- of a single long column and sodium citrate buffer. of a single long column and somulin circate outer.
 DNA was determined by a microadaptation of the method of J. M. Kissane and E. Robbins [J. Biol. Chem. 233, 184 (1958)].
 J. G. Jacobsen and L. H. Smith, Physiol. Rev. 48,
- Chem. 235, 164 (1936);
 J. G. Jacobsen and L. H. Smith, Physiol. Rev. 48, 424 (1968); H. Pasantes-Morales, J. Klethi, M. Ledig, P. Mandel, Brain Res. 41, 494 (1972); A. I. Cohen, M. McDaniel, H. Orr, Invest. Ophthalmol. 12, 686 (1973); S. Macione, P. Ruggeri, F. De-Luca, G. Tucci, J. Neurochem. 22, 887 (1974). W. O. Read and J. D. Welty, J. Pharmacol. Exp. Ther. 139, 283 (1963); M. S. Starr and M. J. Voaden, Vision Res. 12, 1261 (1972); P. Dolora, P. Marino, F. Buffoni, Biochem. Pharmacol. 22, 2085 (1973); E. G. Honegger, L. M. Krepelka, M. Steiner, Experientia (Basel) 29, 1235 (1973); H. Pasantes-Morales, N. Bonaventure, N. Wioland, P. Mandel, Int. J. Neurosci. 5, 235 (1973); H. Pasantes-Morales, J. Klethi, P. F. Urban, P. Mandel, Exp. Brain Res. 19, 131 (1974); N. Bonaventure, N. Wioland, P. Mandel, Brain Res. 80, 281 (1974). C. D. Dickinson and P. P. Scott, Br. J. Nutr. 10, 311 (1956); F. W. Bernhart, Nature (Lond.) 191, 358 (1961).
- 358 (1961)
- Datta and H. Harris, Ann. Eugenics 18, 107

- 8. J. P. Greaves and P. P. Scott, Nature (Lond.) 187.
- J. P. Greaves and P. F. Scott, *Nature* (Lona.) 161, 242 (1960).
 J. G. Jacobsen, L. L. Thomas, L. H. Smith, Jr., *Biochim. Biophys. Acta* 85, 103 (1964).
 L. J. Machlin, *Poultry Sci.* 34, 1209 (1955); W. G. Martin, *ibid.* 51, 608 (1972).
- W. G. Martin, N. L. Sass, L. J. Hill, S. Tark, R. Truex, *Proc. Soc. Exp. Biol. Med.* **141**, 632 (1972); L. J. Hill and W. G. Martin, *ibid.* **144**, 530 (1973).
- J. Hill and W. G. Martin, *Ibid.* 144, 530 (1973).
 P. C. Rambaut and S. I. Miller, *Fed. Proc.* 24, 373 abstr. (1965).
- M. S. Starr, Biochem. Pharmacol. 22, 1693 (1973); M. S. Starr, Biochem. Pharmacol. 22, 1693 (1973); E. Ehinger, Brain Res. 60, 512 (1973); N. Urgu-hart, T. L. Perry, S. Hansen, J. Kennedy, J. Neuro-chem. 22, 871 (1974). E. L. Berson, K. C. Hayes, A. R. Rabin, S. Y. Schmidt, G. Watson, in preparation. These studies were supported in part by a grant-in-aid from the National Institutes of Health (EY-
- old from the National Institutes of Health (EY-00631); the Fund for Research and Teaching, Department of Nutrition, Harvard School of Public Health; the National Retinitis Pigmentosa Foundation, Baltimore, Maryland; and the George Gund Foundation, Cleveland, Ohio.
- 11 February 1975

Moving Visual Phantoms: A New Contour Completion Effect

Abstract. Moving contours surrounding an empty region make phantoms appear to move through the empty region. The phantoms are contours, dimmer than the inducing contours but of the same pattern, color, speed, and direction of movement. The phantoms originate in the brain and may be related to completion effects most often seen with visual pathology.

A localized region of blindness often goes unnoticed. Instead of looking like a hole in the visual field, the blind region (scotoma) takes on the appearance of surrounding intact areas of the field. These completion effects may hide the temporary scotomas that accompany migraines (1) or the permanent scotomas that result from small lesions of the visual cortex (2). Similar processes also render the blind spot (optic disk) in each eye unobtrusive (3). We have discovered an entirely new form of completion that operates over large areas in any normal field. This type of completion produces a dramatic change in the appearance of a large empty region surrounded by a field of moving contours: the empty region seems to be filled with phantom versions of the moving surround contours. We have studied this phantom motion under a variety of conditions and report some of the results here.

Standard electronic methods (4) were used to make a vertical sinusoidal grating drift across an oscilloscope screen. The spatial frequency of the grating was 0.75 cycle/deg, and it drifted horizontally at about 1 hertz. The grating had a space-average luminance of 60 cd/m² and a contrast of 0.25; viewing was in a dimly illuminated room. Observers saw only two sections of this grating, each 1° high, one at the top and one at the bottom of the screen. The sections were separated by several layers of black construction paper 3° high and extending across the entire width

of the screen (the total density of black paper was 15D, where D = density units). A small white fixation mark was painted on the center of the construction paper. Upon staring at the mark in the center of the gap, all observers immediately reported the appearance of a dim grating which seemed to drift across the blank gap in phase with the real pattern flanking the gap. This phantom grating would suddenly disappear when the real grating stopped moving. At this writing, every observer tested has seen the phantom grating (N = 20 observers,from three different laboratories in two countries).

