Mechanisms of Human Motion Perception Revealed by a New Cyclopean Illusion

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A new cyclopean illusion of motion may bear on neural mechanisms of direction selectivity. Stationary flickering patterns were presented to each eye, and the resulting fused pattern was perceived to be moving. To determine direction of motion, the visual system seems to integrate image components differing by 90 degrees in spatial and temporal phase. On the other hand, image speed seems to be derived from displacement of features over time. A model of neural direction selectivity is discussed in light of these results.

A CYCLOPEAN IMAGE CONTAINS FEATURES that cannot be appreciated directly, but that emerge only on integration of signals from the two eyes. A classic example is the random dot stereogram in which a figure in depth is apparent only when patterns presented to the left and right eyes are binocularly fused (*1*). We now describe a new cyclopean illusion of the perception of motion. This is achieved through a novel decomposition of image motion into a pair of stationary flickering patterns. When component patterns are viewed through a stereoscope, the fused percept moves smoothly in one direction.

In its simplest form, one eye views a horizontal sinusoidal grating whose contrast is reversed back and forth in counterphase. The luminance profile of this pattern may be represented as a product of temporal and spatial modulations:

$$L(x,t) = L_0 + mL_0\sin(2\pi\omega t)\sin(2\pi fx) \quad (1)$$

where $L(x,t)$ is luminance at position x and time t, f is spatial frequency in cycles per degree, ω is temporal frequency in hertz, L_0 is mean luminance, and m is peak contrast (*2*).

The other eye views a similar pattern offset by 90° in spatial as well as temporal phase. The luminance profile of the second pattern may be represented by substituting cosine for sine in Eq. 1:

$$L'(x,t) = L_0 + mL_0\cos(2\pi\omega t)\cos(2\pi fx) \quad (2)$$

Simple addition of the two patterns in space and time yields a single sinusoidal grating drifting in one direction, represented by a traveling wave:

$$L(x,t) + L'(x,t) = 2L_0 + mL_0\cos[2\pi(fx - \omega t)] \quad (3)$$

Patterns were presented dichoptically for 1 second, after which the observer signaled the direction in which the grating seemed to move—either up or down (*3*). The actual direction of the fused pattern, represented by the sum in Eq. 3, was varied randomly between trials ($n = 20$) by reversing the interocular temporal phase difference (±90°).

Observers perceived motion in the direction predicted by the sum of left and right patterns over a broad range of spatial and temporal frequencies (Fig. 1). Particularly at low contrasts ($m < 0.1$) the fused image drifted smoothly and gave rise to a motion aftereffect (*4*). The result suggests that an early motion system may be activated dichoptically and is consistent with the physiological observation that neural direction sensitivity occurs after or coincident with binocular integration in primates (*5*). The failure of previous attempts to demonstrate binocular integration of motion cues (*6*) probably arose from the assumption that the visual system must sense motion as a spatial displacement in time. In our display a direction cue may be obtained by integrating image components which differ by 90° in spatial and temporal phase (*7*). Such components are said to form a quadrature pair and contain, in their sum, spatio-temporal energy consistent with only one direction of motion. In the following experiment we show that quadrature pairs may be integrated to yield a cyclopean perception of motion, even when they are not derived from a rigidly moving pattern.

Consider an arbitrary spatial pattern, $L(x)$, expressed as a fourier series:

$$L(x) = L_0 + \sum_n m_nL_0\sin(2\pi nx + \theta_n) \quad (4)$$

where m_n and θ_n are the amplitude and phase of the nth component, respectively. A pattern in quadrature may be created by shifting the phase of every component by 90° or, equivalently, by substituting cosine for sine:

$$L'(x) = L_0 + \sum_n m_nL_0\cos(2\pi nx + \theta_n) \quad (5)$$

These patterns may be temporally modulated by sine and cosine functions to yield a pair of flickering patterns in quadrature (Fig. 2) (*8*). When presented dichoptically (or combined on a single display), these patterns do not move rigidly but undergo morphological changes, returning to their original form after each temporal cycle (*9*).

