

The interaction of color and motion

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Abstract

Human vision constructs the experiences of color and motion in coordination. In this paper I discuss recent experiments and computational theories which show, in the case of “dynamic color spreading,” how this coordination can occur.

1. Introduction

On the second of January, 1986, Jonathan I. had an auto accident and suffered a concussion. He recovered within a few days, except in one respect. He lost all ability to perceive, imagine, or dream in color (Sacks 1995, pp. 3–41; Sacks and Wasserman 1987). This would be a difficult loss for anyone, but it was particularly poignant for Mr. I. since he was an artist and, at age 65, had made his living for decades working with color.

His loss of color was due to damage of cerebral cortical, not to selective loss of retinal cones as in typical cases of color blindness, and was therefore diagnosed as *cerebral achromatopsia*. The condition is rare, but documented cases of what appears to be cerebral achromatopsia go back several centuries (Boyle 1688; Collins 1925). Louis Verrey discovered in 1888 that the regions of cortex affected in cerebral achromatopsia are the lingual and fusiform gyri of the inferior occipital lobe. Later work has confirmed Verrey’s finding. There is now substantial evidence that area V4 of inferior occipital cortex is critical to the perception of color (Desimone *et al.* 1985; Desimone and Schein 1987; Dufort and Lumsden 1991; Heywood *et al.* 1992; Lueck *et al.* 1989; Motter 1994; Yoshioka and Dow, 1996; Yoshioka *et al.* 1996; Zeki 1973; 1980; 1983a; 1983b; 1985; Zeki *et al.* 1991), that magnetic stimulation of V4 in

normal subjects can cause color experiences called “chromatophenes” (Sacks 1995, p. 28; Zeki 1993, p. 279), and that magnetic inhibition of V4 in normal subjects can cause temporary achromatopsia (Sacks 1995, p. 34).

In short, without V4 you can't construct color. You might still discriminate different wavelengths of light, but you won't experience different hues.

In October of 1978, L.M. entered a hospital after suffering for three days with headaches and vomiting. A series of tests indicated a stroke that damaged the lateral border between the occipital and temporal lobes of cortex in each hemisphere. She recovered from the stroke and was, in most respects, normal, with one notable exception. She could not see motion. She could see objects and colors, and otherwise had normal vision. But, as Zihl reported in 1983, “She had difficulty, for example, in pouring tea or coffee into a cup because the fluid appeared to be frozen, like a glacier. In addition, she could not stop pouring at the right time since she was unable to perceive the movement in the cup (or a pot) when the fluid rose.” (Zihl *et al.* 1983, p. 315).

Her condition is an instance of *cerebral akinetopsia* (Zeki 1991). There is now substantial evidence that cerebral akinetopsia results from damage to area V5 of cortex (Zeki 1991), and that V5 is critical for the perception of motion in monkeys (Newsome *et al.* 1985; Newsome and Paré 1988; Salzman *et al.* 1990) and in man (Riddoch 1917; Zihl *et al.* 1983; Baker *et al.* 1991; Zihl *et al.* 1991; Zeki *et al.* 1991). Moreover it has been found that magnetic inhibition of V5 in normal subjects by Transcranial Magnetic Stimulation can cause temporary akinetopsia (Beckers and Homberg 1992; ffytche *et al.* 1995; Beckers and Zeki 1995).

In short, without V5 you can't construct much motion.

It is tempting to interpret these findings, and a wealth of related anatomical and physiological findings, as evidence for independent processing of color and motion in human vision (Livingstone and Hubel 1987). There is, for instance, neuroanatomical and neurophysiological evidence for segregated processing of color and motion by, respectively, distinct parvocellular and magnocellular pathways. These separate pathways are evident as early as the retina, and continue well into prestriate cortex (Albright 1984; DeYoe and van Essen 1988; Maunsell and van Essen 1983; Newsome and Paré 1988; Siegel and Andersen 1986; van Essen 1985; Zeki 1974). And there is psychophysical data which suggest their segregated processing. It was noted in 1911 by Stumpf, for instance, that the perception of motion in color displays is greatly reduced at isoluminance (Stumpf 1911; Todorović 1996; Cavanagh, Tyler, and Favreau 1984).

A natural question is, How independent are color and motion? Do we construct motion and color separately, or does our construction of one affect our construction of the other?

That the two interact, at least in part, has been known since the French monk Benedict Prevost, in 1826, observed colors near his fingers when he waved his hands in the dimness of the cloisters (Cohen and Gordon 1949; Gregory 1987). Similar interactions between motion and color were subsequently rediscovered many times, including rediscoveries by Gustav Fechner and Sir David Brewster (Cohen and Gordon 1949). Perhaps the most famous rediscovery was by Benham, who in 1894 marketed a popular disk with this black and white pattern:

Figure 1 near here

This “Benham’s top” is mounted on a spindle so that it can spin about its center. If you spin it counterclockwise at modest speed, you see an artificial spectrum: the innermost arcs form dark violet rings, the next arcs form pale blue rings, the next green, and the outermost red. If you spin it clockwise, the sequence of colors reverses, from dark violet at the innermost to red at the outermost.

