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Miniature Eye Movement

The pattern of saccades made by man during maintained fixation may be a refined but useless motor habit.

Robert M. Steinman, Genevieve M. Haddad, Alexander A. Skavenski, Diane Wyman

When a human being is asked to fixate, he rotates his eye causing the image of the fixation target to fall within his foveal bouquet—the part of his retina where he sees details best. If he is then asked to maintain fixation on the target, his eye makes a consistent but idiosyncratic pattern of slow and fast miniature eye movements. This maintained fixation pattern has traditionally been considered to be "involuntary," "spontaneous," or "reflexive," largely because these eye movements are extremely small (much smaller than ordinary voluntary motor acts), and also because the individual is not ordinarily aware of intending to make or of actually making any of these small eye movements (*1*). We believe that the traditional view is not entirely correct.

A typical maintained fixation pattern of a human being is shown in Fig. 1. This pattern is composed of three kinds of movements: saccades, drifts, and physiological nystagmus. Saccades are small, very fast changes in eye position. They occur one to three times each second, shifting the line of sight abruptly by a small amount. Their average size is about 6 minutes of arc (the same size as the head of a thumbtack 2.5 meters away from the eye). The eye slowly drifts back and forth in the intervals between saccades. These saccades and drifts are superimposed upon a high frequency tremor called physiological nystagmus (*2–4*). All subjects make these three kinds of miniature eye movements but the size and most frequent direction of saccades vary considerably from subject to subject.

Although the eye is continually moving, it does not wander very far from its mean position during maintained fixation (standard deviations are only about 2 to 5 minutes of arc on both horizontal and vertical meridians). This permits the retinal image of the target to remain within the foveal bouquet where detail vision is best and relatively uniform (the foveal bouquet has a diameter of about 20 minutes of arc) (*5*).

Origin of Modern Interest in Miniature Eye Movements

Modern interest in the fine details of the maintained fixation pattern was provoked by dynamic theories of visual acuity first proposed by Weymouth *et al.* (*6*) about 50 years ago and developed by Marshall and Talbot (*7*) and Jones and Higgins (*8*) in the 1940's. It is assumed in such theories that physiological nystagmus and reciprocal overlap in the visual pathways sharpen a target image blurred by optical defects of the normal human eye. The tremor causes the target image to sweep rapidly back and forth across a number of receptors. The cortex averages messages from the maximally stimulated population of these receptors. This average restores edges given only as shifting gradients of illumination in the blurred retinal image. Quantitative details of this theory were based on findings that were accepted as accurate estimates of physiological nystagmus made by Alder and Fliegelman who measured tremor by photographing light reflected from a small mirror resting on the limbus of the fixating eye (*9*). These authors reported that physiological nystagmus had a frequency of 50 to 100 hertz and an average amplitude of slightly more than 2 minutes of arc (such characteristic frequencies and amplitudes are required if eye movements are to provide the proposed statistical sharpening mechanism). The Marshall-Talbot dynamic theory of visual acuity was extended by Osgood and Heyer (*10*) in whose hands it became a statistical theory of form perception, an alternative to the volume conductor brain model which had been proposed by Köhler and Wallach a few years earlier (*11*). At about the same time, Riggs and co-workers in this country and Ditchburn and co-workers in England (*12*) as well as Yarbus in Russia (*13*) devised techniques to measure miniature eye movements during

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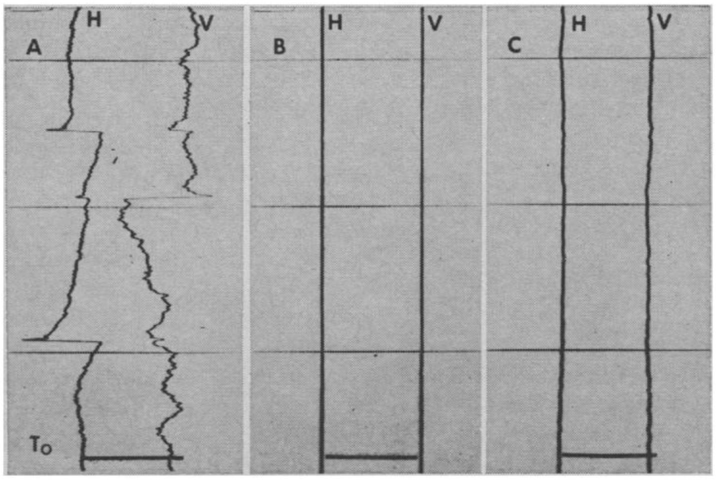


Fig. 1. (A) A 3-second two-dimensional record of the human eye movement pattern during maintained fixation of a bright red point of light viewed in darkness. The record begins at the bottom (T_0). Repetitive horizontal lines mark 1-second periods of time. The record plots voltages proportional to eye position on the horizontal (H) and vertical meridians (V) as a function of time. The eye position scale on both meridians is indicated by the black bar representing 15 minutes of arc under the record. The abrupt changes in eye position are "saccades." "Intersaccadic drifts" are seen in the periods between saccades. The drift is superimposed on "physiological nystagmus," the high frequency tremor seen in both eye position analogs. (B) A similar record made with a mirror attached to the bite board in place of the mirror attached to the subject's eye. This record shows the mechanical and electrical noise in the recording apparatus with the same optical lever length and amplification used to make the fixation record reproduced in (A). (C) A similar record made with a mirror mounted on a plastic pedestal cemented to the bridge of the subject's nose. This record shows noise produced by rotations of the hand pivoting about the bite board (head translations are eliminated by the flat mirror used in the optical system). This record also contains noise that would not contaminate the eye movement record, namely, changes in the orientation of the mirror produced by changes in the tension of the skin whenever the subject's facial expression changes.

fixation in order to test the dynamic theory. They all used a contact lens optical lever to record eye position. This technique is perhaps the simplest means of studying the maintained fixation pattern because very small eye movements (smaller than 1 minute of arc) can easily be recorded free from head movement artifacts. Figure 2 shows a variant of such an instrument currently in use in our laboratory.

Physiological nystagmus, the high frequency tremor which provided the basis for border sharpening in dynamic theories of visual acuity, is shown clearly in Fig. 1. Its frequency is on the order of 50 to 100 hz, but its average amplitude is much less than 1 minute of arc: 5 to 30 seconds is a typical value obtained in modern research. So, the tremor of the human oculomotor system is sufficiently frequent, but much too small to sweep the retinal image of the target object across any appreciable population of cones (there are only about three cone receptors per minute of arc in the foveal bouquet). Because of such measurements, interest in the dynamic theory of visual acuity waned by the middle 1950's [just in time to welcome lateral inhibition then coming back into vogue after 100 years as a mechanism to explain the neurological sharpening of edges blurred by the optics of the normal eye (*14, 15*)].