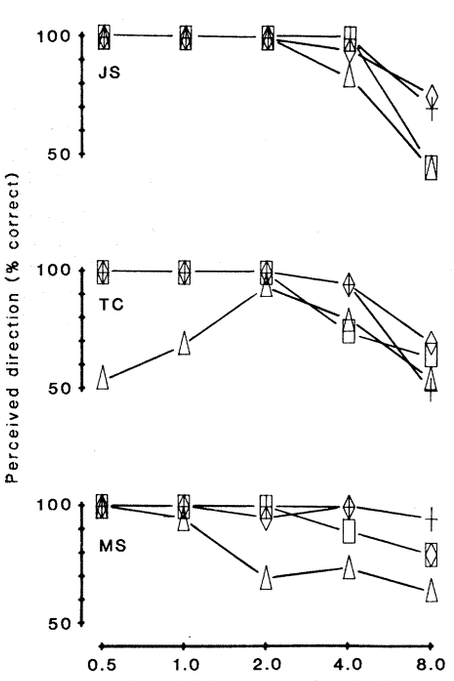

Fig. 1. The probability of perceiving motion in the predicted direction as a function of stimulus spatial frequency plotted for three observers for four temporal frequencies: □, 1 Hz; +, 2 Hz; ◇, 4 Hz; and △, 8 Hz (for 70 percent correct, $z = 1.79$, $P < 0.05$).

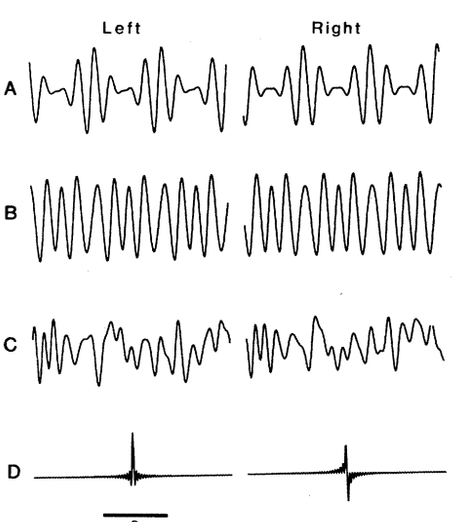

Fig. 2. Luminance profiles of spatial quadrature patterns counterphase flickered before left and right eyes. (A) Amplitude modulated grating; (B) frequency modulated grating; (C) one-dimensional noise texture; and (D) line. The patterns actually used were horizontally oriented (*3*).

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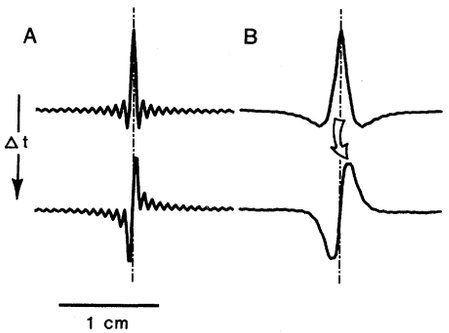

Fig. 3. Luminance profiles representing two frames of the changing line stimulus (A) as it is presented on a single display and (B) as it would appear after filtering with the visual system's modulation transfer function (*18*) (viewing distance, 114 cm). Perceived speed is consistent with displacement of the peaks in (B) (arrow; Δt = 1/4 temporal period = 250 msec).

Nevertheless, they are perceived to be moving in a consistent direction (*10*).

In a rigidly moving pattern, higher spatial frequencies are associated with higher temporal frequencies according to the relationship $\omega = vf$, where v is the image velocity. If individual spatial frequency components participate in our perception of velocity, the patterns in Fig. 2 should give rise to the perception of numerous speeds. Indeed, some do. Yet the line stimulus (Fig. 2D) seems to move at a unique rate. To estimate perceived speed, quadrature components of the line were superimposed on a single screen, and each observer adjusted the speed of a real opposing motion until the line appeared stationary (*11*). At a viewing distance of 114 cm this speed was 4.1 ± 0.2 mm/sec along the display (n = 3 observers, ω = 1 Hz). Oddly enough, perceived speed changed with viewing distance. For example, apparent speed was 2.6 ± 0.2 mm/sec at 57 cm.

