manner in which the subjects indicated their retention of presented items.

Two findings are noted. First, the missing-scan estimate of retention was greater than the digit-span estimate for all subjects (Fig. 1 and Table 1) (5). On the average, the estimate of retention obtained with retrieval by the modified digit span was only 64 percent of the estimate obtained without retrieval by the missing scan (Table 1). Second, in the digit-span test most of the "forgotten" items (errors) were in the second half of any series presented, while in the missing-scan test most of these errors were in the first half (Table 1) (6). All subjects showed this reversal of error distribution (7).

The significance of the finding that the missing-scan estimate of retention exceeds the digit-span estimate is enhanced by the modification of the digitspan test, which would tend to increase the digit-span estimate. Since the numbers used in the digit-span test were selected from a sequence known to the subject, and could be reported in any order, the probability of guessing correctly would be greater in the modified digit-span than in the missing-scan test. However, all subjects usually reported the numbers practically in the order in which they were presented.

The reversal of error distribution shown in Table 1 raises further considerations. If the missing scan were performed by retaining presented numbers as in the digit span and then comparing retrieved numbers with the known sequence to find the missing number, the estimate of retention by the missing scan should be equal to or less than that by the digit span, and the error distribution of the missing scan should be similar to that of the digit span. These predictions are not borne out by the data, for the results of the two tests are clearly different. Thus, it appears either that different modes of short-term storage are used for retention in the digit span and the missing scan, or that the same storage system is used for both but that the missing scan reveals characteristics of retention in storage while the digit span reflects the effects of retrieval. The latter interpretation seems more probable and leaves open for further investigation the possibility that different operations may be performed upon incoming information prior to storage or that different types of scanning may be used on the same storage (8).

The larger estimate of retention given by the missing scan confirms that more is retained in short-term memory storage than may be retrieved, and suggests that methods which do not depend upon retrieval, such as the missing-scan test, may provide the best estimate of retention.

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- At the 99-percent confidence level it may be 5. asserted that the number of correct series in the missing-scan test exceeds that in the digitthe missing-scan test exceeds that in the end of span test for 4, 6, 8, 10, 12, and 14 items per series by -15.9, 8.8, 36.1, 27.4, 12.7, and 3.9 percent, respectively.
- At the 99-percent confidence level it may be asserted that the percentage of errors in the 6. first half of any series in the missing-scan test exceeds that in the digit-span test by 42 percent. In the digit-span test failure to report any number presented was such an error, while in the missing-scan test reporting that any number actually presented was missing constituted such an error
- I thank Dr. Helena Chimura Kraemer, re-search associate in the Department of Biosta-7. of Stanford University School of Medicine, for the statistical analysis.
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# Measurement of a Visual Motion Aftereffect in the Rhesus Monkey

Abstract. A monkey was trained to discriminate between a shrinking and expanding test figure presented after steady fixation of the center of a rotating spiral. Differential shifts in the animal's perception of size constancy were found for clockwise and counterclockwise rotation of the spiral. The magnitude of the aftereffect was within the range found in human subjects.

It has long been known that continued observation of a moving pattern will induce an illusion of motion in the opposite direction upon subsequent viewing of a stationary pattern, or test stimulus (1). A convenient method of eliciting this illusion is to fixate a rotating disk having a spiral figure drawn

on it. During a period of steady gazing at the center of this rotating spiral, it appears to be expanding or contracting, depending on the direction of rotation. When the spiral is stopped suddenly, or when any stationary pattern is viewed, an illusory motion in the opposite direction is clearly seen by virtually all persons.

Nothing specific is known about the physiological mechanisms responsible for this aftereffect, although attempts have been made, perhaps prematurely, to show that brain damage is in some way related to it. Various authors have reported that, among brain-damaged subjects, the aftereffect is absent (2), is enhanced (3), persists longer (4), is of shorter duration (5), or is unaffected (6). These conflicting findings may be clarified by the perfection of measurement techniques (7) and the development of methods for studying the phenomenon in animals, thus making possible selective ablation studies aimed at discovering the mediating structures. This study presents a method of measuring the rate of an aftereffect of this kind in the rhesus monkey.

A three-field mirror tachistoscope was used for alternate presentation of the spiral and a circular test stimulus, both seen at an optical distance of 5 feet. The third field was used for the continuous presentation of a spot of light which served as a fixation point. The fixation point was centered in the field so that it appeared to be in the center of both the spiral and the circle when these were visible. The spiral, which was 8 inches in diameter, is illustrated in Fig. 1 (top). It could be rotated by a synchronous motor in either direction at a speed that was stroboscopically set at 180 rev/min. In a preliminary study with human subjects it was found that this particular combination of spiral and speed of rotation resulted in greater aftereffect rate than any of the other combinations tried (7). The spiral was illuminated by four 1.5-watt incandescent bulbs. with diffusing reflectors, whose average distance to the surface of the spiral was about 6 inches.