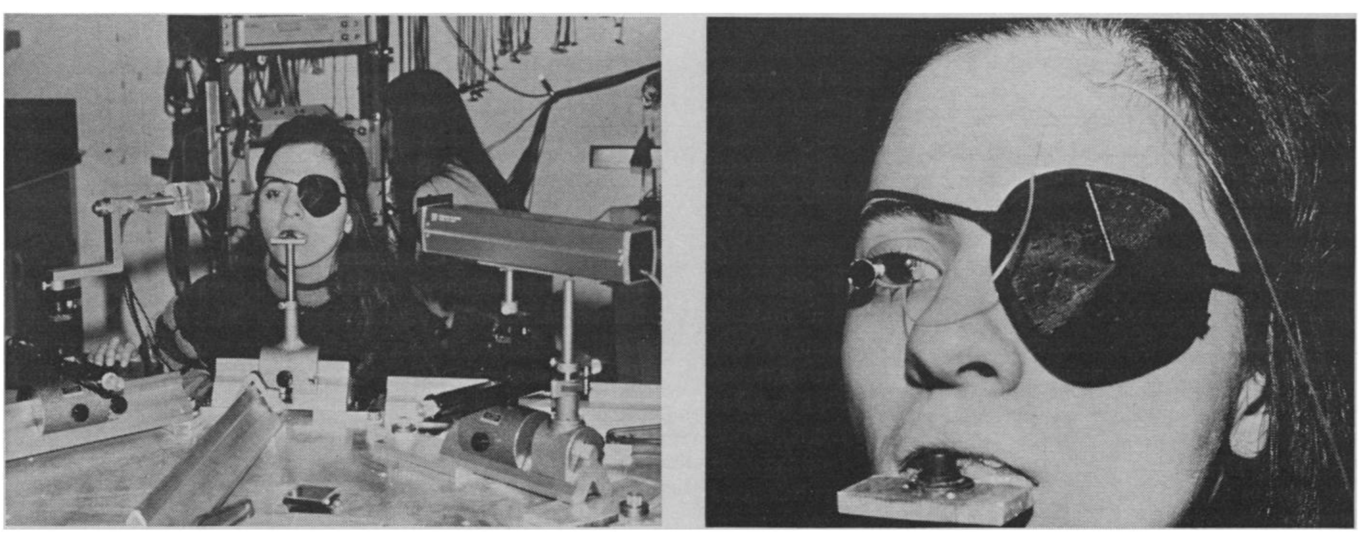


Fig. 2. (Left) A subject positioned for eye movement recording with a contact lens optical lever. The target (not shown) is located 2.04 meters in front of the subject's right eye. Head position is stabilized by a dental acrylic bite board. A narrow beam of collimated light, from the attenuated HeNe laser (0.15 milliwatt at the detector) on the right, falls on the flat front surface mirror which is attached by means of a stalk to a tightly fitting molded scleral contact lens held by suction (30 to 100 millimeters of mercury) on the subject's right eye. The mirror is oriented so that it is perpendicular to the line of sight, permitting horizontal and vertical rotations to be recorded free from confusion with torsions of the eye. The plane mirror also eliminates confusion of eye rotations with head translations. The laser light, after reflection from the contact lens mirror, falls on the surface of the photodetector shown mounted in Lucite on the left. The photodetector gives continuous two-dimensional indications of the position of the laser spot on the detector surface. (Right) Close-up view of the scleral contact lens during use. The flat front surface mirror is attached to the temporal side of the contact lens by means of a rigid aluminum stalk and self-curing acrylic pedestal. The suction tubing, which is connected to the nasal side of the lens, can be seen taped to the subject's forehead as it passes to the suction apparatus (not shown).

Miniature Eye Movements and Visibility

The possibility of the contact lens optical lever being used to make valid measurements of very small rotations of the eye provoked further interest in the miniature eye movements made during fixation and led to questions being asked about the origin and purpose of the movements. It was soon found that continuous eye movement during maintained fixation is very useful to the visual system. If the eye does not move, the target image is stabilized on the retina and the target fades from view after several seconds (*16*). In some sense, then, the subject must move his eye in order to see. But why does he use the particular pattern of slow and fast eye movements observed during maintained fixation? One answer might be that the maintained fixation pattern is the best way a subject can keep the target visible. But this is not the case. If the subject makes eye movements during fixation in order to keep the target from fading, then the disappearance of the target image should initiate or, at least, influence saccades or drifts. In 1956, Cornsweet showed that neither the frequency of saccades nor the size of drift samples correlated with the fading of stabilized targets. He recorded horizontal eye movements under conditions of normal fixation and, also, under conditions where the fixation target was stabilized on the retina (*17*). The stabilized target image was kept visible for different proportions of time by flickering it at various rates, permitting him to correlate target visibility with saccade frequency. The correlation was almost zero, leading Cornsweet to conclude that target disappearance was not the stimulus for saccades. A similar analysis of drift samples gave the same result.

The fading of stabilized foveal targets, then, does not influence fast or slow components of the pattern of eye movements during maintained fixation despite the fact that eye movements are necessary to prevent target fading. Moreover, we know that fixation saccades do not contribute to target visibility. In fact, saccades may affect visibility adversely. Visual threshold is probably elevated when a saccade occurs during fixation (*18*) in much the same way that threshold is elevated when a large voluntary saccade is made to jump between targets spaced several degrees apart in the visual field (*19*). Drifts, however, seem to be necessary as well as sufficient to keep a target from fading when it is stabilized on the retina (*16*). So, target visibility does not require saccades; their occurrence interferes with seeing; and saccades during maintained fixation, if they have any functional significance at all, must serve some other purpose. What might it be?

Saccades as Position-Correcting Reflexes

Cornsweet (*17*) attempted to answer this question by proposing a model consistent with his measurements of the eye movement pattern during maintained fixation. According to this model, the eye drifts because of instability in the oculomotor muscles. As the line of sight drifts away from the center of the target, the target image moves away from the center of the foveal bouquet. This increasing distance between the line of sight and the target center serves as a visual error signal which triggers an involuntary saccade that moves the target image back toward the center of the foveal bouquet. The probability of a saccade increases as the visual error signal grows larger and a visual error as small as 7 minutes of arc is virtually certain to trigger a position-correcting saccade. After the saccade is made, the eye drifts once again until another saccade is triggered. This happens again and again, establishing the eye movement pattern observed during maintained fixation.