These observations may be explained if we accept that the visual system treats the changing image of the line as a unique entity in motion. Speed may then be inferred from the displacement of some common feature, like peak luminance, over successive moments (Fig. 3B). During 1/4 of a temporal cycle, the luminance peak appears to change location. This displacement is consistent with the speed determined experimentally and depends on the degree to which the image is blurred by the visual system. Thus, as one approaches the display screen the image appears sharper, resembling the sequence in Fig. 3A. Peaks are barely displaced and the motion seems slower.

While feature displacement could be used to determine both speed and direction of the line stimulus, it fails to account for observations with visual noise (Fig. 2C), which is characterized by many features, completely disordered and all changing. If matches are to be made between features they would not be restricted to one direction. Thus we would expect a sensation of brownian-like motion, or no motion at all. Yet the display appears to flow in one direction.

Conceivably, feature displacement could predict both the direction and speed in the noise pattern, provided correlations are carried out within spatial representations of the image bandpass filtered. The mechanism would assign different speeds to each frequency band (spatial scale). This is consistent with the appearance of the noise pattern: coarser textures seem to flow more rapidly behind, or over, the finer textures, and pattern motion cannot be canceled by a real opposing motion (*12*). However, this scheme would fail to assign a unique speed to the line stimulus since it, too, would be represented at multiple spatial scales.

We conclude that a single mechanism cannot signal on both direction and speed of motion. Image speed seems to be determined from the change in location of features over time. This process must be sophisticated enough to identify features in an image that change in appearance or shape over time. To determine direction, the visual system uses a less intuitive scheme that attributes certain patterns of luminance in space and time to the movement of a contour. This is accomplished through local integration of quadrature spatio-temporal components and can occur when components are presented separately to either eye, thus providing a cyclopean illusion of motion.

Although the assessment of image speed seems to be a high-level process, direction of motion is probably determined by neurons in the primary visual cortex that use a spatio-temporal decomposition similar to the one we have imposed dichoptically. The mechanism (Fig. 4) works by extracting spatio-temporal energy consistent with one direction but many speeds of image motion. It is based on the concept of an ideal motion sensor derived by Watson and Ahumada (*13*) and resembles a class of models inspired by Reichardt (*14*). A pair of linear spatial filters, $S(x)$ and $S'(x)$, represent binocular subunits of the neuron's receptive field. They exhibit even and odd symmetry about the same spatial axis, thus approximating a quadrature pair (*15*). The signals produced by these subunits will differ by 90° of temporal phase regardless of the spatial frequency content of the moving image. The sign of this phase difference (lead or lag) depends on the direction of image motion. Signals produced by the spatial subunits are then delayed by temporal filters with weighting functions $H(t)$ and $H'(t)$. These functions also approximate a quadrature relation and therefore introduce an additional 90° phase difference between left and right signals. For motion in one direction, the left and right signals differ by 180° and cancel when summed. For motion in the opposite direction, the 90° phase difference introduced by spatial filters is balanced by temporal filters, yielding superposition of left and right signals when summed.

This type of mechanism can signal the

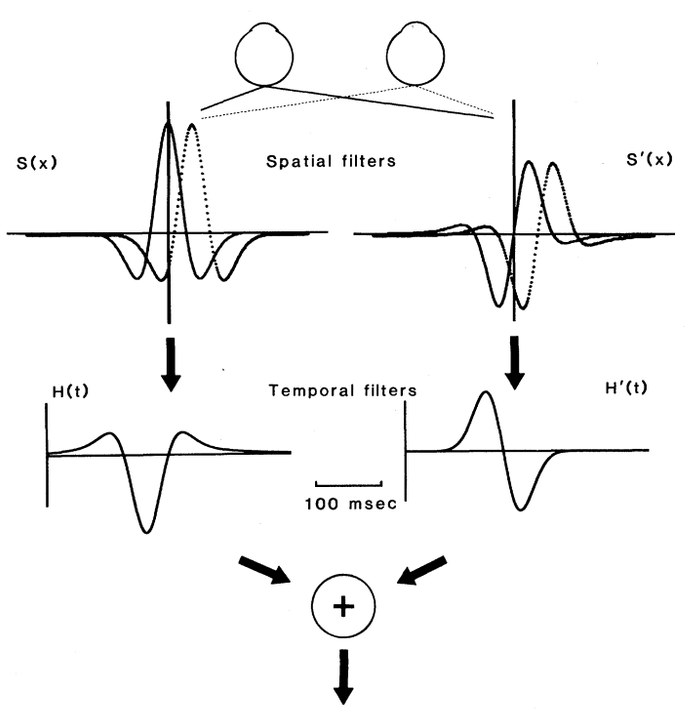

Fig. 4. Model of neural direction selectivity.

