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Color from motion: dichoptic activation and a possible role in breaking camouflage

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Abstract. 'Color from motion' describes the perception of a spread of subjective color over achromatic regions seen as moving. The effect can be produced in a 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, but not dot locations, changing from frame to frame. Evidence is presented 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, which suggests that it may play a role in enhancing the visibility of camouflaged objects.

1 Introduction

A number of reports of color phenomena associated with moving or rapidly changing stimulation have appeared since the nineteenth century (Prevost 1826; Fechner 1838; Brewster 1861). Other related phenomena include Benham's (1894) top, in which one sees subjective colors when viewing a rotating disk of black and white patterns; Bidwell's (1896) ghost, in which—with rapid sequential presentation of white light, colored light, and darkness—one perceives the complement of the colored light; 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 et al 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, but 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 (1997) 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 clear 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

are governed mainly by the luminance and the chromaticity of the dots in the test region, not those of the dots in the surround, 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.

In this report 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 perhaps 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. Amodal completion is not perceived in still views of single frames of this display. In the motion mode, amodal completion is perceived even when a high proportion of the dots in the surround region is of the same color as in the test region, thus making the test region less visible in still view. This suggests that color from motion may play a role in enhancing the visibility of camouflaged objects.

2 Experiment 1: Single-eye views can be binocularly combined to produce color from motion

One frame from the original displays is shown in figure 1a. Each stimulus presentation was comprised of twelve 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

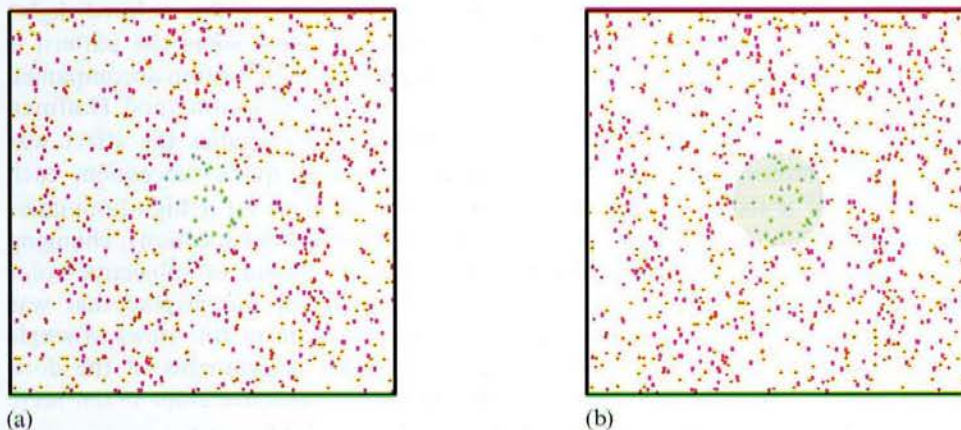


Figure 1. (a) One of the twelve frames from the original display. Each frame was a white square filled with a random array of dots. Colors and luminosities are not accurate matches to the stimuli. From frame to frame the location of each dot was fixed, while the assignment of color for each dot was progressively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

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 in figure 1b. 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.

Earlier results (Cicerone et al 1995; Miyahara and Cicerone 1997) suggest that the perception of motion is yoked to the spread of subjective color into achromatic regions seen as moving. Certainly, unlike neon color spreading in still displays (eg 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 (1997) 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 color spreading effect can be placed at or beyond the site regulating apparent motion. Apparent motion can be perceived with random-texture kinematograms presented