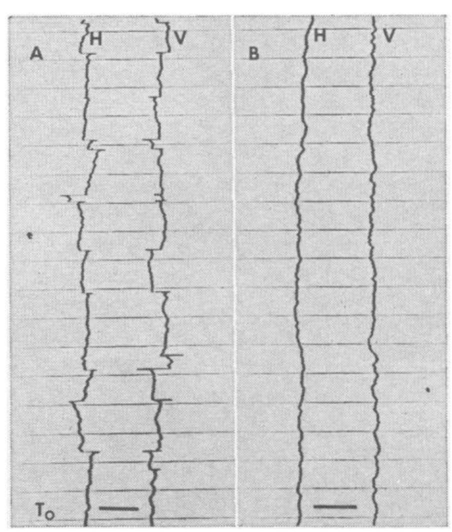


Fig. 3. (A) A 17-second two-dimensional record of the eye movement pattern during maintained fixation of a bright red point of light viewed in darkness. The record begins at the bottom (T_0) and repetitive horizontal lines show 1-second periods of time. Saccades occurred about once or twice each second. Most saccades had a component of motion on both horizontal (*H*) and vertical meridians (*V*). Their size can be estimated by means of the black bar at the bottom of the record which represents 15 minutes of arc. (B) The next record was made immediately after (A). Conditions were the same except that the subject was told to suppress saccades and hold his eye in place with slow control.

The problem with Cornsweet's model is that it does not explain fixation characteristics that have been observed in subsequent experiments. Nachmias showed that drifts on some meridians correct visual errors introduced by other drifts and that increasing the drift rate of the eye did not increase the frequency of saccades, leading him to conclude that the time since the last saccade was a better predictor of when the next saccade would occur than the deviation of the line of sight from the target (*20*). Nachmias's findings were confirmed by Fiorentini and Ercoles (*21*) and most recently by St. Cyr and Fender (*22*). There is other evidence that makes additional difficulties for Cornsweet's model. Boyce (*23*) found that only 30 percent of his subjects' saccades compensated for immediately preceding drifts, and similar characteristics were reported in a larger sample of subjects by Proskuryakova and Shakhnovich in 1968 (*24*). These findings suggest that both saccades and drifts produce, as well as correct, position errors during maintained fixation. So, perhaps both are required to keep the line of sight on the target when a subject tries to maintain fixation. But, we believe that the saccades serve some other purpose because slow control keeps the eye in place when saccades are suppressed.

Slow Control

About 6 years ago, we became interested in the role of drifts in maintaining the line of sight during fixation, and were able to investigate the problem by simply asking subjects (two of us: R.S. and A.S.) to hold their eyes in place without making any saccades. It was exceedingly simple to do this; no special training was required. The experimenter watched a much enlarged analog of the subject's fixation pattern for 2 or 3 minutes during which time he told the subject whenever a saccade had been made. Recordings were then made of alternating 10-second trials during which the subject was asked either to hold his eye still, or to fixate

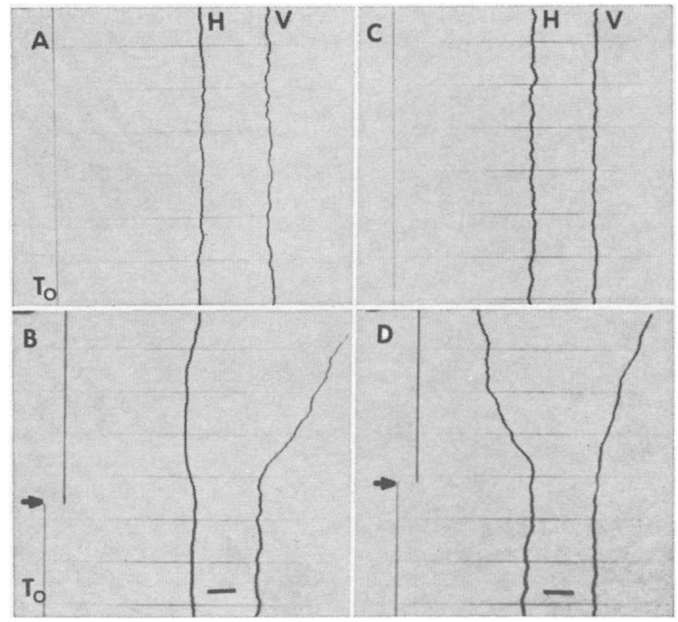
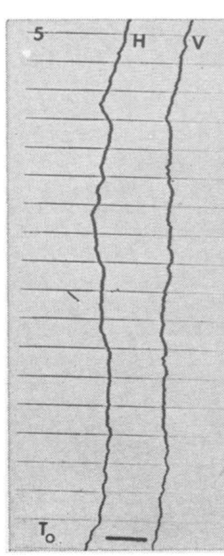


Fig. 4. (A) A 7-second two-dimensional record of the eye movement pattern during maintained fixation of a bright red point located directly in front of the subject's right eye. The subject had been instructed to suppress saccades. The record begins at the bottom (T_0) and repetitive horizontal lines show 1-second periods of time. (B) A record made under similar conditions except that the target was removed from view in the 2nd second at the time indicated by the black arrow. Four seconds later the eye had drifted down [the vertical trace (V) went to the right] and had reached the recording limits of the apparatus. The size of the drift can be estimated from the black bar at the bottom of the record which shows 15 minutes of arc. (C) A record made under the same conditions as (A) except that the target was located about 30 degrees to the right of the subject. (D) A record made with the target in the same position shown in (C) except that the target was removed from view at the time indicated by the black arrow. The eye drifted toward the straight-ahead position when the target was removed [left in the horizontal (H) trace]. It also drifted downward [to the right in the vertical (V) trace]. The size of the drifts in the dark on both meridians can be estimated from the black bar under the record which indicates 15 minutes of arc.

as he usually did. The results were clear-cut. Saccades were suppressed, often completely, and the subjects' eyes stayed in place very well (*25*). This finding is illustrated in Fig. 3. Fiorentini and Ercoles published a similar report of saccade suppression at about the same time (*21*), and Filin and Mizinova subsequently reported that a large sample of subjects could voluntarily suppress saccades when they were asked to do so (*26*).

