

## RESEARCH NOTE

### ADAPTATION ALTERS PERCEIVED DIRECTION OF MOTION<sup>1</sup>

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(Received 21 October 1975)

Detection of a moving target depends not only upon the physical character of the target but also upon the observer's recent perceptual history. Experimental manipulation of this perceptual history has allowed us to identify the mechanisms governing a moving target's visibility. A more important perceptual issue, however, has thus far been ignored: How does the target look when it is visible? In this paper we take a first step toward defining the neural code for one aspect of a moving object's appearance, its perceived direction of motion.

Recent psychophysical experiments have shown that detection of a moving stimulus (at the contrast threshold) is mediated by channels selective for direction of movement (Levinson and Sekuler, 1975; Sekuler and Levinson, 1974; Sekuler, Pantle and Levinson, 1976). Part of the evidence for these channels is derived from measurements of direction-specific adaptation (Sekuler and Ganz, 1963; Sekuler, 1975). Prolonged exposure, for example, to a field of random dots drifting in one direction selectively elevates the contrast detection threshold for subsequently presented moving test dots: threshold elevation is maximal for test dots drifting in the same direction as the adaptation dots, and the amount of elevation falls gradually to zero as the test and adapting directions are made increasingly dissimilar (Levinson and Sekuler, 1974). This selective desensitization which adaptation produces in direction-specific channels should also change the distribution of activity evoked among the channels by a suprathreshold test stimulus, drifting in a direction other than the adaptation direction. In particular, the central tendency of the response distribution should be shifted away from the channel most sensitive to the adapting direction. If the code for perceived direction depends upon the direction-specific channels, then this adaptation-induced change in their pattern of responsiveness should alter the apparent direction of movement of the suprathreshold

test stimulus.<sup>2</sup> Here we report such a shift in perceived direction.

Stimuli used in these experiments were sheets of random dots generated on a cathode ray display under control of a small computer (Fig. 1). The face of the display tube was illuminated at 0.5 ft-L, and the incremental luminance of the dots could be varied up to 5.5 ft-L. The distribution of spectral energy for a dot pattern was approximately the same in all meridians (i.e. the patterns were effectively isotropic). The two-dimensional uniformity of the dot patterns was assessed both statistically and by visual inspection of their optical Fourier transforms. The use of isotropic patterns permitted measurement of changes in perceived direction of movement without variation in apparent orientation or tilt, which can occur when patterns are rectilinear gratings. Patterns were viewed monocularly through a circular aperture (dia 8° visual angle); for most measurements about 400 dots were simultaneously visible. All dots in a sheet drifted uniformly, along parallel paths (velocity 4° visual angle/sec), giving the appearance of an infinite, textured surface moving continuously behind the aperture. Direction of movement was variable over a full 360°, and could be set with an accuracy of better than 1°. Individual dots were positioned using high-resolution (12 bit) digital-to-analog converters. The direction of motion of a dot could therefore be changed without altering either luminance or velocity.

Each experimental session began with 3 min continuous exposure to a pattern of adaptation dots (luminance 5.5 ft-L).<sup>3</sup> After this initial period, the adapting dots were replaced every 3 sec by a 1-sec presentation of test dots (0.7 ft-L) followed by a 1-sec presentation of a luminous line (5.5 ft-L) of adjustable orientation. The observer set the line parallel to the axis along which the test dots appeared to drift. The authors served as principal observers. Careful fixation was maintained throughout. Control measurements indicated that the apparent orientation of the adjustable line was unaffected by adaptation to moving dot patterns. Moreover, intersession time (several min) was always longer than the decay time of the after-effect.

The perceived direction shift is schematically illustrated in Fig. 1. Prior to adaptation, dots moving toward 0° appear to be drifting directly to the right. The observer next views for several minutes a bright sheet of adaptation dots moving toward 30° (anti-clockwise from rightward). Now the sheet of test dots,

<sup>1</sup> Supported by grant EY-00321 from the National Institutes of Health.

<sup>2</sup> The argument is similar to that applied in studies of spatial vision, where adaptation-produced shifts in apparent fineness of gratings can be predicted on the basis of channels selective for spatial frequency (Blakemore and Sutton, 1969; Blakemore, Nachmias and Sutton, 1970).

<sup>3</sup> Baseline measurements were obtained by replacing the adaptation period with 3 min exposure to the 0.5 ft-L background luminance.

still truly drifting toward  $0^\circ$ , appears to move toward  $-10^\circ$ ; the apparent axis of motion is rotated clockwise, away from the adaptation direction.