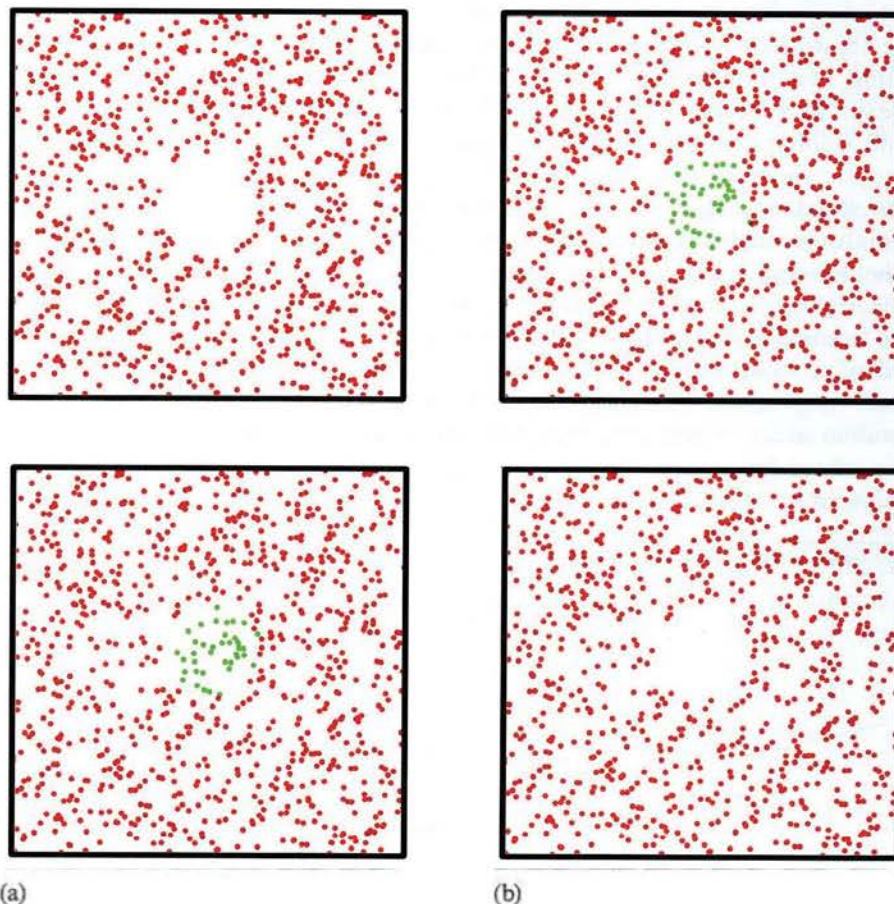


Figure 2. The stimulus used in experiment 1: (a) two frames of the sequence seen by the left eye; (b) the corresponding two frames seen by the right eye. In the dichoptic view, the right eye saw every odd-numbered frame of the standard twelve-frame display, and the left eye saw every even-numbered frame. All specifications of stimulus dimensions, chromaticities, and luminances are given in section 2.1.

dichoptically in spatiotemporal quadrature (eg Carney and Shadlen 1993; but see Georgeson and Shackleton 1992). The idea that apparent motion is achieved at or beyond the site of binocular combination is supported by physiological evidence as well (eg Mikami et al 1986).

Experiment 1 was designed to test the hypothesis 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. The experimental question was 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.

2.1 Method

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

2.1.2 *Stimuli and apparatus.* The stimuli were generated by an Apple MAC IIfx and displayed on a Raster Ops Color Monitor. CIE 1931 (Wyszecki and Stiles 1982) coordinates and luminosity values for stimuli used in these experiments were measured with a Spectracolorimeter (Photo Research, PR-650). The stimuli are shown in figure 2. (The figure accurately portrays the dot density but not the actual colors or luminosities.) In figure 2a are shown two frames of the sequence seen by the left eye, and in figure 2b 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 sequences (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 twelve-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 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 min. Within a circular patch subtending 2 deg, the dots were green (CIE $x = 0.2797$, $y = 0.6102$; luminance = 62.4 cd m^{-2}); all other dots were red (CIE $x = 0.6213$, $y = 0.3444$;

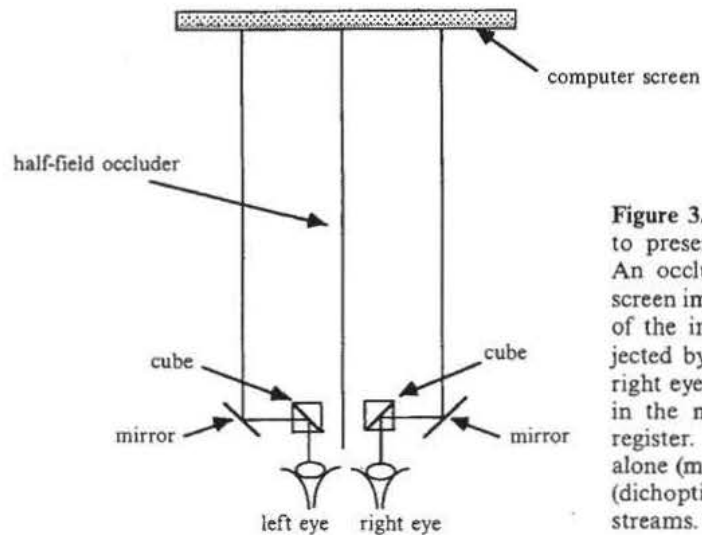


Figure 3. A simple optical device used to present separate stimuli to each eye. An occluding screen kept left and right screen images separate. Left and right sides of the images on the monitor were projected by a mirror and a cube to left and right eyes, respectively. Small adjustments in the mirrors 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.