This manner of eye position control is not a trick; it does not depend on the type or distance of the fixation target, nor does it result from defocusing —saccades can be suppressed and the eye held in place when the lens of the eye is almost completely paralyzed and spectacle correction is added to keep the target image sharp (*27*). Such slow control is an active process: a visible stimulus is required. This is shown in Fig. 4. The top records show effective slow control on both horizontal and vertical meridians when the fixation target was placed in two very different locations. Slow control was effective, regardless of the orientation of the eye in the orbit. But this was true only while the target was visible and a visual error signal was available to drive the slow control system. Slow control is not only an active process requiring a visual stimulus, but the stimulus from one eye can serve to hold the other eye in place when the second eye is not provided with a fixation stimulus. This is illustrated in Fig. 5 where the eye movement pattern of an occluded right eye was recorded while the fixation stimulus was seen only by the left eye and the subject was asked to use slow control exclusively (compare this record with the record reproduced in Fig. 3B which shows the oculomotor pattern of the same subject under the same instruction when the target was seen by the eye from which the record was made) (*28*).

Two of us (R.S. and A.S.) show very effective slow control of the kind illustrated in Figs. 3 to 5. The other subject (G.H.), whose slow control has also been studied extensively, suppresses saccades as well but tends to drift slowly to the right (about 1 to 2 minutes of arc per second). Her slow control on the vertical meridian, however, is completely effective (drifts in one direction are always followed by suitable drifts in the other direction). These characteristics are shown in Fig. 6. So, for some subjects saccades may be necessary to maintain eye position after all. If, for some special reason, it is important for G.H. to keep the target in her foveal bouquet for periods in excess of 5 or 10 seconds, she will have to make a single saccade to the left to recenter the target image. But such deficiencies in slow control would not be of much practical significance for this subject (or others with similar defects) because a great deal of visual information can be processed in 1 or



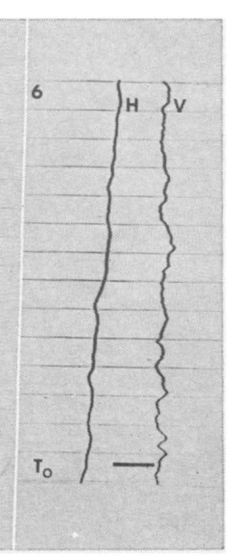


Fig. 5. A 19-second two-dimensional record of slow control. The right eye, from which this record was made, could not see the target. The target, seen only by the left eye, was a bright red point 2.04 meters away in an otherwise dark room. The record begins at the bottom (T_0) and repetitive horizontal lines show 1-second periods of time. The black bar at the bottom of the record shows 15 minutes of arc. The yoking of the two eyes during slow control can be evaluated by comparing this record with the performance of the same subject shown in Fig. 3B where the record was made with the same target at the same recording session except that in Fig. 3B the stimulus was seen by the eye from which the record was made.

Fig. 6. A 14-second two-dimensional recording of subject G.H.'s right eye when using slow control. The record begins at the bottom (T_0); repetitive horizontal lines show 1-second periods of time and the black bar shows 15 minutes of arc. This subject's tendency to drift slowly to the right (temporally) when she suppresses saccades can be seen in this representative record. By the end of the trial she was about 12 minutes to the right of her starting position on the horizontal (H) meridian. Her slow control on the vertical (V) meridian, however, shows no such systematic tendency to drift away from the target.

2 seconds, for example, 300 or 400 milliseconds is a sufficient pause during normal reading for a person to process relatively difficult visual information. During periods ten times as long, the target of interest would remain well within the retinal region of best detail vision even when slow control is relatively ineffective. If human beings can maintain eye position so well using drifts exclusively, why do they typically make saccades every half-second when they are asked to maintain fixation? Why all the jumping around?

Fixation Saccades May Scan a Small Region near the Target

We suspect that the patterns of eye movement during fixation that are recorded in the laboratory are almost confined to the laboratory. Elsewhere, during normal visual search, the eye rests in an attended region for several seconds at most, a sufficient time to take in all relevant information without any tiny fixation saccades. It is only when a subject is asked (or tells himself) to pay very close attention and try very hard to be sure that he is really looking directly at a target that the tiny search pattern we call maintained fixation comes into play. Since a subject is never entirely sure that his line of sight is perfectly centered, he uses tiny saccades to test a variety of regions near the target. If the maintained fixation pattern is seen in everyday life, it is probably confined to threading needles, the rifle range, or possibly, long-distance girl-watching—all situations in which ferreting out and being certain of fine detail are critical. Or, put slightly differently, the human being uses saccades, normally large ones, to search in his visual world—normally he makes large saccades to search his entire visual field. If we ask him (or if he decides) to search an almost microscopic portion of this field, he can do so. We believe that this is what a subject is really doing when we ask him to maintain fixation and we propose that such exquisite oculomotor control is learned. It does not result from the activities of a built-in retinal reflex that corrects tiny fixation errors by initiating involuntary saccades whenever the errors exceed a very few minutes of arc. What evidence do we have for such speculation?

We have not yet done the obvious experiments that would enable us to compare visual search patterns with maintained fixation patterns in naive subjects because we do not have a suitable eye position monitor. We need an instrument capable of registering saccades as small as 1 minute of arc without attachments to the eye because it is absurd to fit naive subjects with scleral contact lenses, line them up in an instrument of the kind shown in Fig. 2, and then expect them to inspect visual scenes as they normally do in everyday life. We have, however, been able to use the contact lens recording technique with subjects experienced in eye movement experiments and to make a similar type of comparison, that is, between maintained fixation and reading (*29*). Two of us (A.S. and R.S.) were asked to maintain fixation on the letter "T" or to read previously unseen paragraphs cut out from *Science* under the expectation that we would be tested on our comprehension of this material at the end of the experiment. We found that the maximum average saccade rate during normal reading and during maintained fixation were very similar, and that tiny saccades of the kind seen during maintained fixation (less than 10 minutes of arc) were exceedingly rare during pauses in reading. On those very rare occasions when a fixation-like saccade did occur during a reading pause, it occurred during a very long pause (more than 500 msec) at the time a reading saccade (about 50 minutes of arc) would have been expected if the subject had decided to make a saccade to continue on or to go backward in the text. The observed similarity of intersaccadic intervals during maintained fixation and normal reading lends plausibility to the notion that maintained fixation and reading may both be overlearned motor skills—reading surely is. That the velocity-amplitude characteristics of small so-called "involuntary" saccades and large voluntary saccades have already been shown to be the same (*30*) also support this notion. Studies with naive subjects, in which comparisons are made between the eye movement pattern during normal free exploration of a visual scene and the eye movement pattern when the subject lets his line of sight linger near some detail within the scene, might lend further support to our speculation. But, recording miniature eye movements while preserving naiveté during visual search is not the only problem we face. Experimental test of the learning notion is also difficult. Parents are not enthusiastic about having their children fitted with contact lenses, and it is possible that the maintained fixation pattern may be learned early in life.

