10. E.A. Wasserman, The pecking pigeon: A model of complex visual processing, *Contemporary Psychology, 36,* 605–606 (1991).

11. E.A. Wasserman, Comparative cognition: Beginning the second century of the study of animal intelligence, *Psychological Bulletin, 113,* 211–228 (1993); E.A. Wasserman, Comparative cognition: Toward a general understanding of cognition in behavior, *Psychological Science, 4,* 156–161 (1993).

Recommended Reading

Commons, M.L., Herrnstein, R.J., Kosslyn, S.M., and Mumford, D.B., Eds. (1990). *Quantitative Analyses of Behavior: Vol. 8. Behavioral Approaches to Pattern Recognition and Concept Formation* (Erlbaum, Hillsdale, NJ).

Wasserman, E.A., and Bhatt, R.S. (1992). Conceptualization of natural and artificial stimuli by pigeons. In *Cognitive Aspects of Stimulus Control,* W.K. Honig and J.G. Fetterman, Eds. (Erlbaum, Hillsdale, NJ).

Color, Luminance, and the Detection of Visual Motion

Karen R. Dobkins and Thomas D. Albright

The movement of an object through the visual world results in spatial displacements of image features across the retinal surface. The ability to detect and perceive object motion necessarily involves "matching" these retinal-image features as they undergo displacement. Characterizing the process of motion detection in this manner, however, merely begs the question. What is it, precisely, that is matched? What are the criteria of similarity that qualify a match? How does a motion detector cope with multiple potential matches? By addressing these questions directly in psychophysical and neurophysiological experiments, visual scientists have sought to reveal the "rules" that govern the *motion correspondence process.* Such knowledge will ultimately lead to a more complete understanding of how people see things move.

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The search for matching tokens naturally begins with the sources of physical contrast that enable people to distinguish objects in the retinal image: luminance, color, texture, distance, and other qualities. Because objects in the visual world generally differ from one another with respect to the intensity of light reflected off their surfaces, most studies of motion correspondence have focused on the influence of luminance contrast. Under many environmental conditions, motion correspondence can be established from the unique patterns of luminance associated with each moving object. In the simplest case, bright image features can be matched (over space and time) with bright features, and dim features can be matched with dim features. Consistent with the arguments for the utility of luminance as a matching token, there exists substantial evidence in support of the possibility that local image contrast is a key determinant of motion correspondence.[1]

But what about color? On the one hand, the chromatic properties of an image certainly afford salient and reliable means for distinguishing objects. It is tempting to speculate that these chromatic properties also facilitate motion correspondence. On the other hand, the sophisticated trichromatic system with which many primates are endowed was a relatively recent acquisition over the course of evolution. As a consequence of its late development, color processing may not have become fully integrated with other visual subsystems, such as that for motion processing. This controversial issue has become amenable to study in recent years, owing in part to advances in understanding of the organization of the primate visual system and to technical developments that facilitate manipulation of the chromatic properties of a visual stimulus.

PARALLEL PROCESSING STREAMS

To understand recent work on the contribution of chromatic cues to motion correspondence, it is useful to know something about color, luminance, and motion processing subsystems in the primate brain. Data from several disciplines have yielded considerable evidence for the existence of two processing streams: parvocellular (P) and magnocellular (M).[2] P and M neurons were first identified on the basis of cell-size differences and by virtue of the stratification of these cell types into separate laminae in the lateral geniculate nucleus (LGN). These anatomical subdivisions arise in the retina and remain largely segregated through several stages of the visual hierarchy.

Neurophysiological studies have revealed that these two classes of neurons encode different types of visual information. At the level of the LGN, cells of the P pathway exhibit wavelength selectivity. Such neurons may, for example, be activated when stimulated with red light but

not when stimulated with green. P neurons also respond to luminance contrast within their receptive fields, but their sensitivities are well below psychophysical thresholds. M neurons, by contrast, exhibit little wavelength selectivity, but they are highly sensitive to luminance contrast. The distinctions between P and M response properties that have been observed in the LGN have also been found in the respective cortical components of these processing streams.[3] At the cortical level, furthermore, selectivity for direction of motion emerges as a salient property of neurons within the M division of striate cortex (V1). Directionally selective neurons respond vigorously to a stimulus moving in one direction, but exhibit little or no response to motion in the opposite direction. Directional selectivity is believed to be almost exclusively a feature of the M cortical projection, whereas selectivity for the chromatic properties of a visual stimulus remains a dominant characteristic of the P stream.