luminance = 20.1 cd m^{-2}). From frame to frame the location of each dot in the stimulus was held constant, while the assignment of color to dots was progressively changed according to an algorithm (Cicerone and Hoffman 1992; 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 deg below the center of the display. On each successive frame the center of the circular region was moved vertically by 0.125 deg .

2.1.3 Procedures. The observer kept his/her gaze centered on the display⁽¹⁾ and was instructed to rate, on a scale from 0 to 4, the perceived color spread for each stimulus presentation: 0 was to be used if the observer was absolutely certain of the absence of color spread, 1 if moderately certain of its absence, 2 if uncertain, 3 if moderately certain of its presence, and 4 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.

2.1.4 Design. We compared three conditions: (i) the right-eye-only view of the reduced stimulus, (ii) the dichoptic view with left and right eyes viewing the reduced stimulus out of phase, and (iii) the monocular or binocular view of the standard stimulus. The independent variable was the update rate of the twelve frames in each presentation. There were four different update rates (equivalent to speeds of 0.37 , 0.92 , 1.38 , and 2.05 deg s^{-1}). 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 were collected in sessions that were separate from those in which the reduced stimulus was used.

2.2 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 implies that the visual system can use the binocular combination of left-eye and right-eye views. Furthermore, a comparison of the dichoptic view of the reduced stimulus with the original, full stimulus shows 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.

When judgments are based on the right-eye-only view of the reduced stimulus, color spread 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 easily be argued that the difference between the monoptic and dichoptic views of the reduced stimulus is due 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

⁽¹⁾Scanning the display, instead, does not alter the effect as compared to maintaining fixation anywhere in the display. Keeping gaze centered on the display standardized the viewing conditions and obviated 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.

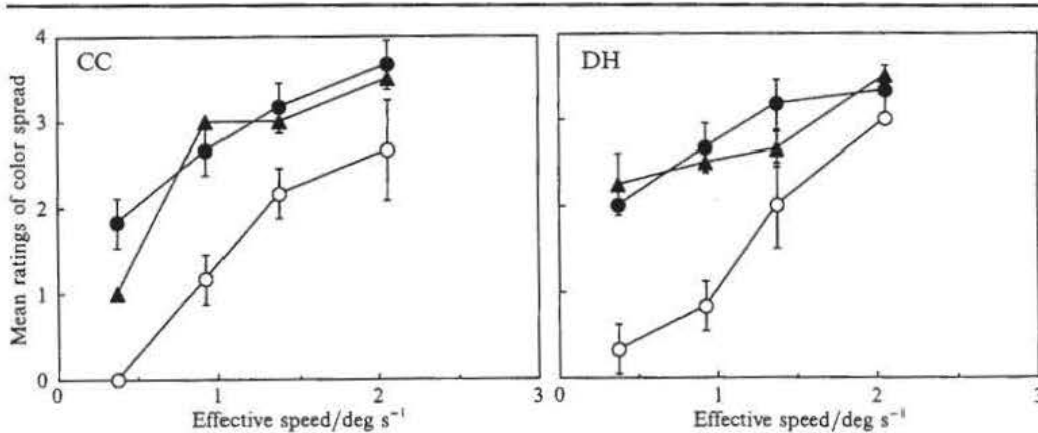


Figure 4. The results of experiment 1 for observers CC and DH. The mean ratings of color spread (± 1 SD) are plotted as a function of the effective speed of the stimulus under three conditions. Results obtained with the original, full stimulus are shown with solid triangles. Results obtained with the 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 solid circles.

solely luminance contrast—can influence the perception of motion (Krauskopf and Farell 1990; Nakayama and Shimojo 1990; Kersten et al 1992; Kooi et al 1992; Dobkins and Albright 1993; Trueswell and Hayhoe 1993). Our results suggest the reverse: that the perception of motion is linked to 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. Experimental evidence suggests that the receptive fields subserving the effect may be reasonably large. Cicerone et al (1995) showed that test regions near 1 deg (over a range of 0.3 to 2.4 deg) produce optimal color spread from motion. Although these sizes are too large to be compatible with the receptive field sizes of color-coded P ganglion cells of the primate retina, size alone does not allow us to specify where in the postretinal motion-processing chain the color spreading might occur.