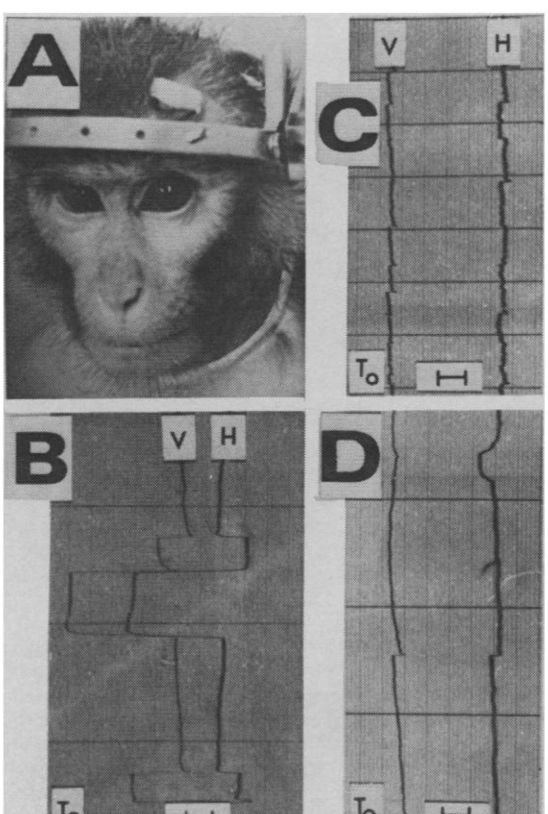


Fig. 7. (A) A rhesus monkey (Henry) positioned for recording eye movement by means of the magnetic field search coil technique. The search coil (not visible) is held to the sclera of the left eye and its leads are carried under the skin to the connector shown screwed to the skull just above the eye. The head is held in place in the magnetic field coils (not shown) by means of the metal band screwed to the skull. (B) Henry's two-dimensional fixation pattern before special training. (C) A representative eye movement record made after 3 months of fixation training. (D) A record of Henry's subsequent performance when he started to use slow control to keep his eye in place. All records begin at the bottom at (T_0); repetitive horizontal lines show 1-second periods of time and the black bars show 15 minutes of arc.

Evidence

There is, however, some recent indirect evidence which suggests that the pattern of saccades made during maintained fixation may be the kind of overlearned voluntary motor habit we wish to propose. One of us (A.S.), working in collaboration with David Robinson, has used a magnetic field search coil to study maintained fixation in primates (*31*). By this technique, the smallest details of the oculomotor pattern in an alert and active monkey can be studied over periods of several months. A fine wire coil is held against the sclera of the animal's eye by passing its leads behind the insertions of the extraocular muscle. A metal band screwed to the monkey's skull is used to hold the head in two alternating magnetic fields kept in temporal and spatial quadrature; and eye orientation is recorded by detecting phases in the voltages generated in the coil. This technique, which has been used to observe the fixation patterns of three young rhesus monkeys (each about 2 years old) was sufficiently sensitive to show miniature eye movements. In one way, the fixation pattern of rhesus monkeys before special training is like ours in that saccades are made one to three times each second; in another way, however, their fixation pattern is not like ours because their saccade amplitudes are, on the average, 40 minutes of arc and never smaller than 23 minutes of arc—that is, they are from four to eight times as large as those of the adult human being. Fixation in a rhesus monkey is sufficiently stable to keep the line of sight within a degree of the target. The human being has similar control of eye position and makes smaller saccades when maintaining fixation in total darkness for long periods of time (40 seconds or more) (*32*).

This initial result suggested that the rhesus monkeys were perhaps (i) incapable of making saccades during maintained fixation that are as small as those of the human being, (ii) not able to determine precisely what we wanted them to do, or (iii) inexperienced and had neither the occasion nor the need to develop a fine fixation microsearch pattern. We examined the first alternative by giving one of these animals (Henry) extensive fixation training. He was required to perform a difficult visual discrimination that required him to keep his line of sight near the fixation target if he wished to receive a squirt of orange juice. He did. And after 3 months (during which time he had about 120 1-hour training sessions), his eye movement pattern became very similar to the eye movement pattern of a typical human subject who is trying to maintain fixation. When we found that Henry had the capacity to make tiny fixation saccades and maintain his line of sight within a very small portion of his visual field, he was changed to an easier discrimination problem (a trivial task for which he apparently decided he did not require saccades) and Henry's eye began to stay on target without saccades (*33*). During maintained fixation his saccade rate has dropped to about one saccade every 2 seconds, and there are frequent periods of about 3 seconds during which he makes no saccades. When saccades are not made, the monkey's slow control is effective and his records are becoming similar to the records of human subjects under the same instruction. These results are shown in Fig. 7. We plan to study development of the fixation pattern in infant rhesus monkeys now that we know that such animals have oculomotor capacities that are similar to those of the human being, and we have worked out training procedures that will instruct the infants to fixate. The outcome of these developmental studies is not known, but the rhesus monkey seems to be a promising subject in which to study the learning of the fixation microsearch pattern.

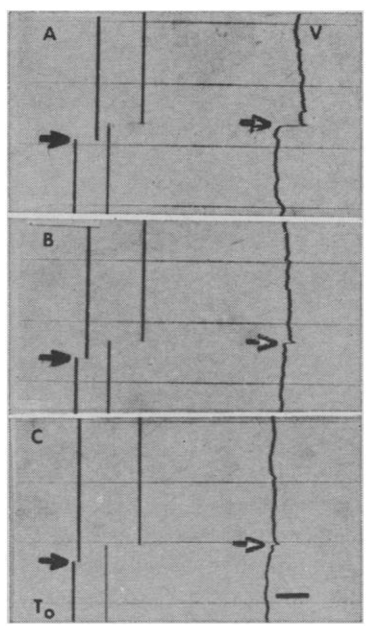


Fig. 8. (A) A representative record of small step tracking on the vertical (*V*) meridian. The record begins at the bottom (T_0) and the filled black arrow points to the time a small point target moved downward 15 minutes of arc. The open black arrow points to the saccade made to follow the instantaneous displacement of the target. (B) A similar record of the saccade made in response to a downward target step of 7 minutes of arc. (C) A similar record of the saccade made in response to a downward step of 3.5 minutes of arc. Repetitive horizontal lines in all records show 1-second periods of time and the black bar at the bottom indicates 15 minutes of arc. The event marker to the left of the eye position analog shows the operation of a trigger that monitored the eye position channel and stopped a timer that was started when the target stepped, permitting us to measure the reaction time for small step saccadic tracking.

