Seeing-More-Than-is-There: A Probe of Retinoid Networks

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ABSTRACT

Dynamic properties of a model post-retinal, short-term visual store called a retinoid are presented. The retinoid model generates specific predictions about visual perception in several variants of the seeing-more-than-is-there (SMTT) paradigm. Three experiments were conducted to test for the predicted effects. Performance curves are presented and discussed. A new visual illusion of motion is shown to follow from the properties of the retinoid model.

INTRODUCTION

A fundamental question in the study of human vision concerns the integration of disparate foveal stimuli into a proper unified representation of a larger real-world scene. Some kind of post-retinal mechanism which can register and appropriately combine inputs from a series of visual saccades or a continuous visual scan, seems to be required. To account for this central process, as well as for a variety of other high-level visual operations, a theoretical neuronal mechanism, called a retinoid, has been proposed and described in detail (Trehub, 1977, in press).

If a target figure is moved back and forth behind a narrow window in an otherwise opaque surface, much more of the figure can be seen at a given instant than is physically present within the window. This phenomenon was reported as long ago as 1862 by Zollner, and by Helmholtz in 1867. It has been called the seeing-more-than-is-there effect (McCloskey and Watkins, 1978). The phenomenon seems to depend upon a post-retinal integrating mechanism like a retinoid to give the subject the perception of a visual pattern which is much larger than the small "slices" of the figure actually stimulating the retina. In the laboratory, one can exercise systematic control over a number of stimulus and contextual parameters for the seeing-more-than-is-there (SMTT) effect. Thus SMTT may be a particularly good paradigm for probing the dynamic properties of retinoid networks. In this paper, we review the basic structure and general operating characteristics of the retinoid model, and test some implications of the theory using the SMTT procedure.

Theoretical Model

A retinoid is a postulated brain mechanism that can organize successive retinocentric visual patterns into a unified egocentric or allocentric representation of object space. The network is called a retinoid because, like the retina, it represents information in visual space and projects afferents to higher visual centers. Retinoids serve as visual "scratch pads" with spatially organized information stored as short-term memory. The mechanism of storage is assumed to be a retinotopically

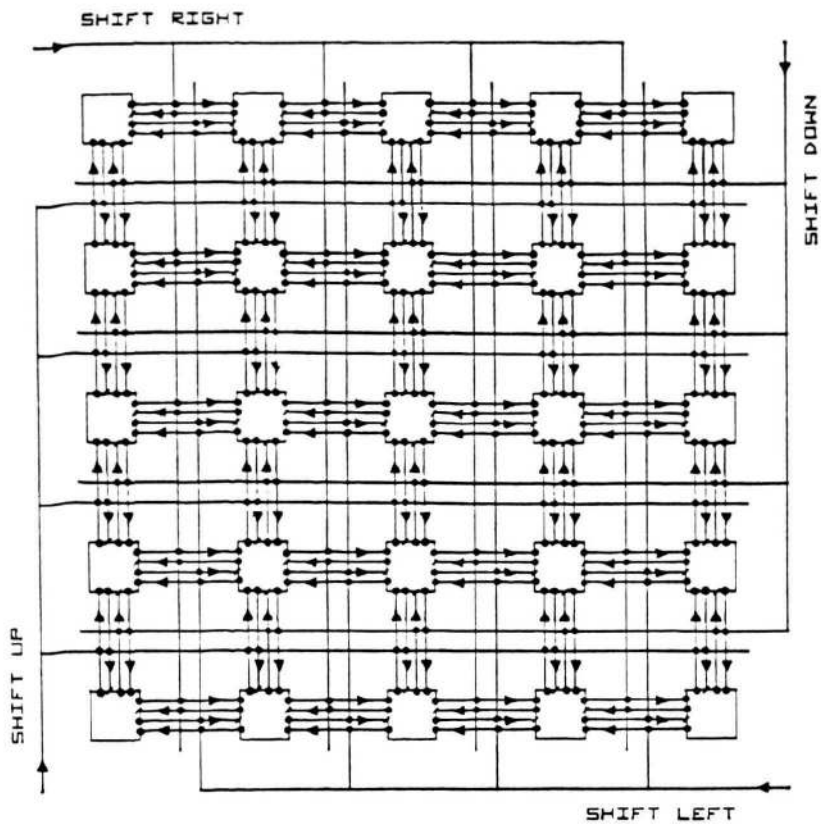

Figure 1. Translation retinoid. Large squares represent autaptic cells serving short-term memory. Small filled triangles represent interneurons. Shift-control cells are designated by direction of effect.