presence of a moving contour and its direction (*16*). The scheme is ideal in that it cannot be fooled by the emergence of new contours, inappropriate speed, or complicated texture (*17*). It represents a means of maintaining direction selectivity over a broad range of spatial and temporal frequencies to which cortical neurons are responsive, but is achieved by sacrificing sensitivity to image speed.

REFERENCES AND NOTES

1. B. Julesz, *Foundations of Cyclopean Perception* (Univ. of Chicago Press, Chicago, 1971).
2. Contrast (m), defined ($L_{max} - L_{min}/2L_0$, was 0.25; L_0 = 1.1 footlamberts (1 footlambert, 3.43 cd/m^2).
3. Horizontal gratings in vertical motion do not introduce horizontal disparity cues for depth perception and are less likely to stimulate vergence eye movements.
4. At higher contrasts, perceived motion is accompanied by flicker.
5. P. H. Schiller, B. L. Finlay, S. F. Volman, *J. Neurophysiol.* **39**, 1288 (1976).
6. M. Green and R. Blake, *Vision Res.* **21**, 356 (1981); O. Braddick, *ibid.* **14**, 519 (1974).
7. The percept is degraded when phase differences other than 90° are used.
8. More complicated temporal modulation functions can be used provided they too exhibit quadrature relationships between left and right eye images.
9. Viewed binocularly, the patterns in Fig. 2 seem to change cyclically: the left pattern fades into the right, then to the negative (reversed contrast) image of the left, to the negative of the right, and back to the left. When the patterns are combined on a single display, the illusion resembles reversed phi [S. M. Anstis and B. J. Rogers, *Vision Res.* **15**, 957 (1975)].
10. On a test similar to the one preceding, each of three observers identified the direction of motion consistent with stimulus spatio-temporal frequency components (percent correct ≥85 for each pattern; $z \geq 3.13$; $P < 0.01$; $n = 20$ trials).
11. In practice this must be done by presenting the spatio-temporal line pattern for brief periods (for example, 250 to 500 msec), because ultimately the real opposing motion will produce a noticeable displacement. (At 114 cm the line contains spatial frequencies ≤25.6 cycle/deg).
12. These observations apply to dichoptic as well as monocular (superimposed) versions of the display.
13. A. B. Watson and A. J. Ahumada, *NASA Tech. Mem. 84352* (1983).
14. W. Reichardt, *Sensory Communication*, W. Rosenblith, Ed. (MIT Press and Wiley, New York, 1961), pp. 465–493. See also E. H. Adelson and J. R. Bergen [*J. Opt. Soc. Am.* **2**, 284 (1985)] and J. P. H. van Santen and G. Sperling [*ibid.* **1**, 451 (1984)].
15. D. A. Pollen and S. F. Ronner [*Science* **212**, 1409 (1981)] reported that such a quadrature relationship is common between adjacent simple cells in the cat's primary visual cortex. Such cells might serve as subunits for other direction-selective cortical neurons.
16. By "direction" we mean orthogonal to a neuron's preferred orientation ±90°.
17. The mechanism does not alias spatially or temporally.
18. We have adapted expressions derived by D. H. Kelly [*J. Opt. Soc. Am.* **69**, 1340 (1979)] describing human contrast sensitivity. The relation between contrast sensitivity data and the visual system's modulation transfer function is unknown and therefore serves only as an approximation.

19. We thank I. Ohzawa and R. D. Freeman for helpful comments on the manuscript and J. Slobin for volunteering her time. Supported by NIH grants EY01175 and EY05636 awarded to T.C. and R. D. Freeman.