The phantom looked as though a portion of the real grating was being viewed through a neutral density filter. To quantify this appearance, neutral density filters were placed over sections of the real grating to mimic the appearance of the phantoms. Filters between 1.7 and 2.0 density units gave a satisfactory match.

Spatial frequency is an important determinant of the phantom grating and the apparent spatial frequency of the phantoms covaried with that of the real, inducing grating. Under our viewing conditions, the phantoms became less distinct as spatial frequency increased by as little as fourfold (to 3 cycle/deg). Moreover, when the drifting, low-frequency (0.75 cycle/deg) grating had a square-wave luminance profile rather than a sinusoidal one, the phantoms took on a square-wave appearance but were reduced in vividness

Finally, the angle between the opaque occluder and direction of grating drift is critical. In most of our observations the vertical gratings drifted either leftward or rightward; the occluded section extended across the screen horizontally. When we rotated the occluding material to vertical but kept direction of drift as before, the phantoms were not seen.

We wondered where in the visual system our phantoms originated. To get a rough answer, we arranged two pieces of Polaroid material on the cathode-ray tube. Oppositely oriented Polaroid analyzers produced a dichoptic display: the top section of inducing grating was seen by the right eye only, the bottom section by the left eye only. No phantom gratings were seen when the display was viewed monocularly, but when it was viewed dichoptically, phantoms of normal vividness were seen. This means that the phantom gratings can be produced by mechanisms in the visual system at or beyond the point where information from both eyes is combined (5).

Another observation is also consistent with a central origin for our effect. We compared the phantoms seen in two different viewing conditions: in the first condition, the motion of the grating's image across the retina was produced as before, with a stationary fixation located midway between two separate sections of moving grating; in the second condition, equivalent motion of the retinal image was produced by tracking a fixation point that moved across the empty region between two sections of a stationary grating. The fixation point in both conditions was produced on the face of an oscilloscope whose image was combined optically with that of the grating. The speed of the fixation point's movement in condition 2 precisely matched the drift rate of the grating in condition 1. Six observers were tested in both conditions and all reported that the phantoms were very much attenuated or were absent entirely (N = 4) in condition 2. Retinal image motion accompanying movement of the eyes is not sufficient to produce pronounced visual phantoms. This implies that the phantoms are generated somewhere in the nervous system central to the processing of information about the state of the extraocular muscles (6).

We wondered what might happen when top and bottom gratings moved in opposite directions. To test this, a Dove prism was set in front of the lower half of one of the observer's eyes and the other eye was occluded. Looking straight ahead, the observer saw the top grating section moving rightward and the bottom section moving leftward. Each section produced a phan-

30 MAY 1975

tom of its own which extended slightly less than halfway through the empty region separating top and bottom sections. Along the center of the blank region the phantoms were absent. The two oppositely moving phantoms could not result simply from independent contributions of the two oppositely moving inducing gratings. In fact, either section of inducing grating alone, top or bottom, could not by itself produce a phantom. For example, when we covered up the top section of the grating, the bottom section failed to produce any phantom. A single section even failed to produce a discernible phantom when it alone was larger than two separated sections that could produce a phantom. So, when oppositely moving inducing gratings produce oppositely moving phantoms, the effect results from a long-distance interaction between the two separate inducing gratings, rather than from the simple summation of their two independent effects. The same argument also applies to conditions wherein top and bottom grating sections move in the same direction. For such conditions, too, the phantoms are the product of an interaction between the two separate sections rather than a sum of their separate effects.

From the start, we were concerned that the phantoms were the product of scattered light within the eyeball. Three observations rule out this possibility. First, the presence of the phantoms in the dichoptic conditions described earlier points to a central rather than a retinal origin for the phantoms. Second, phantom gratings remain quite distinct even when the contrast of the surrounding, real grating is only twice the contrast required to discern the bars of that real grating. Finally, the height of the top and bottom grating sections (contrast = 0.25) could be reduced to only 0.33° and still produce phantoms across a 3° central gap. In these last two conditions it is unlikely that internally scattered light would be of sufficient intensity and spatial extent to produce vivid entopic gratings. Two other facts related to these conditions may be worth noting. When the empty region separating grating sections was quite wide (for example, 3°) observers usually found that several seconds had to pass before the phantoms became apparent; moreover even after this incubation period the phantoms were less vivid than with smaller gaps. Surprisingly, the phantom gratings often appeared more vivid when induced by a low-contrast grating than when induced by a higher-contrast grating. This may reflect the fact that with a weak inducing grating there was less difference between the contrast of the phantom and that of the inducing grating; with a strong inducer the relative contrast of the phantom seemed to suffer by comparison.