organized array of excitatory autaptic neurons. Neurons of this type have at least one of their axon collaterals in recurrent excitatory synapse with their own cell body or dendrite (Shepherd, 1974). In order for an active autaptic neuron to refire itself, there must be other concurrent excitatory input to it. Thus the sheet of autaptic neurons in the retinoid can represent in its sustained firing pattern any transitory organized input for as long as diffuse priming excitation (arousal) is sustained. If the priming background input is removed or sufficiently reduced then the captured pattern on the retinoid is "erased".

Figure 1 shows a retinoid of autaptic neurons connected by a grid structure of excitatory and inhibitory interneurons. Axon collaterals of shift-control neurons are in excitatory synapse with selected groups of interneurons. Any momentary input from an afferent visual array to its homologous autaptic retinoid cells will evoke sustained firing of the retinoid targets if there is a sufficient level of diffuse tonic excitation. Thus any retinal stimulus induces a comparable retinoid pattern of spatially organized discharge. Each active autaptic neuron induces a

sub-threshold, priming excitatory postsynaptic potential (EPSP) in each of the eight contiguous interneurons capable of eliciting excitatory and inhibitory potentials (IPSP) in their targeted autaptic cells. If a primed interneuron receives an increment of excitation from one of the shift-control cells, that interneuron will fire and send a spike input to its target cell. The rules are: (a) if an autaptic cells which is not discharging (i.e., off) receives an EPSP from an interneuron, it will fire (turn on); (b) if an autaptic cell which is on receives an IPSP from an interneuron, it will turn off unless it receives simultaneously an EPSP from another interneuron, in which case it will remain on; (c) if diffuse tonic excitation to the retinoid falls below a critical level, all cells in the retinoid turn off.

If we imagine a standing pattern of excitation evoked on a retinoid, this "captured" pattern can be spatially translated in any direction by appropriate pulses (discharge spikes) from the shift-control command cells. For example, each pulse from the shift-right line will transfer standing activity from any active autaptic cell to an adjacent autaptic cell on its right and, at the same time, erase the activity of the previously active donor (on the left) unless that cell is also receiving transferred excitation from an active autaptic cell to its immediate left. Thus successive command pulses from the shift-control cell will move the entire retinoid pattern to the right in successive increments of a single autaptic cell. The more rapid the pulses, the more rapid the pattern will move; the longer the shift-command pulse train is sustained, the greater will be the distance through which the pattern is moved. Appropriate sequences of shift right/left, shift up/down can move the pattern of cell activity to any position on the retinoid surface. The model assumes that automatic translation of retinoid patterns occurs when shift-control neurons are driven by eye and/or head deviations from the normal foveal axis (the line of sight of the fovea when the eyes are straight ahead, head unturned, shoulders square with the body), and by the discharge of motion detecting cells in the lower-level visual mechanisms.

Explaining SMTT

We theorize that the SMTT phenomenon occurs when the component pattern segments, which are directly observed through the narrow aperture, are swept across the retinoid surface in synchrony with signals from the motion-detector cells. This explanation depends on: (a) the detection of the velocity and direction of the stimulus pattern on the basis of information available in the screen aperture; (b) the short-term memory properties of the retinoid that enable it to assemble a unified representation of the stimulus from the sequence of partial inputs that are registered in its aperture region and then shifted step-wise across adjacent cells.

Figure 2 shows, in schematic form, the significant factors in the SMTT paradigm. The stimulus pattern which is depicted is a triangle moving to the right with its leading edge just entering the aperture in an otherwise occluding screen. The symbols in the schematic figure are to

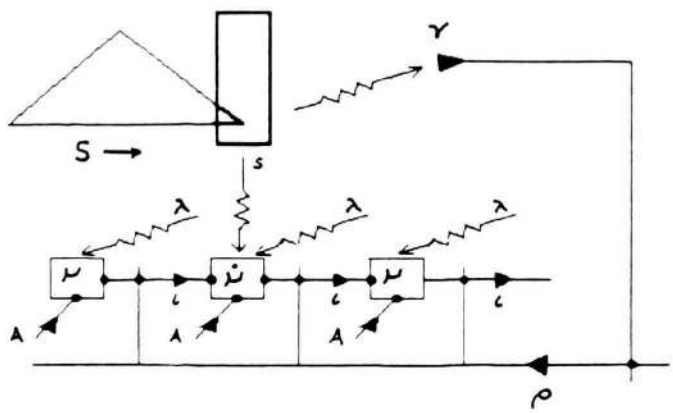

Figure 2. Schematic showing significant elements and parameters in SMTT paradigm.

be interpreted as follows.