3 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 traces 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, separately from the surrounding red dots. When apparent motion is perceived, the region defined by motion is enveloped in subjective color spreading into achromatic regions near the green dots. The color spread is uniform; although it is of low saturation (Miyahara and Cicerone 1997), grouping by color enhances 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 et al 1964; Kanizsa 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.

3.1 Method

3.1.1 *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, Tokyo) matches.

3.1.2 *Stimuli and apparatus.* The stimuli were generated by a Power MAC 7500 and displayed on a Hitachi Color Monitor. CIE 1931 (Wyszecki and 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 5a. Twelve such frames were presented in succession at a rate equivalent to 3.07 deg s^{-1} . Every frame consisted of a background square (CIE $x = 0.2787$, $y = 0.3028$; luminance equal to 0.23, 5.93, 22.3, 51.8, or 105 cd m^{-2} ; 5 deg 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 min. Within a circular patch subtending 1 deg, the dots were green (CIE $x = 0.2854$, $y = 0.5979$; luminance = 73.8 cd m^{-2} ; all other dots were red (CIE $x = 0.6143$, $y = 0.3374$; luminance = 19.9 cd m^{-2}). In all other respects the stimuli were identical to those of experiment 1.

3.1.3 *Procedures.* In preliminary trials, observers reported that the perception of amodal completion was seen at low luminance levels of the background but could be somewhat ephemeral. When amodal completion was not seen, the observers reported seeing apparent motion, but no contours and no disk. Within each trial of 30 s duration, the observer was instructed to start a stopwatch 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 s interval that the observer reported seeing amodal completion of a moving green circle.

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

3.2 Results and discussion

For high luminance levels of the background, observers reported seeing a disk moving over the field of dots and the spread of a desaturated color throughout this disk (Cicerone et al 1995). Under a range of low-luminance backgrounds the observers reported seeing a highly saturated, solidly colored green disk moving in front of a solid red field. Both the red field and the green disk appeared to lie behind a perforated dark screen (amodal completion). Depending on the background luminance, the perception of amodal completion could be somewhat ephemeral. When amodal completion was not seen, the observers reported seeing apparent motion, but no contours and no disk. 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. With backgrounds of high