Another interaction between color and motion was discovered by Bidwell in 1896 and called “Bidwell’s ghost”. In one instance of his demonstration, you see a spinning disk illuminated by an incandescent lamp. The surface of the spinning disk looks to be bluish green. But when the disk slows down, you see that its surface is half black and half white, with a slit through which a red lamp flashes. The bluish green that you see when the disk spins rapidly is, roughly, the color complement to the flashing red.

Wallach discovered an interaction between color and motion in 1935 while studying the aperture problem. He used a pattern of lines seen through a rectangular aperture:

Figure 2 near here

A still view of Wallach’s display gives a faint impression of red color spreading in the upper half of the rectangle. There also appears to be a faint illusory contour passing horizontally through the middle of the rectangle. Wallach found that the color spreading could be enhanced if he put the slanted lines in motion, and if the motion was perceived in a certain way. He rigidly translated the lines horizontally, say to the left. Sometimes observers perceived the lines as translating to the left and

sometimes, due to the ambiguity induced by the rectangular aperture, as translating upwards. When they saw the lines translating upwards, subjects reported that the red color spreading was greatly enhanced. They also reported that the lines looked uniformly black, even in the upper half of the display, but seemed to be sliding under a red filter.

Wallach's display, then, is notable in at least three respects. First, it is the first published example of neon color spreading in a static display. Second, it clearly demonstrates that motion can enhance color spreading. Third, it shows that motion can alter the perceived color of image features such as lines (e.g., changing them from red to black).

Cortese and Andersen (1989) created a display in which apparent motion in an achromatic display leads to the perception of brightness spreading and illusory contours. Their display consists of a black background on which are scattered a few hundred small white dots. The dots never move from frame to frame of the display. But some dots turn on or turn off according to the following algorithm. They simulate the rotation of a rigid (but invisible) ellipsoid that floats in front of the field of white dots. Any dots that are occluded by the ellipsoid are turned off, the rest are turned on. As the ellipsoid rotates from frame to frame, some dots switch on and others switch off, all near the boundary of the simulated ellipsoid. Literally, then, the display just consists of white unmoving dots switching on and off against a black background. But what observers perceive is an ellipsoid in three dimensions whose surface appears "blacker than black", i.e., a black darker and more striking than that of the background. The ellipsoid is bounded by a clear

illusory contour.

Cortese and Andersen's display is notable in at least two respects. First it demonstrates that perceived motion can lead to perceived brightness (or darkness) spreading. In this regard it is like Wallach's display, but without any hues. Second, it shows that this induced brightness spreading can be seen as three-dimensional, for instance as the surface of an ellipsoid which curves in three dimensions. This clearly shows an interaction between motion, brightness, and the visual construction of surfaces (see also Gibson *et al.* 1969, Shipley and Kellman 1993, and Stappers 1989, for related displays and results).

The demonstrations of Benham, Wallach, and Cortese and Andersen suggest that visual motion can affect perceived color. The converse is also true: color can affect perceived motion. Some evidence for this comes from isoluminant displays. Although it is true, as Stumpf discovered, that perceived motion is greatly reduced at isoluminance, it does not completely disappear (Cavanagh and Anstis 1991; Cavanagh and Favreau 1985; Derrington and Badcock 1985). Subjects can reliably discriminate direction of motion in colored displays at isoluminance (Dobkins and Albright 1993; Lindsey and Teller 1990; Sato, 1988). Dobkins and Albright, for instance, have shown that color affects perceived motion at isoluminance in displays like this:

Figure 3 near here

This figure depicts three frames from a movie. Each frame has a band of red and green patches, all of equal luminance. From one frame to the next this band translates horizontally by a precise amount: half the width of a patch. Subjects view

the display through an aperture so that they can't see the left and right ends of the band. The question is, Which way will the band appear to move, left or right? The answer is that subjects prefer to see it move to the right. By so doing they match green patches with green and red with red. In the process of constructing objects and motion, we prefer to construct objects that don't change color. But this suggests that color affects our construction of motion, even if there are no luminance differences around. And this further suggests that the parvocellular pathway, which processes information about color, can affect the magnocellular pathway, which processes information about motion.

2. A Useful Display

In the summer of 1991 I was considering the interaction of color and motion, and wondered if I could construct another display that would demonstrate this interaction. I found a straightforward extension of the displays of Cortese and Andersen that did the trick. An example is as follows:

Figure 4 near here

Here are two frames from a movie. The frame on the left has 900 dots placed at random according to a uniform distribution. The frame on the right has the same dots placed at exactly the same locations. So no dots move at all from frame to frame. The only difference between frames is in the assignment of colors to dots: a slightly different set of dots is colored green on the right than on the left.

This movie was a pleasant surprise. I saw a green disk, much like a spot light or a green filter, moving over the field of red dots. The green disk has a ghostly glow, and a well-defined subjective border surrounding it. You can get some idea of the

effect by cross fusing the two frames of the figure. You'll see a faint disk floating above the field of dots. The color and border, however, are much more striking in the movie, which can be seen online at <http://www.socsci.uci.edu/cogsci/personnel/hoffman/dcs-demo.html>.

This display can be varied through almost limitless combinations of colors and virtual shapes. In place of glowing green disks I have seen, for instance, glowing red squares, glowing blue stripes, and even glowing shapes in three dimensions. My favorite is a glowing blue cigar rotating in space.

