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6. This work was supported by a research grant from the Non-Medical Use of Drug Directorate of the Department of Health and Welfare, Canada.

19 January 1976; revised 26 March 1976

A Multistable Movement Display: Evidence for Two Separate Motion Systems in Human Vision

Abstract. *Two competing sensations of apparent movement were produced by the rapid alternation of two multielement stimulus frames. Either sensation could be made dominant by appropriate manipulations of the stimulus display. The results suggest that there are two systems capable of generating movement signals in man. One system depends on preliminary processing of form, and the second system does not.*

Sensations of stroboscopic movement were produced by a cyclic alternation of two stimulus frames in a tachistoscope. Frame 1 contained three black dots (a, b, c) arranged in a horizontal row on a white background. Frame 2 contained three identical dots (d, e, f), also arranged horizontally but shifted to the right, so that the positions of dots d and e of frame 2 overlapped those of b and c, respectively, of frame 1. With a frame duration of 200 msec and an interval of approximately 40 msec between frames, the spatiotemporal display gave rise to a multistable percept; either the observer perceived a group of three dots moving in toto back and forth (group movement) or he perceived the overlapping dots of each frame as stationary and a third dot as moving back and forth from one end of the display to the other (element movement) (*1*). On the average, the two movement sensations alternated spontaneously about eight times per minute, and the rate of reversal remained stable over a 10-minute period. However, we have been able to bring the multistable percept under stimulus control, that is, to cause either the group movement sensation or the element movement sensation to predominate, by manipulating the duration of the interval between frames, the type of viewing (binocular or dichoptic), or the contrast of the stimulus frames (*2*). The results suggest that there are two systems or channels for generating movement signals in humans, each with different functional properties.

A three-channel Gerbrands tachistoscope was used to superimpose the two alternating stimulus frames (provided by two separate channels) on a continuously illuminated, uniform background (provided by a third channel). The viewing distance was 81 cm; at this distance each stimulus frame and the uniform background subtended a visual angle of 9° horizontally and 6°15′ vertically. The diameter of each black dot was 40′ with a center-to-center separation of 60′ between a pair of adjacent dots. The luminance of the black dots when superimposed on the uniform background was 0.15 millilambert; that of the white area of each stimulus frame when superimposed on the uniform background, 0.35 mlam. During the interval between stimulus frames, only the uniform white background (0.10 mlam) was visible. In all experimental conditions the duration of each stimulus frame was 200 msec. The interval between stimulus frames (ISI) was varied.

In the first experiment there were 12 different stimulus conditions resulting from the factorial combination of six ISI's (5, 10, 20, 30, 50, or 70 msec) and two types of viewing (binocular or dichoptic). In the binocular condition the observer viewed both stimulus frames with both eyes. In the dichoptic condition, with appropriately arranged Polaroid filters, one stimulus frame was presented to the observer's right eye, the other to the observer's left eye (*3*). In both viewing conditions the uniform background provided by the third channel of the tachistoscope was visible to both eyes and allowed the observer to maintain a constant degree of accommodation and convergence.

The dependent measure was the type of movement reported by the observer (either element or group) after he watched four cycles of one of the 12 experimental stimulus sequences (one cycle: frame 1–ISI–frame 2–ISI). While viewing each sequence, the observer was instructed to direct his gaze toward the center of the stimulus display (no fixation point was used) and at the same time to attend to (be aware of) the entire display. Each of the 12 stimulus sequences was presented 10 times, following an order determined by block randomization. Eight observers participated in the experiment (*4*).

The number of times that each observer reported group movement in each of the 12 experimental conditions was converted to a percentage. The pattern of results was the same for all observers. The observers reported group movement very infrequently (most always saw element movement) at short ISI's in the binocular condition (Fig. 1). With binocular viewing and long ISI's (50 or 70 msec), the observers almost always saw group movement. In addition, the transition from the element movement sensation (few group movement responses) to the group movement sensation occurs abruptly at about 40 msec. In contrast to the results with binocular viewing, the mean percentage of group movement responses in the dichoptic condition is equal to or near 100 at all ISI's. The element movement sensation could not be obtained with dichoptic viewing.