Some recent research on human fixation also supports our speculation. A major obstacle to the voluntary motor skill interpretation of the maintained fixation pattern was an experiment by Rashbass (*34*) who concluded that there is a large saccadic "dead zone" (Rashbass's subjects did not track target steps smaller than 15 to 30 minutes of arc). If the fixation pattern is an overlearned habit based on a voluntary search made with saccades as small as 5 or 6 minutes of arc, how could such a habit be learned if subjects cannot voluntarily track target steps three to six times as large? This obstacle proved not to be insurmountable, as is shown in Fig. 8 where typical records of saccadic tracking of small target steps are reproduced. In our experiments both subjects (one at that time completely inexperienced in eye movement experiments) always made saccades to follow target steps as small as 3.5 minutes of arc and even followed steps of 1.7 minutes of arc on a statistically reliable proportion of the trials (*35*). The first tracking saccade began, on the average, less than 450 msec after there was a step as small as 3.5 minutes of arc in the target. With the largest step (28.4 minutes of arc) average latencies were about 200 msec. Values in the range of 200 to 450 msec are what would be expected if these small tracking saccades were voluntary motor acts of the kind commonly studied in simple experiments to determine the reaction time of a subject asked, for example, to press a telegraph key on seeing a light move through a small distance (*36*).

There was one very interesting difference between our subjects' styles of responding when they tracked small target steps. One subject consistently undershot all but the smallest target step (3.5 minutes of arc) with the first saccade. The other subject consistently overshot. These individual differences suggested to us that characteristics of the first tracking saccade depended on an implicit strategy adopted by each subject in the experiment (the subjects did not know that they were under- or overshooting until the data were analyzed). This possibility led to an examination of the manner in which a number of psychological variables affect saccadic tracking of small target steps. We varied the subject's expectations about when and how many different kinds of steps would be presented, his response strategy, and the perceptual complexity of his task. We found that the latency and accuracy of the first tracking saccade were influenced by such variables in much the same way that latency and accuracy would be influenced in any experiment on voluntary sensorimotor reaction times. For example, latency was exchanged for accuracy simply by asking a subject to adopt one strategy or the other. Also, latency decreased when an auditory signal was added to define precisely when each target step had occurred; and latency increased when the time of the target step, as well as its direction, was made completely unpredictable.

So, there is nothing about the saccadic tracking of small target step displacements that rules out a voluntary motor skill interpretation of the saccadic component of the maintained fixation eye movement pattern. Voluntary saccades, as small as those observed during maintained fixation, are in the voluntary behavioral repertoire of the adult human subject. Furthermore, the susceptibility of these saccades to psychological variables does not differentiate them from other voluntary motor acts despite the fact that they are much smaller than any other voluntary change in the position of a part of the body (when the eye makes a voluntary saccade of 6 minutes of arc, a point on the cornea only moves through a distance of about 0.02 millimeter).

However, a large problem still remained before we could say with confidence that the maintained fixation pattern is an overlearned motor habit developed from tiny saccades initially executed voluntarily. It is one thing to know that a subject can follow the target with voluntary saccades when the target moves a small distance in the visual field, and quite another to know that voluntary saccades can be equally small when they are made in the presence of a target that remains stationary. A stationary target does not provide the subject with a visual error signal if his line of sight is centered on it; and a visual error signal might be required for a subject to make voluntary saccades as small as the saccades that are made during maintained fixation. If this were true, small voluntary saccades could be made only after the eye had drifted away from a stationary target, and each subject's pattern of saccades during maintained fixation would be constrained by his tendency to drift in idiosyncratic directions during intersaccadic intervals. Such constraint on the eye movement pattern during maintained fixation would mean that this pattern differs from the eye movement pattern normally used to search within the entire visual field. In ordinary visual search saccades can be used to look in any direction, even to locations where there is no target to guide the eye to the region the subject wishes to inspect.

The evidence already described indicates that saccades during maintained fixation are not constrained in the suggested manner. Some fixation saccades seem to move the line of sight away from as well as toward the fixation target, but it was not known whether such saccades could be made voluntarily. We found that they can (*37*). This was done by asking subjects (G.H. and R.S.) to make the smallest saccade they possibly could in a direction (up, down, right, or left) specified by the experimenter before each 3-second trial. A tone, at the end of the first second, signaled when this small voluntary saccade should be made. Slow control was used to hold the eye on the target throughout each trial, and consequently each record contained only one saccade: the voluntary saccade, whose size and direction relative to the preferred fixation position, was of interest. One hundred and thirty trials were recorded for each subject. Because both subjects always made a saccade in the specified direction, and because the saccades were made at an appropriate time (latencies were about 235 msec, as would be expected in simple determinations of reaction time), it is almost certain that these saccades were voluntary. The average size of these voluntary saccades (5.6 minutes of arc; standard deviation < 3.0) was similar to the average size of saccades made by the same subjects during maintained fixation and well within the range of fixation saccade sizes measured elsewhere (*38*). Moreover, these voluntary saccades created, rather than reduced, visual errors (the distance of the line of sight from the preferred foveal fixation locus was larger after the saccade than before the saccade). The eye was very near (less than 1.2 minutes of arc) its preferred fixation position when the saccade began, and much farther away (more than 4 minutes of arc) at the end of the saccade. This result shows that subjects can use small voluntary saccades to produce as well as to reduce visual errors just as they can when they make large voluntary saccades to look about in the visual world that surrounds them. Representative records from this experiment are reproduced in Fig. 9.

In the same series of experiments (*39*) we found that we could not only make voluntary saccades as small as those that we make during maintained fixation but, also, that we could be aware of having made them. It was desirable to show this because one of the reasons why saccades made during maintained fixation are frequently described as "spontaneous," "involuntary," or "reflexive" is that subjects are not normally aware of making them when asked to maintain fixation. This reason is not really very compelling, however, because awareness is not normally associated with individual acts in any overlearned motor pattern. William James made and developed this point eloquently 80 years ago (*40*). For James it was extremely significant that a motor habit consisting of a sequence of individual acts recedes from consciousness once it has been executed many times. This property of mind serves a very useful function. It continually makes room in consciousness for new learning; and when most necessary motor habits have been learned, we have room for contemplative cognitive processes.