Sometimes, in these displays, instead of seeing the green disk (or other colored shape) in front, observers see it behind. The screen is perceived as an off-white sheet of paper, and all dots are perceived as holes punched in this paper. Through the holes observers see a red sheet of paper behind the white one. And sandwiched between these two sheets they see a moving green disk.

This is an elaborate construction from static dots changing color. But there's more. When observers see the disk in front, they see its surface as transparent, glowing, and a desaturated green. But when they see it behind, they see its surface as opaque, not glowing, and a saturated green. We coordinate the quality of the surfaces we construct with the depth at which we place them.

This motion-induced spread of color is called *dynamic color spreading*. What we do to create it is impressive. We create motion, even though all dots in the display never move. We create an object and give it a shape, either in two dimensions or in three. We often, though not always, endow that object with a border, sometimes smooth and sometimes with sharp corners. We further endow that object with

a surface of a definite quality, either opaque or transparent, either saturated or desaturated. We place that object in space, either in front of a white sheet or behind it. And we move that object in space, either rotating it or translating it or both. And all this from a few dots that change color but don't move. It takes very little to trigger our creative genius.

By the way, it doesn't much matter whether one tracks the moving disk or keeps one's eye fixated at one point of the display. The moving green disk is about equally compelling in either case. This eliminates simple optical smearing as the explanation for the spread of color.

3. Psychophysical Studies

Dynamic color spreading is an engaging effect. Everyone who sees it is surprised and intrigued. They see, say, a moving green disk, and yet also see that there is no green disk and no motion. This paradoxical perception demands further exploration.

But there is an even more compelling reason to systematically explore dynamic color spreading. It is not merely a perceptual curiosity, like a mirage or an afterimage. It is rather a window into one of the central processes of vision: the construction of objects and their properties. The visual world does not come to us prepackaged into objects and their properties. Objects are an achievement, the product of a sophisticated and active process of construction. The shower of photons hitting each retina does not come with objects prelabelled. Photons are not tagged as "I'm a photon that came from the cat over there" or "I'm the photon from

that brown desk.” Their tags are of a quite different nature: position, wavelength, time, and polarization. Anyone who has tried to build a computer vision program that converts showers of photons into a description of a world of objects, can only be struck by the complexity of the task and the facility with which human vision pulls it off.

The shower of photons is discrete. The retina captures, at any moment, an integer number of photons, say 8013 or 12,359. And the photons are captured at a discrete set of locations at the retina. There are roughly 6 or 7 millions cones and 120 million rods in each eye. So human vision must work, at any given time, with a discrete number of photons captured at a discrete set of locations. Yet the objects we construct have, often enough, continuous surfaces. The top of a table, the screen of a television, a sheet of paper, all have surfaces that appear to us continuous, not discrete. This means that we must not only carve the world into objects, we must also endow these objects with continuous surfaces, even though the information available to us from photons is discrete.

Constructing continuous surfaces from discrete information is central to our visual construction of objects (Shipley and Kellman 1993; 1994). And it is precisely this process that is exaggerated and highlighted by the displays of dynamic color spreading. The discrete nature of the information is exaggerated by the wide spacing between the dots. The construction of continuous surfaces is also highlighted: we clearly see a colored and continuous surface *in the gaps between the dots*. What becomes strikingly obvious in these displays is what is true all the time. Every continuous surface we see is something we construct from information that is discrete

and has gaps. We effortlessly fill in these gaps. If we didn't we would never see continuous objects.

So displays of dynamic color spreading give us a method to probe one of the central processes of vision, the construction of objects, their surfaces, and their other properties. And one of the first points that becomes clear from these displays is that motion can greatly facilitate this construction. If you look at a single static frame of a display, you see no motion, no colored disk, no filling in of color, only a scattered set of dots, some green and some red. But put the display in motion, and the moving green disk appears.

These are the extreme cases. What happens if you systematically vary the amount of motion that is seen. Will the perception of the constructed green surface vary proportionately?

Effects of motion

I was soon joined by Carol Cicerone in studying dynamic color spreading, and this was one of the first questions we tried to answer (Cicerone and Hoffman 1991, 1992). We created displays consisting of 12 frames of red and green dots, similar to the frames shown above. Each frame was 5 degrees tall and wide as viewed at a distance of 42 inches. Each had 900 dots placed at random according to a uniform distribution, and each dot subtended 3 minutes of arc. The center of the region in which dots were colored green was translated vertically by 0.125 degrees on each successive frame. This region started 0.75 degrees below the center of the display on frame 1, and reached 0.75 degrees above the center on frame 12. These same 12 frames

were shown at different speeds on different trials. The nine different speeds used were 0.063, 0.125, 0.300, 0.675, 1.08, 1.50, 1.88, 2.53, and 2.93 degrees per second.

Subjects fixated the center of the display, and on each trial rated the perceived motion and color spreading of the green disk. They also rated the perceived difference in depth between the green dots and the red dots. The rating scale went from 0 to 4, where 0 meant that the observer was absolutely certain that the stimulus attribute was absent, 1 that the observer was moderately certain it was absent, 2 uncertain whether it was present or absent, 3 moderately certain it was present, and 4 absolutely certain it was present.