S = input from stimuli in aperture

$\dot{\mu}$ = autaptic cell in the aperture field excited by stimulus segments

μ = autaptic cell beyond aperture field

i = excitatory interneuron

ρ = retinoid shift-control cell (shift-right)

γ = motion detector (senses velocity of motion to right)

A = diffuse input from arousal

λ = diffuse input from ambient illumination

Let us now consider how some of the factors described above affect the rate of spatial translation over the retinoid network. It should be noted that the subset of autaptic cells ($\dot{\mu}$) "looking at" the stimulus segments receive their input from: (1) stimulus excitation (S); (2) arousal excitation (A); (3) ambient illumination (λ); (4) excitation from active interneurons (i). Since neurons integrate all EPSP input over time, the slope of integration and, thus, the frequency ($F_{\dot{\mu}}$) of cell discharge in $\dot{\mu}$ will be a positive monotonic function of the dwell-time of S on $\dot{\mu}$, the magnitudes of A and λ, and the discharge frequency of i. For the subset of autaptic cells (μ) outside of the direct stimulus (aperture) field, their discharge frequency (F_{μ}) will be a positive monotonic function of input from their associated interneurons

$\underline{i}$ and the magnitudes of $\underline{A}$ and $\underline{\lambda}$. These relationships may be expressed as follows.

$$F_{\dot{\mu}} \propto (S, A, \lambda, i) \quad (1)$$

$$F_{\mu} \propto (A, \lambda, i) \quad (2)$$

The discharge frequency (F_i) for any interneuron ($\underline{i}$) is a positive monotonic function of the input pulse rate from its shift-control driving cell ($\underline{\rho}$) and the spike frequency of its donor autaptic cell ($\dot{\underline{\mu}}$ or $\underline{\mu}$). Thus

$$F_i \propto (\rho, \dot{\mu}) \quad \text{or} \quad F_i \propto (\rho, \mu) \quad (3)$$

Given any arbitrary gating pulse rate from a shift-control cell (say $\underline{\rho}$), variation in the actual velocity of translation of an excitation pattern across the surface of a retinoid will be a positive function of the discharge frequency ($\underline{F}$) in those retinoid cells carrying the pattern. This follows from the fact that the latency of discharge in each successive cell on the translation route of the image is inversely related to the $\underline{F}$ of its donor cell. If the translation velocity of the retinoid image is equal to the velocity of the stimulus pattern, then it is assumed that the <u>perceived</u> proportions of the pattern will correspond to the veridical proportions of the stimulus. If, however, translation velocity on the retinoid is less than stimulus velocity, then the stimulus pattern will be perceived as shorter along its axis of motion in relation to its other dimensions.

GENERAL METHOD

Implications that follow from the assumptions about the dynamics of retinoid networks as presented above, were tested in three SMTT experiments. In particular, we probed the effects of stimulus velocity, aperture width, and ambient illumination.

Subjects

Four subjects participated in each of three experiments. The subjects, the two authors of this paper and two graduate student volunteers, were unpaid. The student subjects were unaware of the theoretical background and other details of this study until after their data were collected.

Apparatus

Visual stimuli were presented on the screen of a CRT which was partially masked by a sheet of gray poster-board with a narrow, vertically oriented aperture in its center. The height of the aperture was fixed and was greater than the height of the stimulus pattern; the width of

the aperture was adjustable and always much less than the width of the stimulus, so that only a small segment of the stimulus pattern could be seen by the subject at any given moment. A hand-held controller was provided the subject that had a potentiometer knob which allowed him to vary the rate of stimulus motion across the face of the CRT from 1.0 degrees/second to a maximum velocity of 12.5 degrees/second at the viewing distance used in this study. The controller also had a button which, when pressed by the subject, signalled that a perceptual criterion was met. After instructions were read to the subject, all experimental trials were controlled by an Apple II+ computer. Stimulus presentation, recording and analysis of the subjects' responses were performed automatically according to a pre-programmed protocol.