The circular test stimulus was produced on the face of a 5BPl cathode ray tube, as shown in Fig. 1 (bottom). The circle, which always appeared with an initial diameter of 3 inches, could expand or contract at preselected linear rates, or it could remain motionless. Its rate of change in size was quantified in percent per second units, based on the initial diameter of the circle. The rates used were 0, 2, 4, 6, and 10 percent per second. The medium persistence phosphor of the 5BPl produced no detectable aftertrace at the rates used. Since the intensity of the electron beam was held constant, there were small, but usually subliminal changes in the brightness of the trace as the circle changed in size.

The response mechanism consisted of a panel in front of the monkey at hand level which contained a food cup in its center and a lever on each side.

After a period of initial training (described below) the 3-year-old male rhesus monkey, seated in a restraining chair, looked into the tachistoscope (see Fig. 1). He fixated a spot of light at the center of the spiral for 10 seconds. At the end of this fixation period the spiral vanished and was replaced



Fig. 1. The monkey (top) fixating the clockwise-rotating spiral. When the circle appears (bottom) he presses the left lever, signaling apparent shrinkage of the circle, even though the circle is objectively of constant size.

not more than 5 msec later by the test stimulus. To make a "correct" response the monkey pressed the right-hand lever when an expanding circle appeared and the left-hand lever when a contracting circle appeared. A whole diet food pellet was released into the food cup for every second "correct" response. A lever response turned off the circle and caused the spiral to reappear for the next trial. If the monkey did not respond with a lever press the circle vanished after 4 seconds and another trial was begun. Either an "incorrect" response or a lever press during the spiral fixation resulted in a mild electric shock. A lever press made during the presentation of a motionless circle resulted in neither shock nor food.

Any aftereffect produced by the rotating spiral would thus influence the monkey's responses to circles having varying rates of shrinkage and expansion. Clockwise rotation would be expected to produce apparent shrinkage while counterclockwise rotation would be expected to produce apparent expansion.

To bring about the complex performance just described the animal first learned to discriminate between an expanding and a contracting circle. This discrimination training required about 4 months, during which the animal was trained to a criterion of at least 98 correct responses in 100 successive trials. Next, the animal was trained to fixate the spot of light by operant conditioning, with the appearance of a circle as the reinforcement. At first, only the fixation point was presented, without the spiral. It was found that this procedure was necessary to insure fixation of the center of the field. During this period the rate of change of circle diameter, which had initially been 50 percent per second, decreased to a minimum value of 2 percent per second. When the animal had learned to fixate for 10 seconds and had reached a criterion of 160 correct responses in 2 hours, the illumination of the spiral was gradually increased to its maximum over a period of about 2 weeks of daily sessions. The fixation training required about 2 months.

The experiment proper was carried out on 12 successive days. On oddnumbered days the spiral was stationary and only circle speeds of 2 percent per second were presented to keep up the desired sharpness in discrimination. On each even-numbered day the animal



Fig. 2. Proportion of left lever responses as a function of rate of change of circle diameter for three different conditions of preexposure to spiral: stationary spiral (open circles), counterclockwise rotation (squares), and clockwise rotation (triangles).

performed under three conditions: a stationary spiral, a clockwise rotation, and a counterclockwise rotation. These conditions were presented in the six possible orders on the six even-numbered days. Order of presentation of the different rates of expansion and contraction of the circle always followed the same counterbalanced program for each condition. During the conditions involving rotation of the spiral, shock was not administered for responses made to the 2- or 4-percent per second rates, since this would have constituted negative reinforcement for responses indicative of aftereffect. This change in reinforcement schedule was trivial, since it resulted in no appreciable change in the proportion of shocked responses. In preliminary experiments, even complete elimination of shock was found to have no detectable effect on the animal's performance during runs of length similar to those of the experiment proper.

Figure 2 is based upon the data obtained on the even-numbered days and shows the results of 1442 presentations of the circle, in response to which 1406 lever responses were made. Almost all of the 36 failures to respond occurred on difficult discriminations. The ordinate shows the proportion of responses made with the left lever. The abscissa represents the rate of change of circle diameter in percent-per-second units, based on the initial diameter of 3 inches. Contraction is indicated by the negative sign. The open circles on the graph show the results from the stationary spiral condition.