Four different diameters of green disk were used: 0.30, 0.60, 1.2, and 2.4 degrees of visual angle. The total design of the experiment was 9 speeds \times 4 diameters \times 20 repetitions. The trials were presented over 4 experimental sessions. Within each session 5 repetitions of each combination of speed and diameter were presented in pseudorandom order. The results showed that as the speed of the display increases so too does the perception of apparent motion and color spreading of the disk. The construction of motion and the construction of color go hand in hand.

The results also illustrated another interesting aspect of the perception. In a static frame of the display, the red dots and green dots seem to be at slightly different depths, with the green dots slightly in front of the red. As the display speeds up, this difference in apparent depths decreases, until all dots appear to be in a single plane. Concomitantly, the green dots cease to look green, and instead are perceived as red just like all the surrounding dots. The green of the green dots is somehow detached from them and reattached, in modified form, to the newly-created disk.

And the entire field of dots is then made of uniform depth and color.

The diameter of the disk matters. The ratings of color spreading were strongest for the 1.2 degree diameter suggesting that the effectiveness of the process for constructing color spreading depends on the size of the region over which color must spread. It also depends, experiments conducted by Fidopiastis *et al.* (1998) now suggests, on the number and placement of dots within this region.

Effects of dot density and dot placement

Fidopiastis *et al.* varied the number of dots in each display: 100, 400, or 900 dots. They also varied the way in which dots were placed: random, pseudorandom, and aligned. The random condition was as before, with dots placed at random, according to a uniform distribution, within the square. In the pseudorandom condition the square was tessellated into an array of smaller squares. The arrays were composed of either 10×10 , 20×20 , or 30×30 squares, depending on the total number of dots in the display. Within each small square was placed one dot at random, according to a uniform distribution within that small square. In the aligned conditions, the dots were evenly spaced in rows or columns, again either in arrays of 10×10 , 20×20 , or 30×30 dots. Examples of the three types of dot placement for the 400 dot displays are shown below:

Figure 5 near here

Fidopiastis *et al.* found that ratings of color spreading and boundary clarity increase as the number of dots increases. This is no surprise. A higher density of dots means more information from which to construct motion and color, and less

area over which that motion and color must be spread. A similar result is reported by Shipley and Kellman (1993) in an achromatic display. Instead of changing dot colors, Shipley and Kellman gave their dots a small displacement as a virtual object passed by. This leads to no color spreading, but it does lead to the perception of a shape with a clear boundary. Instead of collecting ratings, they had subjects discriminate among 10 different shapes in a forced-choice procedure. They found that subjects' accuracy in discrimination increased significantly as the number of dots increased from 50 to 400.

Fidopiastis *et al.* also found that the ratings of color spreading increase with increasing regularity in placement of the dots. The perfectly aligned dots give by far the most compelling color spreading, followed by the pseudorandom placement, with the random placement giving by far the weakest color spreading. They found that this result holds for green disks and green squares, and so probably doesn't depend on the precise shape of the virtual object that is constructed.

Why does dot placement matter? We don't know yet. One possibility is that the more regular the spacing of the dots the less likely there are to be big gaps which must be filled during the process of constructing the color spreading. For perfectly aligned dots, the gaps are consistently the same modest size everywhere. For the randomly placed dots there are regions with large gaps and other regions in which dots crowd together closely. If the efficiency of the spreading process is limited by the largest gap that must be filled, then the randomly placed dots would in general lead to less efficient spreading.

A pilot experiment by Fidopiastis *et al.* also found that dot placement affects

performance in a shape detection task. In this pilot experiment, they replaced the green disk with a green square whose corners could be either sharp or slightly rounded. The subjects' task was to decide if the corners in a given trial were sharp or rounded. Detection, as measured by d' , increased significantly as the dots were more regularly placed, confirming the results obtained by ratings judgments. More careful studies of the effects of dot placement must be done to determine what exactly is responsible for the changes in strength of color spreading. This will give us some insight into the precise processes that create color spreading.

Effects of dot color

I have discussed, so far, displays which use green and red dots, but these colors are not special. Many different color combinations give clear perceptions of motion, color spreading, and boundaries. One can, for instance, use blue dots rather than green, black dots instead of red, and see striking color spreading in the form of a blue disk (Shipley and Kellman 1994). Systematic experiments have not yet been run to compare the relative effectiveness of different colors in producing color spreading and subjective boundaries in displays of dynamic color spreading. Casual observations suggest that blue is more effective than green in producing convincing color spreading, but less effective than green in producing subjective boundaries. Casual observation also suggests that green is more effective than red in producing color spreading. These would be interesting observations to follow up, given that the ratio of L to M cones is about 2:1 (Nerger and Cicerone 1992), and that S cones are even less densely distributed than M cones. There may be a relationship between

effectiveness of color spreading and cone density, with lower density cones yielding better color spreading. Lower density cones may also yield poorer subjective boundaries.

The color of the spreading within the disk depends primarily on the color of the dots within the disk, and little if at all on the color of the dots in the surround, according to Miyahara and Cicerone (1997). They obtained this result with a color matching task. Subjects viewed displays of color-spreading disks and adjusted the hue, saturation, and brightness of two solidly-colored test disks until they matched the color-spreading disk. Miyahara and Cicerone used red and green dots of various luminances in their experiment. If the dots inside the spreading disk were red, then the disk itself was red, and didn't vary with changes in the luminance of the dots in the surround. Similarly, *mutatis mutandis*, if the dots inside the spreading disk were green. It remains to be seen if this result extends to other combinations of hues. If so, then it suggests that color contrast is not the mechanism that drives dynamic color spreading.