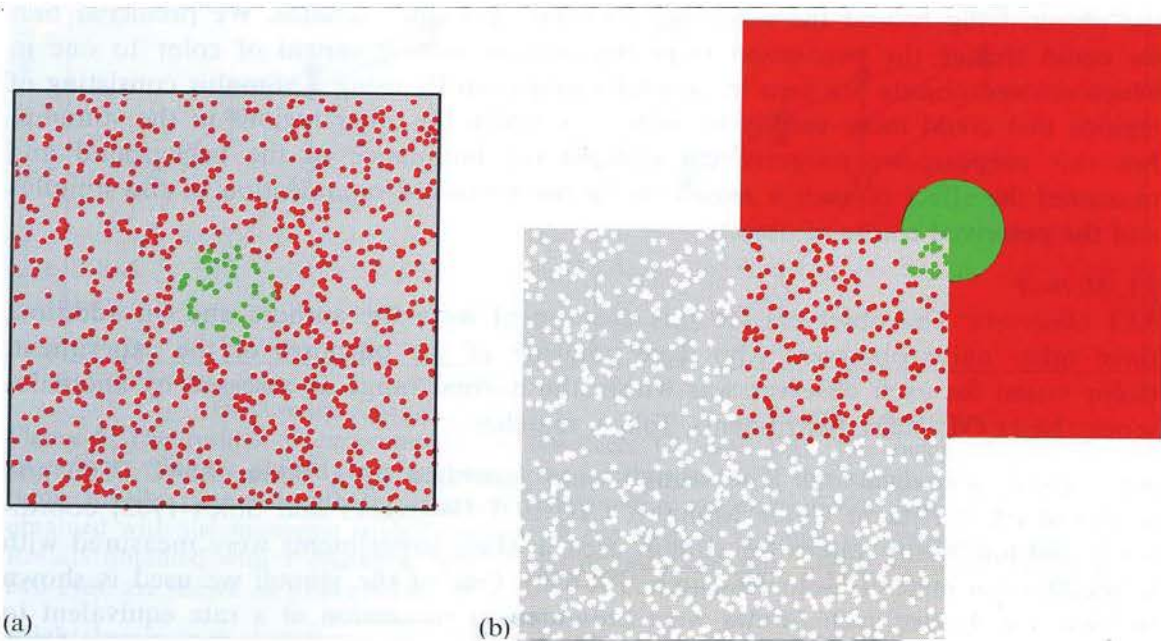


Figure 5. (a) One of the frames from one of the stimuli used in experiment 2. The figure accurately portrays the dot density but not the actual colors or luminosities of the dots or the background. Twelve such frames were presented in succession at a rate equivalent to 3.07 deg s^{-1} . Five different luminance levels (0.23 , 5.93 , 22.3 , 51.8 , or 105 cd m^{-2}) of the background were used. (b) The observer's description of amodal completion when the background luminance was dim and apparent motion was 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 through it.

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 1997). For backgrounds of low luminance, the observers reported seeing one of two percepts: (i) 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 for this percept the observer sees a contour but no color spread. (ii) 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 through it (as illustrated in figure 5b). We designated the latter description as amodal completion. Neither percepts described here is seen in still view of single frames of the stimulus, nor is it 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 (0.23 and 5.93 cd m^{-2} for CC and DN; 5.93 and 22.3 cd m^{-2} for PG; and 0.23 , 5.93 , and 22.3 cd m^{-2} for VC). With these dim backgrounds, when amodal completion is not seen, observers reported seeing the stimulus as described in verbal report (i) above. It should be emphasized that none of the observers reported seeing amodal completion of a green disk in still view. When the background was of high luminance— 105 cd m^{-2} which matches the original condition—all observers saw a low-saturation veiling spread of color over the region seen as moving. Amodal completion was never seen.

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,

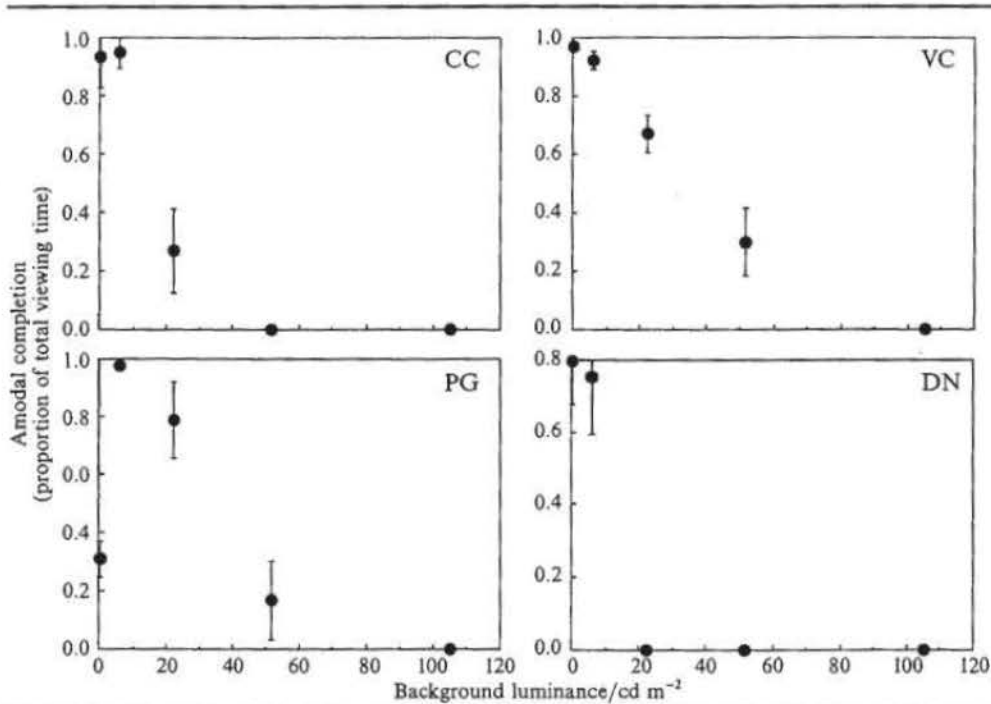


Figure 6. The results of experiment 2 for observers CC, VC, PG, and DN. The mean proportion of total viewing time (30 s per trial) during which the green disk was seen in amodal completion is shown as a function of background luminance. Error bars mark the 90% confidence intervals about the mean values.

the amodal completion of the green disk is a percept mediated by motion and color. As compared with color from motion seen with the original stimulus (Cicerone et al 1995; Miyahara and Cicerone 1997), 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 is linked to 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.