The association between specific response properties and processing streams has led to the proposal that the P and M pathways are involved in the analysis of color and motion, respectively.[4] Other evidence for this functional division of labor between P and M channels comes from neuropsychological studies. Lesions of the M laminae of the LGN in monkeys, for example, produce selective deficits in motion discrimination. Lesions of the P laminae of the LGN, by contrast, lead to deficits in color discrimination. Notably, lesions of neither P nor M laminae lead to marked deficits in luminance contrast sensitivity, demonstrating that either pathway can subserve luminance vision.[5]

SEEING COLORED PATTERNS MOVE

The evidence for independent color and motion processing chan-

nels suggests that, despite the obvious utility of color as a means to distinguish objects, the chromatic properties of a moving object may have little influence over motion correspondence. To explore this prediction, investigators have devised moving patterns that contain only chromatic cues for form. An example of such a stimulus is a pattern of repetitive red and green stripes (a red-green heterochromatic grating) for which the two contrasting hues are of equal luminance (i.e., they are *isoluminant*; Fig. 1). Although the individual stripes in the grating are salient when stationary, a striking perceptual anomaly occurs when the pattern is moved along the axis perpendicular to the stripes: Human observers report that the perceived speed of the isoluminant grating is markedly slowed in comparison to a grating in which the red and green stripes differ in luminance.[6] These results, and others of a similar nature, have been hailed as support for the belief that the chromatic properties of a moving pattern are insufficient to establish motion correspondence. This notion remains, however, a matter of much debate.[7,8] To demonstrate a contribution of color to motion processing, one need merely observe that, despite a somewhat degraded motion
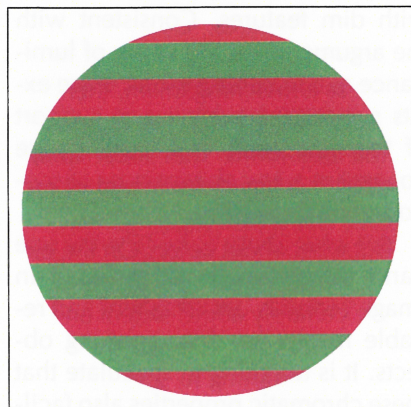

Fig. 1. Heterochromatic (red-green) grating used as a visual stimulus in psychophysical and neurophysiological experiments on the motion correspondence process. The red and green stripes are approximately isoluminant.

percept at isoluminance, motion can still be perceived, and direction discrimination performance is nearly normal. In the remainder of this review, we discuss recent experiments designed to explore the mechanisms through which color exerts these influences over motion detection.

Neurophysiological experiments designed to investigate the contribution of color to motion correspondence have focused on the middle temporal area (area MT) of monkey visual cortex. A principal component of the cortical M pathway, area MT is distinguished by a high proportion of directionally selective neurons and is believed to play a crucial role in the processing of visual motion.[9] Befitting their position in the M pathway, however, MT neurons are not selective for the color of a visual stimulus. Although much emphasis has been placed on this latter finding in the context of color–motion channel independence, a more interesting and relevant question concerns the potential for MT neurons to use chromatic information for establishing motion correspondence. In recent neurophysiological experiments, this issue has been addressed by monitoring MT responses elicited by moving patterns defined solely by chromatic cues. In line with the psychophysical evidence for residual motion perception at chromatic isoluminance, many MT neurons do indeed signal direction when stimulated with moving patterns that vary only in their chromatic content.[10,11]

There are at least two means by which the chromatic properties of a moving image might influence motion correspondence. Testing the predictions of these hypothetical mechanisms may reveal much about the nature of chromatic contributions to motion processing circuits. The simplest possibility is that the tokens for motion correspondence are chromatically defined boundaries in an image—not the colors themselves. This *unsigned chromatic*

contrast hypothesis supposes that chromatic contrast is used to establish object boundaries at an early stage in the visual hierarchy. Subsequent motion processing areas have access to these chromatically defined boundaries, but information about the colors that make up those boundaries is not forwarded through the motion pathway; the *sign* of chromatic contrast is lost (Fig. 2a, solid arrow). Relevant to this possibility, a notable, yet underemphasized, property of many M neurons in retina and LGN is their ability to detect chromatically defined image contours without regard for the sign of chromatic contrast.[12] In this respect, the M pathway carries information sufficient for the hypothesized unsigned mechanism.