Miyahara and Cicerone (1997) also report that luminance differences between the dots within and without the disk are not required to obtain color spreading. They used 12-frame displays of dynamic color spreading, as described above, with red and green dots whose luminance relations were systematically varied. Six color-normal observers rated the apparent motion, color spreading, and subjective boundary on a 5-point scale. They found that the best color spreading is obtained if the dots within the disk are more luminant than those without. However color spreading is obtained even near isoluminance. This suggests that differences in

chromaticities alone, without differences in luminance, are sufficient to drive dynamic color spreading. Near isoluminance, subjective boundaries almost disappear suggesting that subjective boundaries are not required for the perception of dynamic color spreading. Similar results hold for spreading and contour in static neon color spreading (Redies, Spillmann, and Kunz 1984). Again, the results of Miyahara and Cicerone have been obtained using only red and green dots. Other chromaticities need to be explored to see if their results hold more generally.

In the displays discussed so far, the color spreading is homogeneous if it is seen at all. However it is possible to alter the displays so that the spreading is not homogeneous. Consider, for instance, a display in which the dots inside the disk are green and those outside are red. On each frame of the display, one can make a certain fraction of dots inside the disk some color other than green. Suppose the fraction is 10%. Then on each frame each of the dots that should be green has a 10% chance of being another color, say red. Which dots are actually flipped to the other color varies randomly from frame to frame. When this display is viewed, one still sees a disk-shaped unit moving, and this disk is primarily filled with green color spreading. However little holes appear in this color spreading around the dots that have flipped to another color. Since these flipped dots change from frame to frame, one sees a dynamic pattern of holes appearing and disappearing in the green color spreading. Nevertheless one sees a coherent unit moving, even if the percent of dots which are flipped to red is as much as 50%.

Shipley, Cunningham, and Kellman (1993) have obtained a similar result in dynamic displays using black and white dots. They used a static field of black and

white dots, randomly intermixed, against a black background. As they moved an invisible virtual shape over this display, they simply changed the colors of the dots (from black to white or vice versa) within the boundaries of the virtual shape. These changes of dot colors were the only information available to observers for judging the virtual shape. In a 10-alternative forced choice experiment, subjects were well above chance in discriminating the virtual shapes.

Effects of stereo disparity

It has long been known that subjective contours can be fused to produce subjective surfaces in three dimensions. Lee, for instance, found that subjective contours obtained in motion displays by accretion and deletion of texture elements can be fused to create the perception of an object in depth (Gibson *et al.* 1969; Lee 1970; Shipley *et al.* 1993). Static subjective contours may also be fused (Bloomfield 1973; Lawson *et al.* 1974; Gregory and Harris 1974; Ramachandran and Cavanagh 1985; Nakayama *et al.* 1990). With crossed disparities the resulting subjective surfaces appear in front of the inducing elements; with uncrossed disparities they appear behind. The phenomenal appearance of the subjective surface and contours can change dramatically with a simple shift between crossed and uncrossed disparities (Nakayama *et al.* 1990), as illustrated by this figure:

Figure 6 near here

By fusing this figure you can see both the crossed and uncrossed cases. In the crossed case the surface appears to be a diaphanous film; in the uncrossed case it appears to be opaque (a distinction in surface qualities clearly described by Katz in

1935).

Displays of dynamic color spreading can also be viewed in stereo. The trick is simple. All dots remain at zero disparity throughout the display. The only disparity is in the assignment of color to dots. This technique is illustrated above with two frames from a display placed side by side. When fused with crossed disparity, the two frames in static view lead to the perception of transparent filter floating above the field of dots. When fused with uncrossed disparity, they sometimes lead to a weak perception of an opaque disk floating behind the field of dots. Pilot studies by Elisabeth Luntz indicate that these effects are dramatically enhanced when the display is put in motion. In the crossed case, ratings of transparent color spreading are very high, whereas in the uncrossed case ratings of an opaque surface are very high. In these displays we have strong evidence of motion, disparity, and color all interacting in our construction of objects and their surfaces.

Effects of dichoptic presentation

The stereo experiments just described show that dynamic color spreading can be affected by stereo disparity, thus indicating that at least part of the color-spreading effect can take place in the visual system at or beyond the point of binocular combination of the inputs from the two eyes. A minor modification of these stereo displays provides further evidence for the role of more central neural processing in the construction of dynamic color spreading.

The modification turns the stereo display into a dichoptic display as follows. On every odd frame of the stereo movie simply remove all green dots from the left

side of the frame, and leave the right side untouched. On every even frame remove all green dots from the right side of the frame, and leave the left side untouched. When the resulting movie is shown, the green dots defining the disk region are shown first to the right eye alone, then the left eye alone, and so on. If the display is viewed in stereo, these alternating presentations of green dots can still be fused to produce compelling dynamic color spreading (Cicerone and Hoffman 1997). It is possible to find frame presentation rates for which the display viewed monoptically produces no dynamic color spreading, but which when viewed dichoptically produces strong dynamic color spreading (Cicerone and Hoffman 1997). This again suggests that central neural mechanisms are involved in dynamic color spreading. (Dichoptic displays have been used before to study apparent motion. See Carney and Shadlen (1993), and critiques of the approach by Georgeson and Shakleton (1992). Physiological evidence by, e.g., Mikami *et al.* (1986), also suggests that apparent motion may be achieved by neural mechanisms at or beyond the site of binocular combination.)