Before our work with gratings we studied another, less vivid form of phantom movement produced by a surround (10° by 10°) of 950 moving, spatially random dots. The dots drifted continuously in one direction across a cathode-ray tube at 5.5° per second. The central region (4° by 4°) of the screen was free of all dots but one, a stationary fixation point. When observers fixated the point provided, they saw moving dots over the entire screen, even in the center, where none was present. The illusory dots in the middle of the screen seemed like phantom versions of dots in the surrounding area; the center dots appeared to move with the same speed and direction as the surround dots, but were dimmer. The phantoms were so compelling that several naive observers insisted that dots were really moving uniformly across the whole screen and that we had simply placed a dark filter over the middle section. The phantom dots were rarely seen when (i) only a fixation point was present in the field or (ii) the surround dots were present but stationary. Here, too, surround movement is critical for producing phantoms.

After informal testing established that most naive observers experienced the phantom dots, we turned to more extensive experimentation with four observers. We began by varying the speed of the surround dots and the size of the center gap. The entire screen subtended a 10° visual angle on each side. Observers judged (i) the presence or absence of the phantoms, (ii) the speed of the phantoms relative to the surround, and (iii) how much the shape of the phantoms resembled that of the surround dots (dot-likeness). In all conditions, the speed of the phantoms was shown by magnitude estimation (7) to be nearly identical to the speed in the surround. The phantoms were reported more frequently as either (i) the speed of the surround dots increased (from 0° to 8.4° per second, the highest velocity we could produce) or (ii) the size of the center, dot-free zone was increased (from 0.5° to 8° on a side). But while the incidence of phantoms increased with larger gaps, they were judged less distinct and less dot-like.

We should stress that the effects we are describing are entirely different from the familiar visual phenomenon of "induced motion." In that illusion, a pattern of moving contours surrounds a region of stationary contours and the surround motion in one direction makes the center contours appear to move in the opposite direction (8). Moreover, this induced motion usually

appears slower than the inducing motion (9). In contrast, the phantom motion described here shares all the characteristics of the surround's motion, including its pattern, speed, and direction. In this respect, it is more like the completion phenomena described earlier or like still other effects in which complete percepts are experienced despite some spatial gap in the stimulus (10)

The unique features of the phantoms described here are (i) their strong dependence on movement, (ii) their ability to spread over extremely large regions of normal visual space, and (iii) their compelling vividness. In fact, we wonder whether the strength of other completion effects might not be enhanced by the use of moving rather than stationary conditions of stimulation.

Completion effects such as the moving phantoms may reflect a general tendency of the visual system to extrapolate across repetitive or redundant spatial distributions. These extrapolations could be the by-product of mechanisms that ordinarily use certain forms of data compression to achieve economies in the processing of neural data (11). The surprising, erroneous extrapolations we have described may offer unique insights into the unnoticed, correct extrapolations that may be an integral part of the visual system's normal operation. But whatever their detailed explanation, the moving phantoms do show that the visual system, like other sensory systems (12), abhors a gap, particularly one in the midst of transient events.

> PAUL TYNAN ROBERT SEKULER

Cresap Neuroscience Laboratory, Department of Psychology, Northwestern University, Evanston, Illinois 60201

References and Notes

- 1. K. S. Lashley, Arch. Neurol. Psychiatr. 46, 331
- K. S. Lasniey, Arch. Iveurot. Tsychiatr. 40, 331 (1941).
 H.-L. Teuber, W. S. Battersby, M. B. Bender, Visual Defects after Penetrating Missile Wounds of the Brain (Harvard Univ. Press, Cambridge, Mass., 1960)
- Mass., 1960).
 Y. LeGrand, Form and Space Vision (Indiana Univ. Press, Bloomington, 1967), pp. 146–151.
 C. Enroth-Cugell and J. G. Robson, J. Physiol. (Lond.) 187, 517 (1966).

- (Lond.) 187, 5\(\bar{1}\)7 (1966).
 5. B. Julesz, Foundations of Cyclopean Perception (Univ. of Chicago Press, Chicago, 1971), p. 6.
 6. H.-L. Teuber, Handb. Physiol. 3, 1595 (1960).
 7. S. S. Stevens, Am. J. Psychol. 69, 1 (1956).
 8. K. Duncker, Psychol. Forsch. 12, 180 (1929).
 9. P. Tynan and R. Sekuler, Vision Res., in press.
 10. T. Shipley, Science 150, 348 (1965); R. L. Gregory, Nature (Lond.) 238, 51 (1972).
 11. F. Ratliff, in From Theoretical Physics to Biology, M. Marois, Ed. (Karger, Basel, 1973), pp. 328–373.
- F. A. Geldard and C. E. Sherrick, *Science* **178**, 178 (1972); R. M. Warren, *ibid*. **167**, 392 (1970).
- 13. We thank R. Blake for his thoughtful comments on this report. Supported by National Eye Institute grant EY-00321. One of us (P.T.) was supported by National Institute of Mental Health training grant MH-11284.

9 December 1974

SCIENCE, VOL. 188