A more significant role for chromatic information is assumed by the *signed chromatic contrast hypothesis*. According to this scheme, the sign of chromatic contrast is preserved, and image color per se is a token for motion correspondence. Thus, image features possessing sim-

ilar chromatic content are matched over space and time (Fig. 2a, dashed arrow). By distinction from the proposed unsigned mechanism, a signed mechanism requires neuronal inputs that are capable of preserving the sign of chromatic contrast. Later, we discuss how known properties of either M or P pathways could account for this service.

For the most part, the stimuli that have been used to characterize chromatic influences on motion correspondence (in both psychophysical and neurophysiological experiments) have confounded the predictions of the signed and unsigned hypotheses: the two types of chromatically based tokens for motion correspondence move in the same direction (Fig. 2a). In an effort to distinguish between these two hypothesized mechanisms, we have developed heterochromatic moving stimuli that should be invisible to a strictly unsigned motion correspondence mechanism (Fig. 2b). These stimuli are composed of red-green periodic gratings (identical to those

shown in Fig. 1) that are moved by repetitively displacing the pattern over a distance equal to one quarter of its period (i.e., a 90°, or 1/4 cycle, spatial phase shift). Chromatically defined or unsigned contours in this stimulus provide ambiguous information for direction of motion because contours are displaced over equal distances in two opposing directions. In order for unambiguous motion to be seen under these circumstances, information about the sign of chromatic contrast must be available as a token for motion correspondence. When presented with stimuli of this type, human subjects report motion in the direction that preserves the sign of chromatic contrast even when the red and green phases of the stimulus are isoluminant.[8] Although these psychophysical results do not rule out the existence of an unsigned mechanism, they support the signed chromatic contrast hypothesis by suggesting that image color per se (or, more specifically, the sign of chromatic contrast) is a sufficient means to establish motion correspondence.

Can the properties of directionally selective MT neurons account for this perceptual phenomenon? Our approach to this question has been to monitor the strength of directional selectivity expressed by individual MT neurons while their receptive fields are stimulated with moving patterns identical to those used in the psychophysical experiments just described.[8] The subjects for these experiments were alert rhesus monkeys trained to fixate during stimulus presentation. The luminance contrast between the red and green phases of the moving pattern was varied over a small range to ensure that our stimulus set included isoluminant conditions. A standard index of directional selectivity was used to measure the degree to which each neuron could discriminate motion in its preferred direction from motion in the opposite (nonpreferred) direction. Direction indices
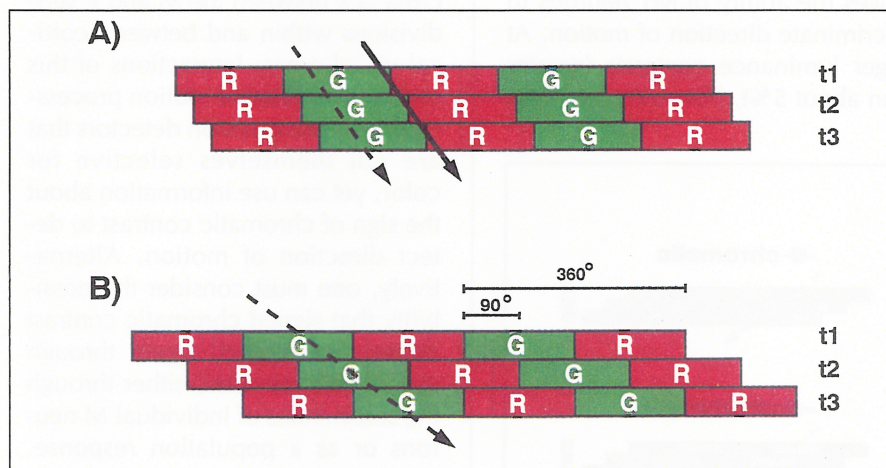