4. Computational Theories

There is as yet no satisfactory computational theory to account for our perception of surfaces and contours in displays of dynamic color spreading. We have just surveyed some of the perceptual phenomena that such a theory must account for. But a brief review of key points is in order:

1. A sparse field of dots in which no dot ever moves, but in which individual dots change hue and brightness, can trigger the perception of subjective contours and of homogeneous color spreading through regions in which there are no dots.
2. The subjective contours and color spreading can be seen as defining a flat surface in two dimensions, or as defining a curved surface in three dimensions.
3. The subjective contours are usually smooth, but can have clear and sharp corners.
4. The subjective contours and color spreading can deform smoothly over time. They are not restricted to rigid motion in two dimensions.
5. The clarity of the subjective contours and color spreading depends on the density of the dots and on the precise placement of the dots. Dots placed in a rectangular array yield better contours and spreading than dots placed at random.
6. Crossed disparity in the assignment of colors to dots can make the color spreading appear transparent. Uncrossed disparity can make it appear opaque.
7. Color spreading can occur, near isoluminance, without an accompanying subjective contour.

This is not an exhaustive list, but a summary of some main points to be faced by computational theories. No theory to date can account for all these points. But there are a few theories that go part way.

Perhaps the most comprehensive theory is Grossberg and Mingolla's (1993)

FACADE neural network, updated to incorporate motion (see also Grossberg 1994). This update includes adding an 8-level motion oriented contrast filter which allows the system to detect and outline moving objects. To account for dynamic color spreading, this network would need to be expanded to detect apparent motion and create subjective boundaries from changes in color of static features (like sparse arrays of dots).

Shipley and Kellman (1997; Cunningham *et al.* 1997) have investigated this problem and taken an interesting step to solve it. They have found that in principle it is possible, in displays of dynamic color spreading, to compute the orientation of a straight-line subjective boundary from the color changes in 3 noncolinear dots. By piecing together many such line segments it may be possible to compute a global subjective boundary.

Prophet, Hoffman, and Cicerone (1998) have also investigated this issue. Their algorithm assigns 3-D coordinates to each dot in each frame of the display. The first two coordinates of a dot are its x and y coordinates in the display, which never change for any given dot. The third coordinate, z , is the frame number. They then save the 3-D coordinates of those dots that change color from one frame to the next. After accumulating the 3-D coordinates of such dots over several frames, they use these coordinates as control points for interpolating a surface (over space and time). The intersection of this surface with the plane $z = t$ gives the subjective boundary of the virtual shape at time t .

5. Conclusion

Color is not simply surface reflectance, or triples consisting of surface reflectances as filtered through cone sensitivity functions. Color is a complex construction of human vision. It is a construction not carried out in isolation, independent of other visual constructions. Instead it is a construction carefully coordinated with the construction of visual motion, surfaces, depths, transparency, and light sources. The nature and complexity of these coordinated constructions has barely been sampled by psychophysics to date. And no existing computational theories are yet adequate to what little of that complexity has been sampled.

Displays of dynamic color spreading provide a fertile area for psychophysical study of our coordinated construction of color, surfaces, motion, and lights. They also provide a challenging arena for testing out computational theories of these constructions. The interaction and convergence of psychophysical and computational studies of color should lead to a more profound understanding of the sophistication and complexity of the processes by which we construct color, an understanding which should be a great aid to certain discussions in the philosophy of mind which turn on theories of color vision.

References

- Albright, T.D. (1984). Direction and orientation selectivity of neurons in visual area MT of the macaque. Journal of Neurophysiology, **52**, 1106–1130.
- Baker, C.L., Hess, R.F., and Zihl, J. (1991). Residual motion perception in a 'motion-blind' patient, assessed with limited-lifetime random dot stimuli. Journal of Neuroscience, **11**, 454–461.
- Beckers, G. and Hömberg, V. (1992). Cerebral visual motion blindness: transitory akinetopsia induced by transcranial magnetic stimulation of human area V5. Proceedings of the Royal Society of London, B, **249**, 173–178.
- Beckers, G. and Zeki, S. (1995). The consequences of inactivating areas V1 and V5 on visual motion perception. Brain, **118**, 49–60.
- Bidwell, S. (1896). On subjective colour phenomena attending sudden changes in illumination. Proceedings of the Royal Society, **60**, 368–377.
- Bloomfield, S. (1973). Implicit features and stereoscopy. Nature, **245**, 256–257.
- Boyle, R. (1688). Some uncommon observations about vitiated sight.
- Cavanagh, P. and Anstis, S.M. (1991). The contribution of color to motion in normal and color-deficient observers. Vision Research,

31, 2109–2148.

Cavanagh, P. and Favreau, O.E. (1985). Color and luminance share a common motion pathway. Vision Research, **25**, 1595–1601.

Cavanagh, P., Tyler, C.W., and Favreau, O.E. (1984). Perceived velocity of moving chromatic gratings. Journal of the Optical Society of America, A, **1**, 893–899.

Cicerone, C.M. and Hoffman, D.D. (1991). Dynamic neon colors: Perceptual evidence for parallel visual pathways. University of California, Irvine, Mathematical Behavior Sciences Memo 91-22.