If one looks only at the percentage data in the binocular condition, it is not possible to determine whether or not the absolute strength of the group movement sensation changed with ISI. The percentages show only that the strength of the group movement sensation decreased relative to that of the element movement sensation as the ISI was made shorter. It is not clear whether the absolute strength of the group movement sensation changed with ISI. The dichoptic data suggest that the absolute strength remained constant. However, supplementary observations indicate that the group movement sensation is more fragile at the short ISI's. When the stimulus sequences were extended beyond four cycles, the group movement sensation adapted within a few seconds with short ISI's (that is, the sensation of movement ceased and was replaced by a sensation of "on-off" flashing of the stimulus frames) but continued indefinitely with long ISI's.

The procedure of a second experiment was identical to that of the first experiment with the following exceptions. Two different stimulus displays were used in the second experiment. In one condition (positive-positive), there were black dots on a white background in both stimulus frames. In the second condition (positive-negative), the dot-to-background contrast was reversed in the two stimu-

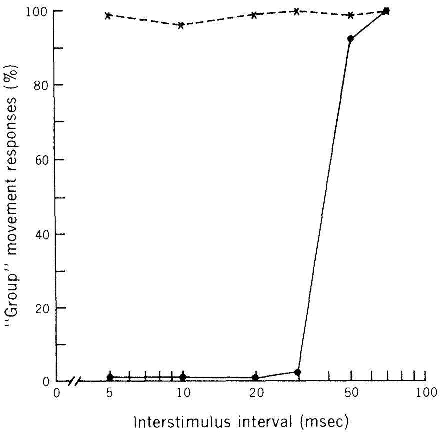

Fig. 1. Percentage of group movement responses (averaged across observers) as a function of the interval between successive stimulus frames (experiment 1). Binocular viewing: solid line. Dichoptic viewing: dashed line.

lus frames. One frame contained black dots on a white background, and the second frame contained white dots on a black background. The luminance of the white areas in each frame was 0.25 mlam; that of the dark areas, 0.05 mlam. There was no continuously present background upon which the stimulus frames were superimposed, and the ISI was completely dark. The ISI's were 10, 20, 30, 50, 70, and 80 msec long. The observers (N = 8) viewed the displays binocularly in all conditions.

The results in the positive-positive condition (Fig. 2) replicate the binocular results obtained in the first experiment. At short ISI's, the observers almost always saw element movement; at long ISI's they saw group movement on 90 to 100 percent of the presentations. By contrast, the mean percentage of group movement responses in the positive-negative condition is equal to or approaches 100 at all ISI's. As with dichoptic viewing, the group movement sensation with the positive-negative display adapted readily with short ISI's but persisted indefinitely with long ISI's.

The major finding of our study is that two competing movement sensations can be elicited by a single spatiotemporal display. By the appropriate manipulation of stimulus conditions, either sensation can be made dominant. The multistability phenomenon suggests that the visual system contains two different motion systems, each with different functional properties.

The group movement sensation predominated (i) when long intervals (> 40 msec) intervened between stimulus frames, (ii) when the two stimulus patterns were presented dichoptically, or (iii) when stimulus contrast was reversed from one stimulus frame to the next. These data indicate that the system that generates the group movement signal is sluggish and is located in the cortex beyond the point where signals from the two eyes are combined. In addition, in order that the group movement sensation survive reversals of stimulus contrast in successive frames, some type of form processing must occur at a site peripheral to or at the site of generation of the group movement signal.

The group movement sensation is similar to the stroboscopic movement of clusters of elements investigated by Ramachandran *et al.* (*5*) and Pantle (*6*). In those studies each of two stimulus frames contained a cluster of elements that were perceptually segregated from surrounding background elements solely on the basis of a form cue. In the study by Ramachandran *et al.* the clusters were defined by the tendency of like elements (dark and light points) in each frame to occur in runs, and in the Pantle study the clusters were defined by a difference in the orientation of rectangular elements in each frame. In both studies pairings of points of light of different intensities across frames were random (uncorrelated), regardless of how the two frames were aligned with each other; such pairings could not have provided any basis for cluster segregation. Consequently, some processing of the form cue was a prerequisite for seeing cluster movement. When the stimulus frames were alternated, the cluster of elements defined by the form cue appeared to move back and forth as a whole. Like the group movement sensation in the present experiments, long ISI's (> 50 msec) were required to generate the cluster movement sensation (*5, 6*), and it could be obtained with dichoptic, as well as binocular, presentation of the stimulus frames (*6*).