Fig. 2. Schematic space-time depiction of visual stimuli used to characterize chromatic influences on motion processing. Actual stimuli were red-green sinusoidal gratings (Fig. 1). Three temporal frames (*t*1, *t*2, *t*3) are shown. Stimuli were moved by repetitive spatial displacement over a constant phase angle. (a) Conventional drifting heterochromatic grating. Rightward motion is detectable from spatiotemporal correspondence of either chromatically defined contours (solid arrow) or actual chromatic identity (dashed arrow). (b) 90° (ambiguous) phase displacement. Chromatically defined boundaries provide ambiguous information about direction of motion (a chromatically defined border at *t*1 is equidistant from either of two potential matches at *t*2). A consistent percept of motion can occur only if information about sign of chromatic contrast is utilized.

obtained under these conditions and averaged over a sample of MT neurons are shown in Figure 3 (red-green curve). For most MT neurons, strength of directional selectivity declined somewhat when luminance contrast was eliminated (accounting for the notable depression in the averaged direction index measurements), but only rarely did directional selectivity vanish altogether. These results suggest that signed chromatic contrast is a sufficient cue for motion correspondence (or, more specifically, directional discrimination) by MT neurons. On a qualitative level, the residual directional selectivity observed under these conditions is comparable to the residual ability of human subjects to perceive motion of isoluminant patterns.[8]

Given that chromatic contrast cues appear to be available for motion detection by MT neurons, we have begun to probe the rules and priorities for motion correspondence even further by examining the possibility of interactions between chromatic and luminance contrast cues. To put it another way, since the visual world is rarely isoluminant, it is crucial to know whether chromatic contrast confers any benefit to mo-

tion correspondence mechanisms when luminance contrast is also present in a moving pattern. We obtained this information by comparing data acquired using the aforementioned chromatic patterns (Fig. 3, red-green curve) with data acquired using achromatic patterns defined solely by luminance contrast (Fig. 3, black curve). In accordance with previous results,[13] we found MT neurons to be highly sensitive to luminance contrast in achromatic stimuli, with directional selectivity typically reaching ceiling levels at about 10% contrast. The most revealing chromatic–achromatic comparison is that between indices of directional selectivity elicited by chromatic versus achromatic patterns possessing identical levels of luminance contrast. As emphasized earlier, chromatic contrast is clearly beneficial in the limiting case of isoluminance (midpoint along the x-axis in Fig. 3). These data also indicate that, for patterns with relatively low—but nonzero—levels of luminance contrast, the addition of chromatic information markedly improves the ability of MT neurons to discriminate direction of motion. At larger luminance contrasts (greater than about 5%), however, the chro-

matic and achromatic curves in Figure 3 converge, suggesting that there is little to be gained from color when luminance contrast is sufficiently large.

BRIDGING THE PROCESSING STREAMS?

Finally, let us consider what these results can reveal about the source of chromatic signals for motion correspondence and about the potential for interaction between color and motion processing streams. The fact that sign of chromatic contrast is a viable cue for motion correspondence implies that cortical M-stream motion detectors receive input from neurons that carry information about chromatic sign, either individually or as a population. Individual P neurons in retina and LGN carry such signals, and there are several routes through which P–M interactions could occur. These include convergent projections from M and P laminae of the LGN to area V1 as well as cross talk between the M and P subdivisions within and between cortical visual areas. Interactions of this sort could influence motion processing by creating motion detectors that are not themselves selective for color, yet can use information about the sign of chromatic contrast to detect direction of motion. Alternatively, one must consider the possibility that signed chromatic contrast signals are carried largely through the M pathway itself, either through the selectivities of individual M neurons or as a population response. Some evidence indicates that individual neurons in the M laminae of the LGN may carry information about chromatic sign.[14] Moreover, even if individual M neurons fail to distinguish chromatic sign, variations in relative sensitivity to red and green light across the population will ensure that any red-green heterochromatic stimulus will activate
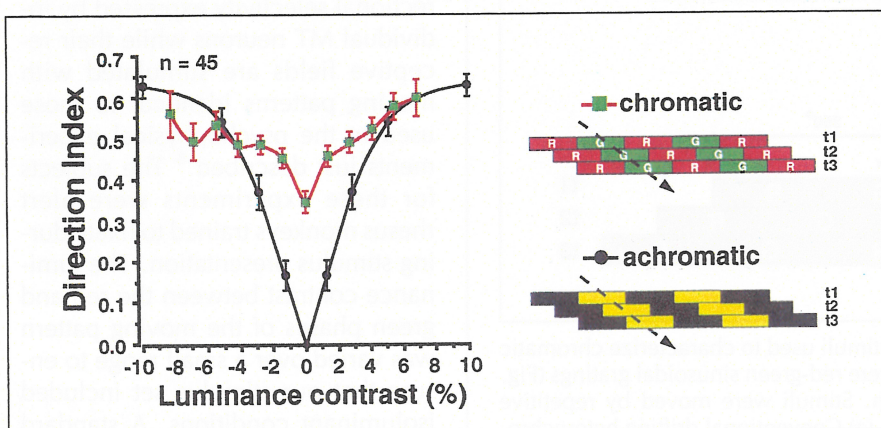