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

Cicerone, C.M. and Hoffman, D.D. (1997). Color from motion: Dichoptic activation and a possible role in breaking camouflage. Perception, **26**, 1367–1380.

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

Collins, M. (1925). Colour-blindness. Harcourt, Brace and Co., New York.

Cortese, J.M. and Andersen, G.J. (1991). Recovery of 3-D shape from

deforming contours. Perception & Psychophysics, **49**, 315–327.

Cunningham, D.W., Shipley, T.F., and Kellman, P.J. (in press). The perception of surface qualities in dynamic scenes: Spatiotemporally defined boundaries and surfaces. Perception.

Derrington, A.M. and Badcock, D.R. (1985). The low level motion system has both chromatic and luminance inputs. Vision Research, **25**, 1879–1884.

Desimone, R. and Schein, S.J. (1987). Visual properties of neurons in area V4 of the macaque: sensitivity to stimulus form. Journal of Neurophysiology, **57**, 835–868.

Desimone, R., Schein, S.J., Moran, J., and Ungerleider, L.G. (1985). Contour, color and shape analysis beyond the striate cortex. Vision Research, **25**, 441–452.

DeYoe, E.A. and Van Essen, D.C. (1988). Concurrent processing streams in monkey visual cortex. Trends in Neuroscience, **11**, 219–226.

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

Dufort, P.A. and Lumsden, C.J. (1991). Color categorization and color constancy in a neural network model of V4. Biological Cybernetics, **65**, 293–303.

- ffytche, D.H., Guy, C.N., and Zeki, S. (1995). The parallel visual motion inputs into areas V1 and V5 of human cerebral cortex. Brain, **118**, 1375–1394.
- Fidopiastis, C. Hoffman, D.D., Prophet, W., and Singh, M. (1998). Constructing surfaces and contours in displays of color from motion: The role of nearest neighbors and maximal disks. University of California, Irvine, Mathematical Behavior Sciences Memo 98–12.
- Gibson, J.J., Kaplan, G.A., Reynolds, H.N., and Wheeler, K. (1969). A study of optical transitions. Perception & Psychophysics, **5**, 113–116.
- Gregory, R.L. (1987). Oxford companion to the mind. Oxford University Press (pp. 78–79).
- Gregory, R.L. and Harris, J.P. (1974). Illusory contours and stereo depth. Perception & Psychophysics, **15**, 411–416.
- Grossberg, S. (1994). 3-D vision and figure-ground separation by visual cortex. Perception & Psychophysics, **55**, 48–120.
- Grossberg, S. and Mingolla, E. (1993). Neural dynamics of motion perception: Direction fields, apertures, and resonant grouping. Perception & Psychophysics, **53**, 243–278.
- Heywood, C.A., Gadotti, A., and Cowey, A. (1992). Cortical area V4 and its role in the perception of color. Journal of Neuroscience, **12**, 4056–4065.

- Katz, D. (1935). The world of colour. Translated from German by R.B. Macleod and C.W. Fox. Kegan Paul, Trench, Trubnov and Co., London.
- Lawson, R.B., Cowan, E., Gibbs, T.D., and Whitmore, C.D. (1974). Stereoscopic enhancement and erasure of subjective contours. Journal of Experimental Psychology, **103**, 1142–1146.
- Lee, D.N. (1970). Binocular stereopsis without spatial disparity. Perception & Psychophysics, **9**, 219–221.
- Lindsey, D.T. and Teller, D.Y. (1990). Motion at isoluminance: Discrimination/detection ratios for moving isoluminant gratings. Vision Research, **30**, 1751–1761.
- Livingstone, M.S. and Hubel, D.H. (1987). Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. Journal of Neuroscience, **7**, 3416–3468.
- Lueck, C.J., Zeki, S., Friston, K.J., Deiber, M.-P., Cope, P., Cunningham, V.J., Lammertsma, A.A., Kennard, C., and Frackowiak, R.S.J. (1989). The colour centre in the cerebral cortex of man. Nature, **340**, 386–389.
- Maunsell, J.H.R. and Van Essen, D.C. (1983). Functional properties of neurons in middle temporal visual area of the macaque monkey. I. Selectivity for stimulus direction, speed and orientation. Journal of Neurophysiology, **49**, 1127–1147.
- Miyahara, E. and Cicerone, C.M. (1997). Color from motion: Separate

contributions of chromaticity and luminance. Perception, **26**, 1381–1396.

Motter, B.C. (1994). Neural correlates of attentive selection for color or luminance in extrastriate area V4. Journal of Neuroscience, **14**, 2178–2189.

Nakayama, K., Shimojo, S., and Ramachandran, V.S. (1990). Transparency: Relation to depth, subjective contours, luminance, and neon color spreading. Perception, **19**, 497–513.

Nerger, J.L. and Cicerone, C.M. (1992). The ratio of L cones to M cones in the human parafoveal retina. Vision Research, **32**, 879–888.

Newsome, W.T. and Paré, E.B. (1988). A selective impairment of motion perception following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. Journal of Neuroscience, **8**, 2201–2211.

Newsome, W.T., Wurtz, R.H., Dürsteler, M.R., and Mikami, A. (1985). Deficits in visual motion processing following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. Journal of Neuroscience, **5**, 825–840.