We believe that the eye movement pattern used by the adult to maintain fixation is like this. The pattern has been overlearned sufficiently that when a subject is asked to maintain fixation, the pattern runs itself off without his making any conscious effort or being aware of making individual movements. This is true of oculomotor control in general, however. Human beings are not ordinarily aware of the much larger saccades they continually make in their ordinary search of their visual worlds. Nor are they aware of the highly overlearned but initially con-

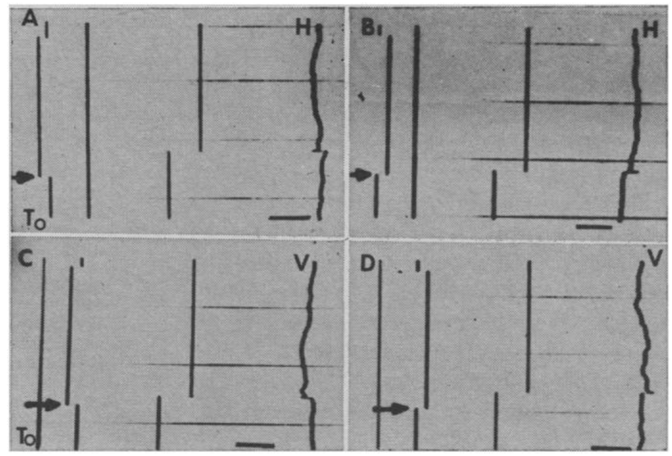


Fig. 9. (A) A record of the eye movement pattern on the horizontal (H) meridian when the subject was asked to make one small voluntary saccade to the left while looking at a point that remained stationary throughout the trial. The record begins at the bottom (T_0). The black arrow indicates when an auditory signal told the subject to make his smallest possible saccade to the left. The eye position trace shows that a small saccade was made to the left after the signal was given. The size of this small voluntary saccade can be estimated from the black bar (15 minutes of arc). The event marker to the left of the eye position analog shows the operation of the trigger which stopped a reaction timer when the saccade was made. The other three records show small voluntary saccades made in the other directions: (B) to the right, (C) up, and (D) down.

scious, as well as voluntary, eye movement pattern used whenever they read. However, if asked to pay attention to such large voluntary saccades, human beings readily become aware that their eyes are jumping around. Once they pay attention to each movement and become aware of each individual saccade, however, the overlearned pattern no longer runs itself off in exactly the same way. The tiny saccades made during maintained fixation show similar characteristics. We found that they can be detected but their frequency is influenced by the attentional act and the maintained fixation pattern loses its typical idiosyncratic characteristics.

Now that we know that voluntary saccades, as small as the saccades made during maintained fixation, can be made in the presence of a stationary target, we plan to find out whether such small voluntary saccades can be used to execute novel oculomotor patterns. If each individual originally learned to pattern the direction, size, and timing of fixation saccades to best serve his visual search of small parts of his visual field, he should be able to learn to execute novel saccade patterns on command much the way musicians can learn to execute and then run off automatically specific finger patterns on the keyboard. We have been constructing a musical saccade organ to examine this problem. Subjects will be asked to execute a pattern of small saccades whose directions, sizes, and temporal spacings will be prescribed by the experimenter. First they will learn that saccades to the right produce one tone, saccades to the left another tone, and that saccade size is proportional to the loudness of the tone. Then they will be given a tune made up of a particular combination of these tones and be asked to play it back by making an appropriate pattern of eye movements. If subjects can learn to play the tune with miniature saccades and if the tunes have rhythms similar to those observed during ordinary maintained fixation, it becomes increasingly plausible to assert that the eye movement pattern used during maintained fixation came to be patterned in much the same way. We have just begun these experiments and our first attempts suggest that any difficulties we may encounter will arise at least as much from the modest musical talents of the subjects as from any intrinsic limitations on their oculomotor control.

Concluding Remarks

We have described progress made in our effort to show that the characteristics and probable functions of miniature saccades made during maintained fixation are not different from the characteristics and probable function of large saccades made during visual exploration. If subsequent work supports this view, what has been gained?

1) The task of understanding human oculomotor performance is simplified because the distinction between large voluntary saccades and miniature involuntary saccades has been discarded. Once this is done, human oculomotor performance becomes not only simpler but also more similar to the performance of other foveate animals who are not known to make miniature saccades but who do use large saccades to make gross changes in the orientation of their eyes. Discarding the distinction between large and miniature saccades, however, raises new questions about oculomotor physiology. For example, rhesus monkeys, although they do not ordinarily make miniature saccades, have the capacity to make them. We must now find out whether the same machinery is used to initiate and guide their miniature saccades as is used for the physiological control of their large saccades (*41*).

2) In our effort to understand the role of miniature saccades in the maintained fixation pattern, we found that both man and the rhesus monkey have an effective slow control system that keeps a target image relatively stationary on the retina when saccades are not made. A slow control system has also been described by Collewijn (*42*) in the rabbit: a nonfoveate animal that does not need to make saccades to bring details in its visual world to fall in a specialized receptor region. The characteristics of slow control in the rabbit seem similar in a number of ways to those of man. If these similarities prove to be marked in subsequent studies of slow control in human beings and the rhesus monkey, there is a gain in our understanding of comparative oculomotor physiology which will have resulted from the treatment of miniature saccades in a manner different from the way they had traditionally been treated.

3) The third gain is methodological. Knowing that miniature saccades are voluntary gives human subjects the option of suppressing them. This option allows studies of slow control characteristics free from contamination by periodic high velocity eye movements that alter the characteristics of intersaccadic drifts. Also, an appreciation of the voluntary origin of the pattern of saccades during maintained fixation leads to the expectation of large individual differences in the use of saccades. This expectation encourages the development of techniques to reduce such differences. For example, in our laboratory subjects tend to under-

or overshoot target step displacements, but we have no idea about the extent to which these errors are representative of saccadic tracking precision. If the subject is explicitly asked to be as accurate as possible and is given feedback at the end of each saccade which tells him how well he did, reasonable estimates of this characteristic might be made. This kind of methodology would not be adopted if one did not begin with the assumption that all saccades are typical voluntary motor acts. As such, saccades are expected to be profoundly influenced by a large number of psychological variables. Saccades viewed as reflexes do not place this burden on the experimenter. Any savings, however, are, in our opinion, subject to interpretive risk and unnecessary variability as well.

4) Last, and probably the most intriguing outgrowth of our approach to the eye movement pattern of maintained fixation, is the realization that miniature saccades are busy work. They seem to accomplish nothing. Miniature saccades may have adverse effects on visibility; they are not required to prevent target fading; and they are not required to keep the eye in place for long periods of time. If these miniature high velocity eye movements are not laboratory curiosities (and they may be), it seems odd that the human being should be so busy doing things that seem to accomplish nothing (*43*).