We measured the direction shift, for several directions of test motion, as a function of adaptation direction (Fig. 2). No change in perceived direction occurred when test and adapting directions were the same (zero normalized adaptation direction in Fig. 2). However, large shifts ( $10^\circ$  or more) were observed for adaptation directions near the test direction ( $\pm 30^\circ$ ); the size of the perceived direction shift decreased as the adapting direction was made less similar to the test direction. Note that the shifts were always away from the adaptation direction. Similar shifts in perceived direction were also measured using a two-alternative forced-choice technique, with an observer naive as to the purposes of the experiment.

The shift in perceived direction of movement is formally similar to the well known tilt aftereffect. The direction shift is unique, however, because it is a truly direction-specific aftereffect. For example, if the direction shift depended upon axis of movement without regard to direction along an axis, then the shift produced by adaptation in any given direction would exactly equal that produced by adaptation  $180^\circ$  away, since these opposite directions would lie along the same axis. We have found, on the contrary, that adaptation directions separated by  $180^\circ$  do not produce shifts which are the same, in either magnitude or polarity. We consistently measured shifts in perceived direction of several degrees for adaptation farther than  $90^\circ$  from the test direction, and these shifts were away from the adapting direction (Fig. 2). The perceived direction shift, then, must arise in directionally selective mechanisms.

It might be argued that the shift in perceived direction is related to the conventional motion aftereffect

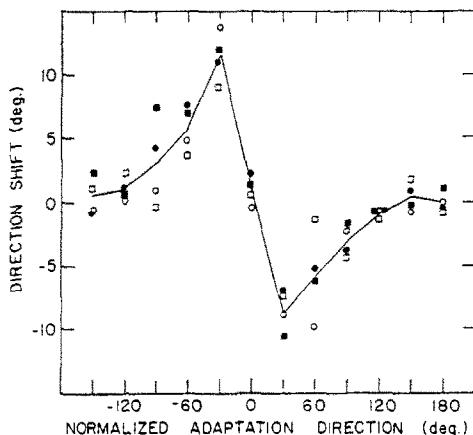


Fig. 2. Shift in perceived direction as a function of the direction of adapting movement. Adaptation directions have been adjusted such that zero normalized adaptation direction is the point where test and adapting directions are the same. Positive values are anticlockwise directions, negative values clockwise directions. Filled circles are for observer EL, test direction  $0^\circ$ ; open circles for EL, test direction  $90^\circ$ ; filled squares for observer RS, test direction  $0^\circ$ ; open squares for RS, test direction  $180^\circ$ . Each point is based on six adjustments, and standard errors are generally less than  $1^\circ$ . The continuous curve shows the mean of the four data points at each normalized adaptation direction.

(the waterfall illusion). With our random dot patterns, the motion aftereffect appears as illusory movement of stationary test dots in the direction opposite that of the adaptation dots. One might try to account for the data of Fig. 2 by assuming that this illusory movement can sum with real motion of the test dots. To test this possibility we devised an adaptation stimulus which could not produce a motion aftereffect. This stimulus consisted of two simultaneously presented sheets of dots, moving at the same velocity but in opposite directions. The density of each of the component sheets was one third that of the test dots; the reduced density prevented extensive overlap of dots in the composite adaptation stimulus. Such a stimulus gives no waterfall illusion because the effects of the oppositely-drifting sheets cancel one another (Wohlgemuth, 1911). One of these sheets of adaptation dots, presented alone and moving  $30^\circ$  away from the test direction, produces about a  $10^\circ$  shift in perceived direction. Addition of the second, oppositely-moving sheet of adapting dots in no way reduces the size of direction shift (see Fig. 3). The conventional motion aftereffect, then, does not contribute to the shift in perceived direction of movement.

Directionally selective channels in human vision are presumably collections of direction-sensitive neurons, similar to those found in cat visual cortex. Such cells can give vigorous direction-specific responses to dot patterns like those used in the present study (Henry, Bishop and Dreher, 1974; Hammond and MacKay, 1975). Perceived direction may therefore depend upon the response distribution among direction-selective neurons, and an adaptation-induced shift in perceived direction may be caused by alteration of this distribution. The perceived direction shift thus provides an initial insight into the neural code for perception of movement.

