here. Colors and luminosities are not accurate matches to the stimuli. From frame to frame the location of each dot was held constant, while the assignment of color for each dot was progressively changed according to an algorithm that colored all dots within a shifting circular area green and all other dots red. When such frames are shown in rapid succession, one sees a moving, luminous region, uniformly colored green, that can be bounded by a circular subjective contour (right).

Figure 2. Shown here is the stimulus used in Experiment 1. Different stimuli were presented to each eye. At the left are shown two frames of the sequence seen by the left eye, at the right the corresponding two frames seen by the right eye. In the dichoptic view when the observer's right eye saw the first frame of the standard display, the left eye saw an identical array of red dots minus the green dots normally located in the central region. The next frame in the standard sequence was presented to the left eye while simultaneously a frame without the green dots was presented to the right eye. Thus, the right eye saw every odd-numbered frame of the standard 12-frame display, and the left eye saw every even-numbered frame. All specifications of stimulus dimensions, chromaticities, and luminances are given in the Methods section.

Figure 3. We used the simple optical device shown here to present separate stimuli to each eye. An occluding screen kept left and right screen images separate. Left and right sides of the images on the monitor were projected by a mirror and a cube to left and right eyes, respectively. Small adjustments in the mirrors brought the images into register. Each eye could be stimulated alone (monoptic view) or at the same time (dichoptic view) with different stimulus streams. The drawing is not to scale.

Figure 4. Shown are the results of Experiment 1 for Observers CC (top) and DH (bottom). The mean ratings of color spread ( $\pm 1$  s.d.) are plotted as a function of the effective speed of the stimulus under three conditions. Results obtained with the original, full stimulus are shown with closed triangles. Results obtained with the monoptic (right) eye view of the reduced stimulus are shown as open circles. Results obtained with a dichoptic view of the reduced stimulus, presented out of phase to the two eyes, are shown as closed circles. The results show that a single eye view of the reduced stimulus is less effective than the view of the full stimulus in producing color from motion. However, a dichoptic view of the reduced stimulus produces color spread equal to the full view of the standard stimulus.

Figure 5. At the left (a) is shown one of the frames from one of the stimuli we used in Experiment 2. The figure accurately portrays the dot density but not the actual colors or luminosities of the dots or the background. Twelve such frames were presented in succession at a rate equivalent to 3.07 deg/sec. Five different luminance levels (0.23, 5.93, 22.3, 51.8, or 105 cd/m<sup>2</sup>) of the background were

used. At the right (b) is illustrated the observer's description of amodal completion when the background luminance is dim and apparent motion is seen. A uniformly colored and highly saturated green circle was seen to be moving in front of a uniformly colored and highly saturated red field. All was viewed through a screen seen as a dark sheet with holes punched into it.

Figure 6. Shown are the results of Experiment 2 for Observers CC, VC, PG, and DN. The mean proportion of total viewing time during which the green disk was seen in amodal completion is shown as a function of background luminance. Error bars mark the 90% confidence intervals about the mean values. All four observers see a moving green, highly saturated disk in amodal completion for a large proportion of the viewing time when the background luminance is low (0.23 and 5.93  $\text{cd/m}^2$  for CC and DN; 5.93 and 22.3  $\text{cd/m}^2$  for PG; and 0.23, 5.93, and 22.3  $\text{cd/m}^2$  for VC). None of the observers reports seeing amodal completion of a green disk in still view. When the background is of high luminance – 105  $\text{cd/m}^2$  which matches the original conditions – amodal completion is never seen. Instead, observers see a veiling color spread of low saturation over the region seen as moving.

Figure 7. A single frame of one of the stimuli of Experiment 3 is shown at the left (a). All aspects of the stimuli were identical to those of Experiment 2 with the following exceptions: The background was fixed at 5.93  $\text{cd/m}^2$  and the surround dots were varied in color such that all, three-quarters, one-half, or one-quarter of the total number were red. All other dots, including dots in the test region were

green. In the example shown here, half of the surround dots were green and half were red. As shown at the left (a), in still view the test region, consisting of all green dots, is well camouflaged. At the right (b), a green circle is used to mark the location of the test dots.

Figure 8. Shown here are the results of Experiment 3 for Observers CC , VC, PG, and DN. The proportion of total viewing time during which the region seen to be moving was perceived in amodal completion is shown as a function of the proportion of surround dots colored red. Error bars mark the 90% confidence intervals about the mean values. All observers see objects in amodal completion when apparent motion is perceived even for conditions with the central cluster of green dots difficult to distinguish in still view, for example with surrounds composed of half-red and half-green dots. Observer DN sees amodal completion under all conditions, even with three-fourths of the dots in the surround painted green.