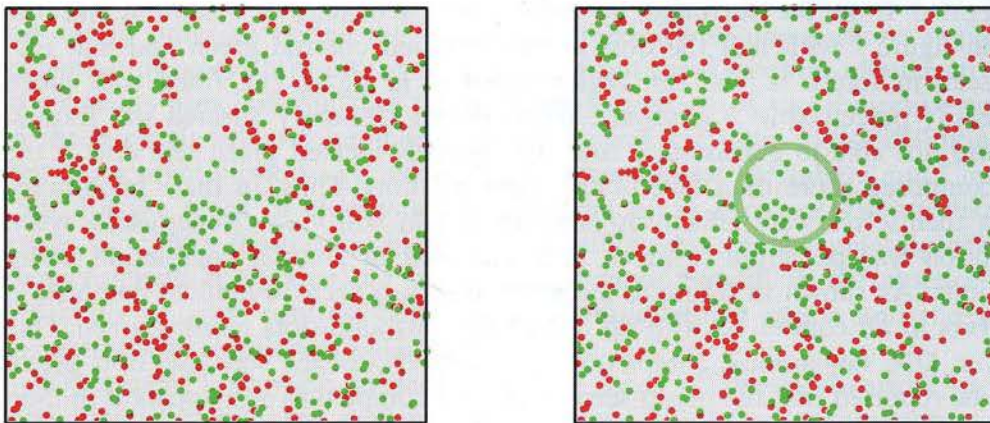


Figure 7. (a) A single frame of one of the stimuli of experiment 3. All aspects of the stimuli were identical to those of experiment 2 with the following exceptions. The background was fixed at 5.93 cd m^{-2} and the surround dots were varied in color such that all, 75%, 50%, or 25% of the total number were red. All other dots, including dots in the test region were green. In the example shown, half of the surround dots were green and half were red. As shown in (a), in still view the test region, consisting of green dots, is well camouflaged. In (b), a green circle is used to mark the location of the test dots.

4 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 was 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, as before, 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.

4.1 Method

4.1.1 *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, Tokyo) matches.

4.1.2 *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^{-2} and the surround dots were varied in chromaticity such that all, 75%, 50%, or 25% of the total number were red. All other dots, including dots in the test region, were green.

4.1.3 *Procedures.* The procedures were identical to those of experiment 2.

4.1.4 *Design.* We varied the color composition of the background dots over five values—25% red and 75% green; 50% red and 50% green; 75% red and 25% green; and all red—in pseudorandom order. The results are based on mean values of the trials over three sessions.

4.2 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 in figure 7a, the test region (marked in figure 7b), filled with green dots is not easily perceived as a grouping. When shown randomly selected still frames, observers were not able to consistently find the centrally located green test dots if the 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 was perceived, a green disk was seen in amodal completion under these conditions. As shown in figure 8, the green disk was seen in amodal completion by all observers in all conditions with up to half the surround dots painted green. One naive observer, DN, saw amodal completion even with 75% of the surround dots green. In this case, he reported that the object seen in amodal completion and apparent motion was no longer circular in shape. 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 the perceptual grouping produced by apparent motion is enhanced by the spread of subjective color within the area seen as moving, with color spreading into even those regions occluded from view. This grouping by motion and color helps organize a scene into objects, foreground, and background and thus enhances the visibility of camouflaged objects.