Prophet, W., Hoffman, D.D. and Cicerone, C.M. (1998). Contours from apparent motion: A computational theory. University of California, Irvine, Mathematical Behavior Sciences Memo 98–13.

Ramachandran, V.S. and Cavanagh, P. (1985). Subjective contours cap-

ture stereopsis. Nature, **317**, 527–530.

Redies, C., Spillmann, L., and Kunz, K. (1984). Colored neon flanks and line gap enhancement. Vision Research, **24**, 1301–1309.

Riddoch, G. (1917). Dissociation of visual perception due to occipital injuries, with especial reference to appreciation of movement. Brain, **40**, 15–57.

Sacks, O. (1995). An anthropologist on Mars. Vintage Books, New York.

Sacks, O. and Wasserman, R. (1987). The case of the colorblind painter. New York Review of Books. November 19.

Salzman, C.D., Britten, K.H., and Newsome, W.T. (1990). Cortical microstimulation influences perceptual judgements of motion direction. Nature, **346**, 174–177.

Sato, T. (1988). Direction discrimination and pattern segregation with isoluminant chromatic random-dot cinematograms (RDC). Investigative Ophthalmological Visual Science, **29**, 449.

Shipley, T.F., Cunningham, D.W., and Kellman, P.J. (1993). Spatiotemporal stereopsis. In Studies in perception and action II, (eds. S.S. Valenti and J.B. Pittenger), pp. 279–283. Erlbaum, New Jersey.

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.

Siegel, R.M. and Andersen, R.A. (1986). Motion perceptual deficits following ibotenic acid lesions of the middle temporal area (MT) in the behaving rhesus monkey. Society for Neuroscience Abstracts, 12, 1183.

Stappers, P.J. (1989). Forms can be recognized from dynamic occlusion alone. Perceptual Motor Skills, 68, 243–251.

Stumpf, P. (1911). Über die Abhängigkeit der visuellen Bewegungsempfindung und ihres negativen Nachbildes von den Reizvorgängen auf der Netzhaut. Zeitschrift für Psychologie, 59, 321–330.

Todorović, D. (1996). A gem from the past: Pleikart Stumpf's (1911) anticipation of the aperture problem, Reichardt detectors, and perceived motion loss at equiluminance. Report 25/96 of the Center for Interdisciplinary Research, Bielefeld, Germany.

Van Essen, D.C. (1985). Functional organization of primate visual cortex. In Cerebral cortex Vol. 3 (eds. A. Peters and E.G. Jones), pp. 259–327). Plenum, New York.

Wallach H. (1935). Über visuell wahrgenommene Bewegungsrich-

tung. Psychologische Forschung, **20**, 325–380.

Yoshioka, T. and Dow, B.M. (1996). Color, orientation and cytochrome oxidase reactivity in areas V1, V2, and V4 of macaque monkey visual cortex. Behavioural Brain Research, **76**, 71–88.

Zeki, S.M. (1973). Colour coding in rhesus monkey prestriate cortex. Brain Research, **53**, 422–427.

Zeki, S.M. (1974). Functional organization of a visual area in the posterior bank of the superior temporal sulcus of the rhesus monkey. Journal of Physiology, **236**, 549–573.

Zeki, S.M. (1980). The representation of colours in the cerebral cortex. Nature, **284**, 412–418.

Zeki, S.M. (1983a). Colour coding in the cerebral cortex: the reaction of cells in monkey visual cortex to wavelengths and colours. Neuroscience, **9**, 741–765.

Zeki, S.M. (1983b). Colour coding in the cerebral cortex: the responses of wavelength-sensitive cells in monkey visual cortex to changes in wavelength composition. Neuroscience, **9**, 767–781.

Zeki, S.M. (1985). Colour pathways and hierarchies in the cerebral cortex. In D. Ottoson and S. Zeki (Eds.), Central and peripheral mechanisms of colour vision. Macmillan, London.

Zeki, S.M. (1991). Cerebral akinetopsia (cerebral visual motion blind-

ness). Brain, **114**, 811–824.

Zeki, S.M. (1993). A vision of the brain. Blackwell, Boston.

Zeki, S.M., Watson, J.D.G., Lueck, C.J., Friston, K.J., Kennard, C., and Frackowiak, R.S.J. (1991). A direct demonstration of functional specialization in human visual cortex. Journal of Neuroscience, **11**, 641–649.

Zihl, J., Cramon, D. von, and Mai, N. (1983). Selective disturbance of movement vision after bilateral brain damage. Brain, **106**, 313–340.

Zihl, J., Cramon, D. von, Mai, N., and Schmid, CH. (1991). Disturbance of movement vision after bilateral posterior brain damage: Further evidence and follow up observations. Brain, **114**, 2235–2252.

Figure Captions

Fig. 1. The Benham top.

Fig. 2. Wallach's (1935) neon color display. Red lines are depicted as gray.

Fig. 3. The stimulus of Dobkins and Albright (1993). Green is depicted as light grey, red as dark grey.

Fig. 4. Two frames from a display of color from motion. Green dots are depicted as smaller, red dots as larger.

Fig. 5. Stimuli used by Fidopiastis *et al.* (1998). Green dots are depicted as smaller, red dots as larger.

Fig. 6. Subjective surfaces from stereo.