EXPERIMENT 1

Hypothesis I

Given a horizontally oscillating figure in the SMTT paradigm, the perceived width of the figure will contract as stimulus velocity increases.

This follows from the fact that dwell-time of $\underline{S}$ on $\dot{\underline{\mu}}$, hence $\underline{F}_{\dot{\mu}}$, will decrease with an increase of stimulus velocity, causing the rate of translation over the retinoid to decrease relative to stimulus velocity.

Hypothesis II

For any given stimulus velocity, the perceived width of the figure will increase as the aperture width increases.

This follows from the fact that the proportion $\dot{\underline{\mu}}/\underline{\mu}$ will increase as the aperture for direct stimulation increases. Since $F_{\dot{\mu}} > F_{\mu}$, the velocity of translation over the retinoid will be greater for the larger aperture.

Procedure

The subject was seated at a distance of approximately 58 cm from the CRT. A laterally oscillating triangle on the face of the CRT was exposed to the subject through the narrow aperture in the masking screen. The triangle disappeared behind the screen on both left and right excursions. The height of the triangle was always 0.7 degrees of visual angle, whereas the base of the triangle varied randomly on each trial within a range of 0.8 degrees to 1.9 degrees in visual angle. Incident illumination on the CRT mask was set at approximately 8.0 foot-candles. The subject was instructed to fixate the center of the aperture on each stimulus presentation, and to adjust the knob on the controller until the width of the perceived triangle was equal to its height. As soon as this oc-

curred, the subject was to press the controller button which recorded the rate setting, cleared the screen, and terminated the trial.

Data were collected from each subject under the two aperture conditions in five 20-trial blocks for each condition. Two subjects were tested on five blocks with the 0.1 degree aperture, followed by five blocks with the 0.2 degree aperture. The other two subjects viewed the stimulus first through the 0.2 degree aperture followed by the 0.1 degree aperture. During each block of trials, there was an interstimulus interval of five seconds following each response. A rest interval of 90 seconds was given after each block of trials.

Results

In this experiment, the independent variables were: (1) the height/width ratios of the stimulus patterns; (2) the width of the aperture. The dependent variable was the stimulus velocity set by the subject to give the perception of height/width equivalence. At each velocity setting required to meet the criterion of equivalence, the ratio of perceived-width/true-width is expressed as a contraction ratio. Figure 3 shows the results plotted separately for each of the four subjects. Hypothesis I is confirmed by the response curves obtained from each subject under the two aperture conditions. Using a binomial test, the confidence levels for each of the four subjects are as follows: (AP) $p<.025$; (JH) $p<.025$; (JP) $p<.005$; (AT) $p<.005$. Thus it can be concluded that in the SMTT paradigm, perceived width contracts as stimulus velocity increases.

To test Hypothesis II, we analyzed the stimulus velocity settings selected by the subject to achieve the contraction ratios required for the perception of height/width equivalence for the 0.1 degree vs. the 0.2 degree aperture. If the subject sees a wider triangle given a wider aperture, then he must increase the velocity of the stimulus to perceive equivalence. Examination of the differences in response under the two aperture conditions for each subject reveals that Hypothesis II is confirmed. Using a binomial test, the confidence levels for each of the four subjects are as follows: (AP) $p<.005$; (JH) $p<.005$; (JP) $p<.005$; (AT) $p<.005$. Thus it can be concluded that in the SMTT paradigm, perceived width increases as aperture width increases.

EXPERIMENT 2

Hypothesis III

For a given aperture, the perceived width of the figure will increase as ambient illumination increases.

This follows from the assumption that ambient illumination increases both $\underline{F}_{\dot{\mu}}$ and $\underline{F}_{\mu}$. The velocity of translation over the retinoid should be greater with higher general illumination.