In the present study the element movement sensation was produced only (i) if the interval between stimulus frames was short (< 40 msec), (ii) if the successive stimulus frames were presented to the same eye, and (iii) if the direction of stimulus contrast remained the same from one stimulus frame to the next. Since the element movement sensation disappears with a reversal of stimulus contrast, the sensation must depend upon a process for which the relative intensity of points in the two stimulus frames is critical. The data are consistent with the hypothesis that the element movement sensation is produced by a spatiotemporal cross-correlation process, that is, results from a neural computation that is functionally equivalent to a cross-correlation of the spatial intensity distributions of the two successive stimulus frames. Independent evidence for such a process is provided by experiments with random-dot patterns (*7*). When a subject is alternately presented with a pair of random-dot patterns, each of which contains a region of dots that are identical except for a uniform displacement, the region appears to move back and forth as a whole. Because the moving region is defined only by the spatiotemporal relationship between the intensities of points in the two patterns, the movement sensation does not depend upon preliminary processing of form cues. This type of apparent movement can only be obtained with short ISI's (optimally with ISI's of approximately 10 to 20 msec), and it cannot be obtained with dichoptic presentation. This movement sensation behaves like the element movement sensation.

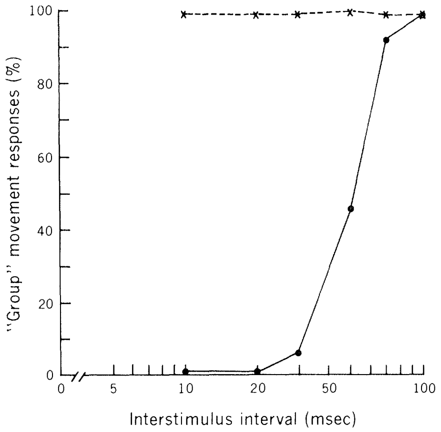

Fig. 2. Percentage of group movement responses (averaged across observers) as a function of the interval between successive stimulus frames (experiment 2). Positive-positive condition: solid line. Positive-negative condition: dashed line.

Information from our experiments is not sufficient to specify the exact anatomical locus of the cross-correlation process presumed to underlie the element movement sensation. However, our data do indicate that the neural substrate for such a process is organized so as to require successive stimulation of the same eye. The substrate might be located peripherally in the visual system, in the retina or lateral geniculate nucleus, but there is little evidence for motion selectivity at these early stages. It is more likely that the cross-correlation process depends on the action of a neural network that contains monocular cortical elements. Because the group movement sensation can be obtained with dichoptic viewing, its substrate must contain elements with binocular inputs.

The most popular explanation of multistable phenomena is that proposed by

Attneave (*8*). According to his model, the alternation between stable states is the result of inhibitory competition between parallel neural structures. We have explored a multistable phenomenon whose stable states are sensations of movement (element versus group) that are qualitatively different (that is, the two states cannot readily be ordered along a single perceptual dimension). By manipulating stimulus conditions, we have been able to favor either the element or the group movement sensation and, thereby, to infer some of the response properties of the neural mechanisms which underlie each stable state. The response properties parallel those of movement mechanisms studied in isolation in other experiments (*5*–*7*). However, by allowing the two mechanisms to compete, we can see more directly the differences in the functional characteristics of the mechanisms. In other experiments (*9*) we have selectively adapted the mechanisms that underlie the two movement sensations and have further delineated differences in their response characteristics.

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References and Notes

1. We use the terms "element movement" and "group movement" merely as descriptive labels for the movement sensations.
2. J. Ternus [in *A Sourcebook of Gestalt Psychology*, W. D. Ellis, Transl. (Humanities Press, New York, 1950), pp. 149–160] reports his experiments on stroboscopic movement with a variety of multielement displays. One of his displays contained two stimulus frames with three dots each, whose spatial arrangement was like that of the dots in the present experiments. While Ternus does not give detailed information about the spatial and temporal characteristics of his display, he does report that his display evoked mainly the movement sensation defined as group movement in our report. Under circumstances considered special by Ternus (direct fixation of the overlapping dots, continuous illumination of the overlapping dots and rapid alternation of the third dot of each frame, or observation at very close ranges), it was possible to see the movement sensation defined as element movement in the present article. None of the stimulus variables were explored systematically by Ternus.
3. Appropriate neutral density filters were used in the binocular condition to keep stimulus luminances equal to those during dichoptic viewing with Polaroid filters.
4. When an observer arrived for the first session of the experiment, he was shown (i) a stimulus sequence with an 80-msec ISI and binocular viewing and (ii) a stimulus sequence with a 10-msec ISI and binocular viewing. After looking at each sequence, the observer was asked whether he perceived any movement of the dots, and if so, which dots moved and in what direction. All observers spontaneously reported the movement sensation defined as group movement with the 80-msec ISI and the movement sensation defined as element movement with the 10-msec ISI.
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9. J. T. Petersik and A. Pantle, in preparation. Recent work by other investigators [for example, P. Tynan and R. Sekuler, *J. Opt. Soc. Am.* **64**, 1251 (1974); B. Breitmeyer, *Vision Res.* **15**, 1411 (1975)] has shown that the processing of different spatial frequencies occurs at different temporal rates. If the spatial response properties of the element and the group movement mechanisms are different, it might be expected that the spatial characteristics of our movement display would have an important bearing on the type of movement seen.
10. Supported in part by Air Force contract F33615-74-C-4032, Wright-Patterson Air Force Base, Ohio.