It can be seen that when the spiral was not turning the animal seldom made an error in judging circles whose rate of expansion or contraction was 6 percent per second or more. The nearly equal left and right lever responses to the motionless circle indicate that little if any lever preference was present. A rate of change to which the monkey responds equally often with the left and right levers is used as a measure of his point of subjective size constancy. This point on the ogive can be estimated by interpolation. The point of subjective size constancy when the spiral was not rotating was 0.2 percent per second with an estimated standard error of .3. Thus, the monkey's subjective size constancy point is less than one standard error away from the objective size constancy point (0.0 percent per second).

Inspection of the results from the counterclockwise condition (squares on the graph) shows a systematic shift to the left. The point of subjective size constancy for this curve is at -1.9 percent per second, with a standard error of about .3. This means that a circle objectively contracting at 1.9 percent per second would be responded to as if it were motionless. Inspection of the results from the clockwise rotation condition (triangles on the graph) shows a marked shift to the right. The point of subjective size constancy for this curve is 3.8 percent per second, with a standard error of about .4.

These results are in the expected directions for the spiral used. The aftereffect rates are not as great as the average of 5.4 percent per second obtained with human subjects (3) but they are well within the range of individual differences. These data clearly show the feasibility of measuring this type of visual motion aftereffect in the rhesus monkey, thus providing a method for the psychophysiological study of this perceptual process.

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## Vegetation, Climate, and Coastal

### Submergence in Connecticut

Abstract. Pollen analysis of a coastal marsh sediment at Guilford, Connecticut, indicates that there was a period of warmth and dryness preceding 3000 years ago. The subsequent increase of conifers at the expense of oak indicates a reversal that could account for decreasing rates of ice melt and rise of sea level. The record of herbaceous vegetation (grasses vs. sedges) suggests that the rise in the water table has been pulsating in character.

In July 1960, at the request of Arthur L. Bloom, Sra. Bopp-Oeste, then working at Yale, assisted him in taking cores from a coastal marsh at Guilford, Conn. Before returning to Mexico she prepared samples for pollen analysis. Additional preparations and initial counts were made by Edna Fox, and the entire suite was re-counted by myself. The results are shown in Fig. 1, for which percentages have been calculated separately for arboreal (AP) and nontree (NAP) pollen (1).

Good counts were obtained from the basal sample at 270 cm, as indicated by heavy dots. The next 25 cm were too heavily oxidized to reveal enough pollen for counting. This oxidation may be due either to the chemical activity of ground water from the underlying sand or to the dry and warm conditions which are indicated by the high basal count of oak and grass and low count of sedge. The shift from fresh- to salt-water deposits occurs at about 95 cm.

Beginning with the 245-cm level. pollen preservation appears to have been continuous and rate of sedimentation fairly uniform. Upward from 240 cm, pine, and later hemlock, increases, while oak diminishes. Such a trend, with the intermediate rise of hickory and beech, I take to indicate a drift toward cooler and moister conditions than those shown at the base of the core. The least-square approximation of increase in pine, hemlock, hickory, and beech, combined, amounts to about 300 percent between depths of 240 and 50 cm.

The reciprocal behavior of grasses and sedges shows a recurrent pattern. Since slight rises in the water table normally favor sedges at the expense of grasses, and vice versa, the general rise appears to have been pulsating rather

than steady. Intensive study of this phenomenon along the coast might yield valuable information about climatic periodicity.

The influence of human activity is clearly reflected by the marked increase of composites and cheno-ams in the uppermost levels. Similar behavior of these ruderal or "weed" groups is a well-known index of clearing and disturbance in both the Old and New Worlds.

Sample Y-855, cited by Bloom and Stuiver (2) as having been dated by the radiocarbon method at  $1180 \pm 80$  years ago, was taken at a depth of  $3.8 \pm 0.2$ feet near the edge of this basin of peat accumulation and is our only guide to chronology. It is not an unreasonable approximation to assume that the basal interval of xeric conditions ended at some time around 3000 years ago, which correlates well with other information.

Although the long period of higher temperature known to have preceded a date of 3000 years ago was interrupted by a moister and cooler episode, about 6000 to 5000 years ago (3) it should account for rapid glacial melting and a corresponding rate of rise in sea-level. Further, Bloom and Stuiver show a reduced gradient of submergence hinged at their sample Y-1175  $(3020 \pm 90)$ years ago), which was taken at a depth of  $9.1 \pm 0.6$  feet from nearby Clinton. This is practically the same depth as that at which the end of the xeric



Fig. 1. Pollen diagram of important indicators in the Guilford, Connecticut, coastal marsh. Depth in centimeters is shown from right to left; percentages, calculated separately for arboreal and nonarboreal pollen, are shown vertically.