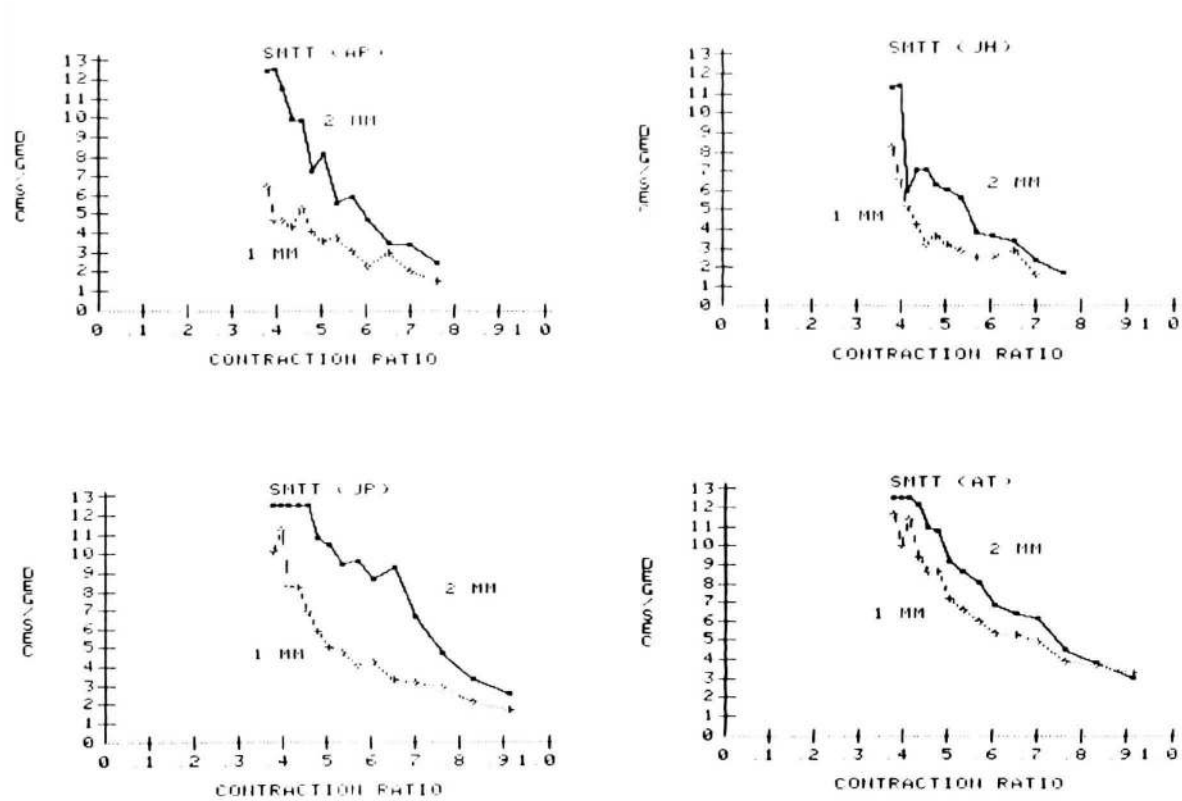

Figure 3. Experiment 1. Plot of adjusted stimulus rates against contraction ratios needed to achieve a perceived width-to-height match for each of four subjects.

Procedure

The apparatus, instructions, and procedure were the same as in Experiment 1, except for the following differences. The width of the aperture in the mask was fixed at 0.2 degrees and data were collected under two different intensities of incident illumination. Two subjects were tested with 8.0 foot-candles of incident illumination followed by 2.0 foot-candles, and for the other two the order of the illumination conditions were reversed.

Results

In this experiment, the independent variables were: (1) the height/width ratios of the stimulus patterns; (2) the levels of ambient illumination. The dependent variable was the stimulus velocity set by the subject to give the perception of height/width equivalence. Figure 4 shows the results plotted separately for each of the four subjects. Using a binomial test, three subjects showed no significant effect of illumination level, while one subject (AT) showed a highly significant effect