29 December 1975; revised 7 April 1976

Constancy and Uniqueness in a Large Population of Small Interneurons

Abstract. *The anatomy of 61 of the smallest interneurons in the brain of the locust shows the same tendency toward uniqueness, constancy of neuropil arborizations, and frequency of occurrence of supernumerary cells as does that of 17 large interneurons; the size and number of neurons thus have no obligatory relation to the concept of the unique identifiable neuron.*

Over the past decade, and particularly with the introduction of intracellular dyes (*1*), increasing numbers of studies have described unique identified neurons. Among conspecific animals, these cells are constant and unique in axon destination, major branching patterns, soma position, and physiological properties. Although the concept of the unique identifiable neuron makes no reference to neuronal size, most studies have, for technical reasons, described large neurons in invertebrate (*2*) and vertebrate (*3*) preparations. In addition, the constancy and variability of 17 large interneurons has been evaluated in a large sample of conspecific animals (*4*). There are no accounts, however, of the constancy and variability of the small interneurons that form the bulk of the nervous system.

Table 1. The tendency toward uniqueness of the large and small ocellar interneurons. Entries are the total numbers of neurons found in particular configurations. Numbers in parentheses are the numbers of unique neurons or clusters (each with contralateral homologs). For example, 36 small interneurons found in three-cell identified clusters refers to six unique three-cell clusters, each with a complementary set of contralateral homologs.

Uniqueness of neurons (*6*)	Large interneurons	Small interneurons
Identified neuron, located along midline	1	1
Identified neuron with contralateral homolog	2 (1)	16 (8)
Identified two-cell cluster with contralateral homolog	8 (2)	8 (2)
Identified three-cell cluster with contralateral homolog	6 (1)	36 (6)
Identified cluster with more than three equivalent cells	0	0
Identified class	0	0
Total	17	61

I now report on the anatomy of 61 of the smallest interneurons in the locust brain and compare them to 17 large interneurons previously studied (*4, 5*).

That the terms "identified neuron," "identified cluster," and "identified class" have been used recently with a wide diversity of meanings by different authors suggests the need for definitions (*6, 7*). In this report, neurons are described as belonging to one of these three categories and can thus be described as occurring along a spectrum of equivalence, from large numbers of equivalent neurons (identified classes) to small numbers of equivalent neurons (identified clusters) to neurons with zero-equivalence (identified neurons) (*8*). The term "tendency toward uniqueness" refers to the tendency for cells to occur near the zero-equivalence end of the spectrum.

The neurons studied here are the small ocellar interneurons in the brain of the locust (*Schistocerca vaga*). In addition to their large compound eyes, most insects have simple eyes (dorsal ocelli). In locusts there are three ocelli, two lateral and one median; each consists of a common lens, a few hundred receptor cells, and a peripheral neuropil. In each ocellus, the receptor cells synapse peripherally with the processes of both large and small ocellar interneurons whose axons form the ocellar nerve, which extends from the ocellus to the brain. There are 17 large ocellar interneurons (*4, 5*) and at least 61 small interneurons (*9, 10*).

The anatomy of the 17 large interneurons, representing some of the largest cells in the locust central nervous system (axons, 15 μm; somata, 45 μm), has been determined by "diffusion" (*11*) of $CoCl_2$ through the distal ends of the ocellar nerves followed by subsequent precipitation of the cobalt ions as a sulfide salt (*4, 5*). The brains were then