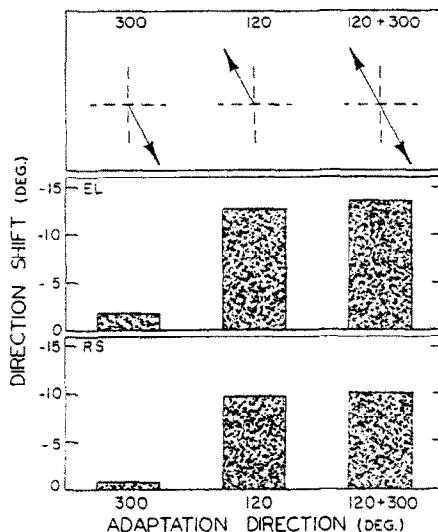


Fig. 3. Shift in perceived direction for a sheet of dots truly drifting toward  $90^\circ$ , produced by adaptation to a composite pattern or to either of its components. The arrows in the upper panel depict the directions of movement components of the adaptation patterns. The two lower panels show data for each of two observers. Individual bars represent averages of 12 measurements.

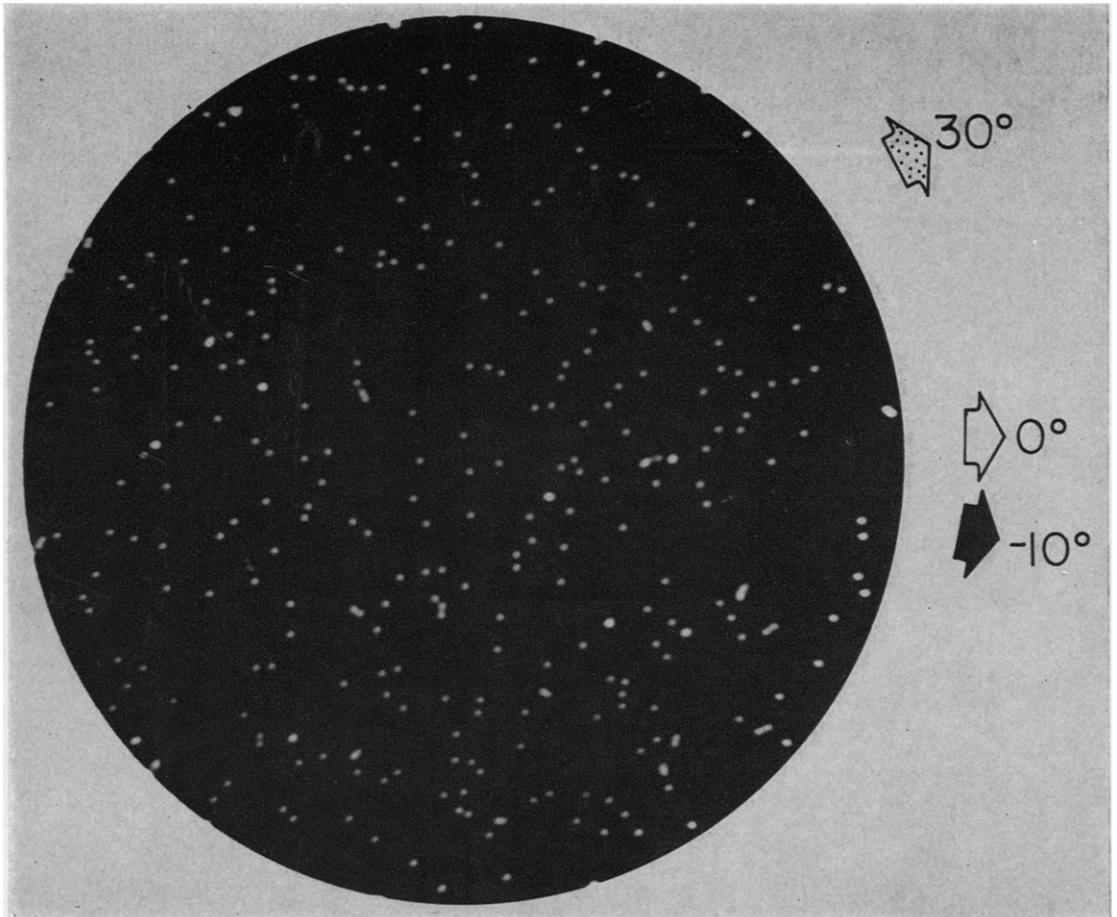


Fig. 1. Photograph of a random dot pattern used in the present experiments. A fixation point was also present, although it is not shown in this figure. The arrows around the circumference of the pattern represent directions of movement for a typical demonstration of the perceived direction shift. The open arrow is the true test direction (toward  $0^\circ$ ), the stippled arrow is the adaptation direction (toward  $30^\circ$ ), and the filled arrow is the perceived direction of the test dots following adaptation (toward  $-10^\circ$ ).

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