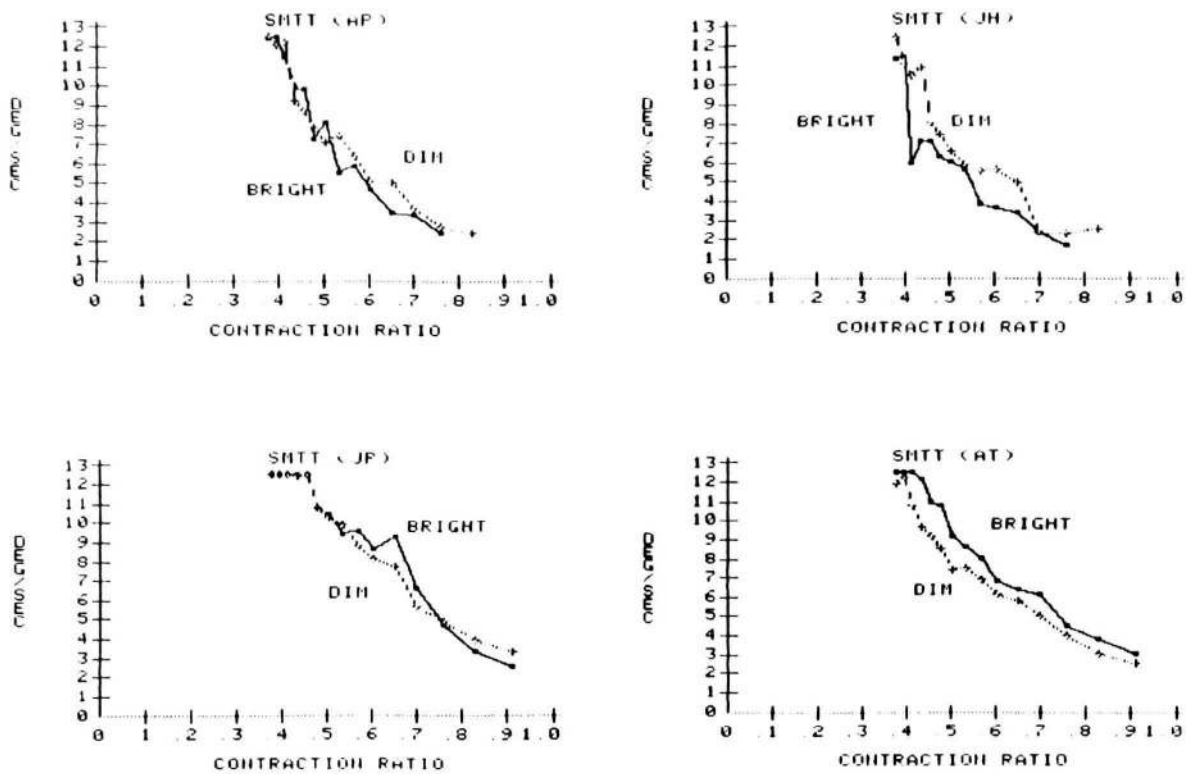

Figure 4. Experiment 2. Plot of adjusted stimulus rates against contraction ratios needed to achieve a perceived width-to-height match for each of four subjects.

in accord with Hypothesis III ($p<.005$). On the basis of these results, we are unable to confirm Hypothesis III.

EXPERIMENT 3

Hypothesis IV

In the SMTT paradigm with stimulus parameters held constant, the absolute number of stimulus sweeps required to squelch the SMTT effect will increase as ambient illumination increases.

This follows from the assumption that the small interneurons $\underline{i}$ will fatigue under prolonged driving. Thus $\underline{F}_i$ will decrease to the point that it no longer adds sufficient excitation to the target autaptic cells ($\underline{\mu}$) for them to reach discharge threshold. When this occurs, pattern translation over $\underline{\mu}$ ceases and SMTT will be squelched. Since the theoretical model assumes that ambient illumination (λ) also adds excitation to $\underline{\mu}$, it follows that SMTT squelching should occur later (more stimulus sweeps will be required) under higher general illumination. Note that

this prediction is opposite what might be expected given differences in control, since one would expect the lower background illumination (higher contrast) figure to survive longer.

Procedure

The apparatus in Experiment 3 was the same as used in Experiments 1 and 2. The mask aperture was fixed at 0.2 degrees in visual angle. The stimulus presented on each trial was a triangle with a height of 0.7 degrees and a base of 1.7 degrees of visual angle. The triangle oscillated horizontally at a constant rate of 10.0 degrees/second in visual angle, and disappeared behind the mask on both left and right excursions. In this experiment, the subject could not vary the rate of stimulus motion. Instead, the subject was instructed to fixate the center of the aperture on each stimulus presentation, and to press the controller button as soon as the perceived pattern clearly shifted from a horizontally oscillating triangle to a short, vertically oscillating line segment above a short, stable line segment (the veridical retinal input). When the button was pressed, the number of stimulus sweeps required for the perceptual shift was automatically recorded; the screen was cleared, and after a 5-second interval, a warning buzzer sounded and was followed a second later by another trial.

Each subject was given ten consecutive trials under each of two intensities of incident illumination. Two subjects were tested first with 8.0 foot-candles, followed by 2.0 foot-candles, while the order of illumination was reversed for the other two subjects. A rest interval of five minutes was allowed between the illumination conditions.