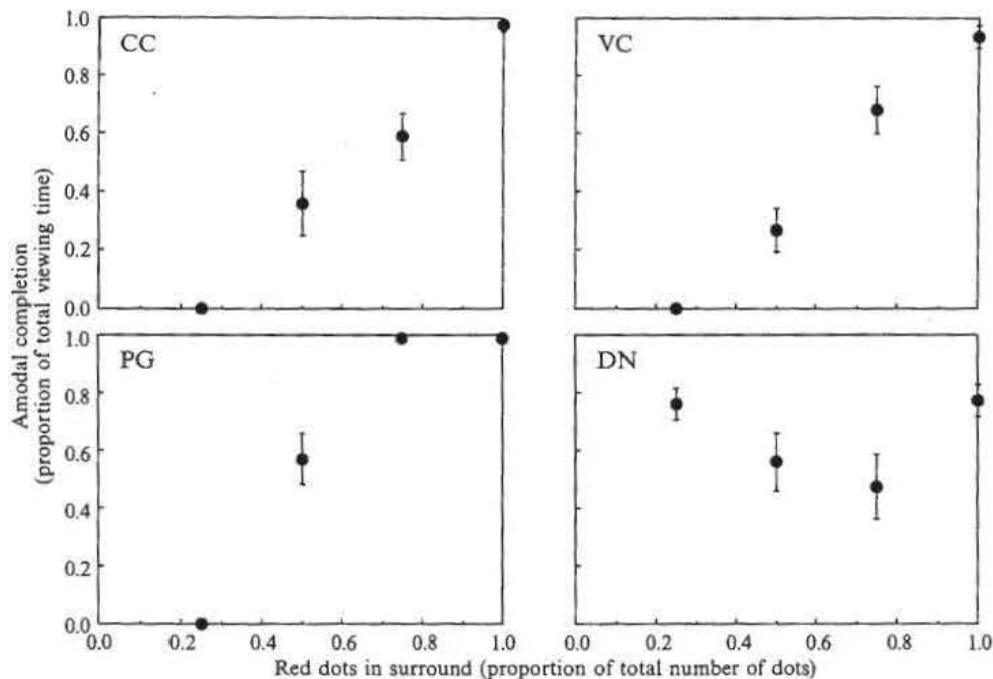


Figure 8. The results of experiment 3 for observers CC, VC, PG, and DN. The mean proportion of total viewing time (30 s per trial) during which the region seen to be moving was perceived in amodal completion is shown as a function of the proportion of surround dots colored red. Error bars mark the 90% confidence intervals about the mean values.

5 General discussion

'Color from motion' (Cicerone and Hoffman 1992; Cicerone et al 1995; Miyahara and Cicerone 1997) 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 1997). In this case, a clear 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 (Miyahara and Cicerone 1997). 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, in the absence of contour formation or color contrast between the motion-defined region and the surround, is linked to the perception of color from motion.

Experiment 1 provides evidence that the locus of the mechanisms regulating the perception of color from motion is at or beyond binocular combination of monocular inputs. Monocular and binocular views of the original full stimulus produced identical results: A desaturated but distinct subjective color was seen to spread over regions defined by apparent motion. Observers described the effect by saying that they saw a green spotlight move over a fixed array of red dots. A reduced stimulus, consisting of a set in which the central green dots were removed in every other frame of the stimulus, was then created. The perception of color spread was weaker for the reduced stimulus than for the original full stimulus. However, when the reduced stimulus was presented

temporally out of phase to the two eyes separately, color from motion was judged to be as compelling as with the original stimulus. Furthermore, as figure 4 shows, there is an enhancement in perceived color spread with the dichoptic view as compared to the monoptic view of the reduced stimulus. This further reinforces the idea that the visual system can use the binocular combination of left-eye and right-eye views and that 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 (eg 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 in section 2, 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. Within this context, our results suggest the reverse: that the perception of motion may influence the perception of color and the spread of subjective color over achromatic regions defined by 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. The effect is 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 can be 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 perforated dark screen. One explanation of the change in perception is as follows. When camouflage is broken, the entire object is perceived even if parts of the object are still occluded because they lie behind 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 (eg Kaplan 1969; Gibson 1979; Andersen and Braunstein 1983; Yonas et al 1987; Andersen and Cortese 1989; Stappers 1989; Shipley and Kellman 1993, 1994). Amodal completion is another effective way to organize the visual scene and break camouflage (Michotte et al 1964; Kanizsa 1979;

Nakayama et al 1990; Nakayama and Shimojo 1990, 1992; Yamada et al 1993; Grossberg 1994). Here we propose that color from motion, arising at a central site, can also be used by the visual system to produce amodal completion and thereby break camouflage.

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