31 May 1985; accepted 1 November 1985

Receptor-Coupled Activation of Phosphoinositide-Specific Phospholipase C by an N Protein

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Cleavage of phosphatidylinositol 4,5-bisphosphate by phospholipase C results in the production of two important second messengers: inositol-1,4,5-trisphosphate and 1,2-diacylglycerol. Although several receptors promote this cleavage, the molecular details of phospholipase C activation have remained unresolved. In this study, occupancy of a Ca^{2+}-mobilizing receptor, the oligopeptide chemoattractant receptor on human polymorphonuclear leukocyte plasma membranes, was found to lead to the activation of a guanine nucleotide regulatory (N) protein by guanosine 5′-triphosphate. The activated N protein then stimulated a polyphosphoinositide-specific phospholipase C by reducing the Ca^{2+} requirement for expression of this activity from superphysiological to normal intracellular concentrations. Therefore, the N protein–mediated activation of phospholipase C may be a key step in the pathway of cellular activation by chemoattractants and certain other hormones.

THE MECHANISMS BY WHICH OCCUPANCY of certain hormone receptors leads to cellular activation by elevating intracellular Ca^{2+} levels have been the subject of intense investigation (*1, 2*). According to the current paradigm, agonist binding to these receptors leads to the phosphodiesteric cleavage of phosphatidylinositol 4,5-bisphosphate (PIP_2), yielding inositol-1,4,5-trisphosphate (IP_3) and 1,2-diacylglycerol. These products mediate the release of Ca^{2+} from intracellular stores (*2*) and the activation of protein kinase C (*3*), respectively. Studies of polyphosphoinositide-specific phospholipase C, however, have demonstrated that expression of this activity in vitro requires superphysiological concentrations of Ca^{2+} (>100 μ*M*) (*4–6*). Therefore, some other mechanism must exist for activating this enzyme at physiological Ca^{2+} concentrations (0.1 to 0.2 μ*M*).

Accumulating evidence suggests that a guanine nucleotide regulatory (N) protein is important in regulating the activity of phospholipase C. For example, addition of analogs of guanosine 5′-triphosphate (GTP) to permeabilized cells produces responses similar to those elicited by some hormonal stimuli (*7, 8*). In addition, *Bordetella pertussis* toxin, which catalytically inactivates certain N proteins (*9*), interferes with chemoattractant-induced responses of phagocytes including stimulated polyphosphoinositide hydrolysis (*10, 11*). More directly, we have recently shown (*12*) that occupancy of the oligopeptide chemoattractant receptor on human polymorphonuclear leukocyte (PMN) plasma membranes (*13*) by the chemotactic peptide *N*-formyl-methionyl-leucyl-phenylalanine (fMet-Leu-Phe) leads to the hydrolysis of PIP_2 only if GTP is included during the incubation. Similarly, hydrolysis of PIP_2 in membranes prepared from blowfly salivary glands can be induced by the addition of serotonin and GTP (*14*).

In the present study, we defined the role of the N protein in the transduction mechanism of the oligopeptide chemoattractant receptor on human PMN's. When activated by a guanosine triphosphate, the N protein appears to reduce the concentration of Ca^{2+} required for activation of a polyphosphoinositide-specific phospholipase C to physiological levels.

Incubation of plasma membranes isolated from human PMN's with adenosine [γ-^{32}P]-triphosphate ([γ-^{32}P]ATP) leads to the synthesis of radiolabeled phosphatidic acid, phosphatidylinositol 4-phosphate (PIP), and PIP_2 (*12*). Further incubation of these labeled membranes with fMet-Leu-Phe (0.1 μ*M*) plus GTP (10 μ*M*), but not with either agent alone, in the presence of 1 μ*M* $CaCl_2$ resulted in hydrolysis of the labeled PIP_2 (Table 1). Guanosine di- and monophosphate (GDP and GMP), as well as ATP and adenosine di- and monophosphate (ADP and AMP), were not active in promoting PIP_2 breakdown either alone or in the presence of fMet-Leu-Phe. The GTP analog guanosine 5′-*O*-(3-thiotriphosphate) (GTPγS) stimulated PIP_2 hydrolysis both in the absence and presence of fMet-Leu-Phe. These results indicate that coupling of the occupied oligopeptide chemoattractant re-

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