Results

In this experiment, the independent variable was the level of ambient illumination. The height/width ratio of the stimulus pattern as well as its velocity were held constant. The dependent variable was the number of successive stimulus sweeps required to squelch the SMTT effect. Figure 5 shows the results plotted separately for each of the four subjects. Examination of the differences in response under the two illumination conditions for each subject reveals that Hypothesis IV is confirmed. Using a binomial test, the confidence levels for each of the four subjects are as follows: (AP) $p<.005$; (JH) $p<.025$; (JP) $p<.025$; (AT) $p<.005$. Thus it can be concluded that in the SMTT paradigm with stimulus parameters held constant, the number of stimulus sweeps required to squelch the SMTT effect will increase as ambient illumination increases.

GENERAL DISCUSSION

The SMTT phenomenon provides a strong argument against a static "iconic" representation in visual short-term memory, and argues for a more dynamic form of storage (McCloskey and Watkins, 1978). The retinoid mechanism offers a well-articulated and biologically plausible model of what such

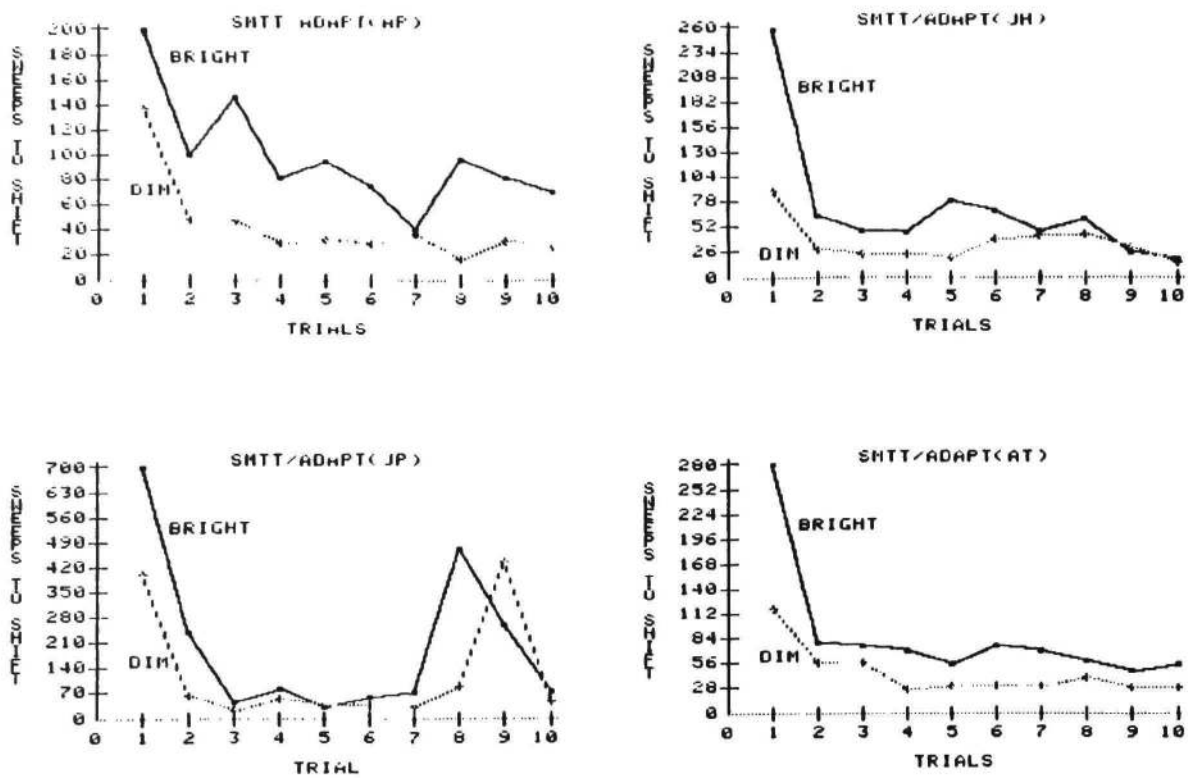

Figure 5. Experiment 3. Plot of the number of successive stimulus sweeps required to squelch the SMTT effect over ten successive trial blocks for each of four subjects.

a dynamic storage system would look like. It explains the SMTT phenomenon and makes several confirmed predictions about the effects of changing stimulus parameters.