Fig. 3. Direction indices obtained using either chromatic (red-green curve) or achromatic (black curve) moving stimuli. Indices are averaged over a sample of MT neurons. A direction index was computed for each neuron from responses to motion in the preferred and nonpreferred directions: (preferred − nonpreferred)/(preferred + nonpreferred). Note that the addition of chromatic contrast improves directional selectivity when luminance contrast is low, but confers no such benefit at higher luminance contrasts.

some M pathway neurons.[15] This residual M-stream population response (present even at some behaviorally determined isoluminant point) could, in principle, be used to establish motion correspondence.

Perhaps the most direct way to determine whether P input to the M pathway contributes to the observed chromatic influences over motion correspondence would be to deactivate the P laminae of the LGN and test, both psychophysically and neurophysiologically, for selective disruptions of chromatically facilitated motion correspondence. Such experiments will soon be under way and promise to reveal much about functional interactions between motion and color processing streams.

Notes

1. S.M. Anstis, Phi movement as a subtractive process, Vision Research, 10, 1411–1430 (1970).

2. P. Lennie, Parallel pathways: A review, Vision Research, 20, 561–594 (1980).

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

4. M.S. Livingstone and D.H. Hubel, Psychophysical evidence for separate channels for the perception of form, color, movement, and depth, Journal of Neuroscience, 7, 3416–3468 (1987).

5. P.H. Schiller, N.K. Logothetis, and E.R. Charles, Functions of the colour-opponent and broad-band channels of the visual system, Nature, 343, 68 (1990).

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

7. P. Cavanagh and S.M. Anstis, The contribution of color to motion in normal and color-deficient observers, Vision Research, 31, 2109–2148 (1991).

8. K.R. Dobkins and T.D. Albright, 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 (1993).

9. J.A. Movshon and W.T. Newsome, Neural foundations of visual motion perception, Current Directions in Psychological Science, 1, 35–39 (1992).

10. H. Saito, K. Tanaka, H. Isono, M. Yasuda, and A. Mikami, Directionally selective response of cells in the middle temporal area (MT) of the macaque monkey to the movement of equiluminous opponent color stimuli, Experimental Brain Research, 75, 1–14 (1989).

11. K.R. Dobkins and T.D. Albright, What happens if it changes color when it moves? On the nature of chromatic input to macaque visual area MT, manuscript submitted for publication (1993).

12. P.H. Schiller and C.L. Colby, The responses of single cells in the lateral geniculate nucleus of the rhesus monkey to color and luminance contrast, Vision Research, 23, 1631–1641 (1983).

13. G. Sclar, J.H.R. Maunsell, and P. Lennie, Coding of image contrast in the central visual pathway of the macaque monkey, Vision Research, 30, 1–10 (1990).

14. A.M. Derrington, J. Krauskopf, and P. Lennie, Chromatic mechanisms in lateral geniculate nucleus of macaque, Journal of Physiology, 357, 241–265 (1984).

15. N.K. Logothetis, P.H. Schiller, E.R. Charles, and A.C. Hurlbert, Perceptual deficits and the activity of the color-opponent and broad-band pathways at isoluminance, Science, 247, 214–217 (1990).