A different explanation, depending upon a homunculus called the "executive agency", has been proposed by Rock (1983). The perceived shortening of the moving figure in the SMTT paradigm has been commented upon by several investigators (Parks, 1965; McCloskey and Watkins, 1978; Rock, 1983). Rock postulates that the motion detection system underestimates the velocity of the moving object, and the "executive agency" then uses the erroneous velocity estimation to calculate where all the points of the figure should be if they were all visible. Presumably, in Rock's theory, since missing parts of the figure should be in a particular location, they are seen in that location. In our view, this begs the central question. A major functional difference between the two models can be framed in these terms: computations and representational processes in the retinoid model are local and non-inferential, while in the Rock model they are global and inferential at the level of the unexplicated "executive agency".

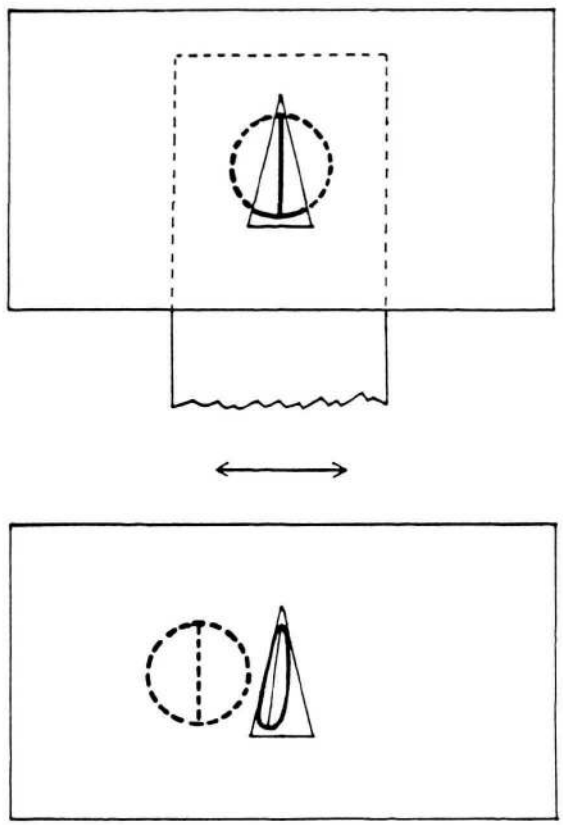

Figure 6. (Top) Screen with triangular aperture through which a part of the stimulus pattern (circle with vertical line) can be seen. (Bottom) Appearance of pendulum illusion when stimulus is moved horizontally back and forth at approximately 2 cycles/sec.

The following demonstration tests the adequacy of a local versus global explanation of SMTT and supports the superiority of the retinoid model over Rock's homunculus. If a figure were to oscillate behind a triangular aperture instead of a rectangular slit, the Rock model would predict only the usual perceived contraction along the axis of motion with no other perceptual distortion related to the shape of the aperture. The dynamics of the retinoid model, on the other hand, takes account of the change in the number of autaptic cells collinear with the direction of stimulus motion which are directly exposed to retinal stimulation as a function of the triangular shape of the aperture. This model predicts that horizontal translation rate over the retinoid surface should increase from the apex to the base of the triangular aperture. Thus, a figure which is moving back and forth should be seen to be swinging in pendular fashion as though pivoting near the apex of the triangular opening. In fact, this pendulum illusion can be clearly seen with simple materials. Using a heavy black line, draw near the top of a strip of white cardboard a circle approximately 25 mm in diameter with a vertical line through

its center. In a sheet of gray cardboard, cut out an isosceles triangle approximately 30 mm high and 15 mm wide. Holding the gray cardboard screen at normal reading distance, position the circle on the white strip behind the triangular aperture and slide it laterally back and forth at a rate of about 2 cycles/sec (taking care to move the circle beyond the aperture in each direction. If the center of the cutout is fixated, an egg-shaped figure will be perceived swinging like a pendulum within the aperture (see Fig. 6). The apparent contraction of the figure along the axis of motion occurs because the rate of translation on the retinoid is less than the veridical rate of stimulus motion. Moreover, the rate lag is greater at the apex of the window than at the base, which accounts for the egg-shaped transformation of the circle. Thus the retinoid model correctly predicts a complex illusion which should not occur according to Rock's theory.

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