However, these tiny saccades, although not beneficial, cannot be very detrimental to vision either. They only draw a veil over the visual world for a few milliseconds and do not move the target away from the part of the retina where things can be seen well. Perhaps, they are made because they cost little in energy. The frequent occurrence of miniature saccades during maintained fixation may merely confirm something we already know. Human beings are uncertain and human beings are curious. After all, how can you be sure that you are really looking exactly at a target, and how can you resist the temptation to look for something more interesting nearby?

References and Notes

1. We know of no explicit discussion of the reflexive or voluntary nature of miniature saccades used to maintain fixation. Titles of many articles, however, refer to these movements as reflexive, involuntary, or spontaneous and it has become commonplace to treat them in this manner in physiological texts that include a treatment of eye movements. See for example: G. H. Bell, J. N. Davidson, H. Scarborough, *Textbook of Physiology and Biochemistry* (Williams & Wilkins, Baltimore, 1959); N. B. Mountcastle, Ed., *Medical Physiology* (Mosby, St. Louis, ed. 12, 1968).
2. See M. Alpern [in *The Eye*, H. Davson, Ed. (Academic Press, New York, ed. 2, 1970), vol. 3] for an extensive review of the literature on oculomotility.
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4. M. Alpern [in *Handbook of Sensory Physiology, Visual Psychophysics*, D. Jameson and L. Hurvich, Eds. (Springer-Verlag, New York, 1972), vol. 7, part 4] describes recent developments in oculomotility, and gives an evaluation of our interpretation of the role of microsaccades during maintained fixation.
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14. F. Ratliff [*Mach Bands* (Holden-Day, San Francisco, 1965)] gives a summary of early work on lateral inhibition as well as more recent physiological developments. Or, see Cornsweet (*15*) for a particularly lucid brief treatment; also, P. H. Lindsay and D. A. Norman [*Human Information Processing* (Academic Press, New York, 1972)] for an introduction to these phenomena.
15. T. Cornsweet, *Visual Perception* (Academic Press, New York, 1970).
16. See E. G. Heckenmueller [*Psychol. Bull.* **63**, 157 (1965)] for a review, or Alpern (*4*) for a recent evaluation of the role of miniature eye movement and target visibility.
17. T. Cornsweet, *J. Opt. Soc. Amer.* **46**, 987 (1956). See also his book (*15*).
18. R. W. Ditchburn [*Opt. Acta* **1**, 171 (1955)] and G. W. Beeler, Jr. [*Vision Res.* **7**, 769 (1967)] reported an elevation of visual threshold during "involuntary" miniature saccades. But, J. Krauskof, V. Graf, and K. Gaarder [*Amer. J. Psychol.* **79**, 73 (1966)] did not find that visual threshold was elevated when these saccades occurred. The cause of elevation in threshold is controversial; there are alternative points of view, for example, D. MacKay, *Nature* **225**, 90 (1970); or W. Richards, *J. Opt. Soc. Amer.* **59**, 617 (1969). There is no good evidence, however, that they enhance or are essential for target visibility even if they prove ultimately not to be deleterious. It is perhaps worth noting that the importance of eye movements of any kind (drifts or saccades) to visibility may have been overemphasized since it was found that stabilized images disappear. It is difficult to imagine an animal whose normal head or body movements are not adequate to guarantee sufficient motion of the retinal image to prevent stabilization and image fading. Oculomotility probably evolved for quite different reasons, such as (i) to stabilize images on the retina in the face of eye movements caused by instability of the eye (slow control); (ii) to maintain the orientation of the eye with respect to objects in space when the orientation of the body or head changes (optovestibular response); (iii) to stabilize the images of moving objects so they can be recognized (smooth pursuit); or (iv) to permit targets to be moved rapidly to a specialized retinal region where acuity and recognition is far superior to other parts of the eye (saccades). Even in foveate animals such as ourselves eye movements during normal vision probably do not serve to prevent stabilization and fading because fading does not occur within the few hundred milliseconds we let our line of sight fall on some detail within our visual fields. It is only when we maintain fixation for long periods of time (a second or more) that eye movements might become important, but even this is unlikely in everyday life because we do not ordinarily stabilize our heads on bite boards to prevent head movements. Head movements would be sufficient to prevent image stabilization and target fading. In fact normal head movements should be large enough to force us to make relatively large saccades (more than 10 minutes of arc) to recenter a target if we wish to continue to inspect it for any appreciable length of time without artificial supports for our heads. In everyday life, target fading is only noticed when feeble targets fall in the peripheral retina where receptive fields are large and large image displacements would, therefore, be required to prevent target fading. Once you look at such targets, however, so that their image falls in the fovea, they are not likely to fade providing they are sufficiently intense to be seen at all (the fovea is relatively insensitive to light). In short, it seems to us that oculomotility probably evolved to stabilize moving images or to bring them to a specialized region within an inhomogeneous receptor and not to keep images moving so that image stabilization and fading would not occur. It is really much harder to stabilize retinal images than to keep them moving in freely moving biological systems. We suspect that the development of the oculomotor system reflects evolutionary pressures toward image stabilization rather than toward guaranteed retinal image motion to prevent neural adaptation, particularly since such motion is guaranteed by nonoculomotor activities of the organism. See D. A. Robinson [*Science* **161**, 1219 (1968)] for a theoretical treatment of the various oculomotor systems used by the primate to establish and maintain image stability.
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28. Slow control is effective if the target is located much nearer to the eye than 2 meters when the subject views the target monocularly and recordings are made from the eye that sees the target. However, if the target is near and seen by the left eye while an occluded right eye's performance is recorded, slow control is disturbed and relatively large oscillatory drifts are observed. We suspect that these drifts probably reflect vergence movements and phorias accompanying changes in accommodation which occur when near targets are kept in focus. The relationship between small vergence movements and drifts is an interesting matter for study. We can say nothing about this relationship because we have not made binocular recordings. See St. Cyr and Fender (*22*) for binocular data and a discussion of the relationship between drift and vergence movements.
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42. H. Collewijn and collaborators have worked out the occulomotor system characteristics of the rabbit in an elegant series of experiments; for example, H. Collewijn, *Vision Res.* **9**, 117 (1969); *Exp. Neurol.* **28**, 132 (1970); C. Oyster, E. Takahashi, H. Collewijn, *Vision Res.* **12**, 183 (1972). Recently, H. Collewijn and F. Van Der Mark [*Brain Res.* **36**, 47 (1972)] explicitly pointed out similarities between slow control in the human being and the rabbit, and suggested that the two species may have a similar primitive oculomotor system. This suggestion will now have to be examined by making a quantitative analysis of the human scotopic slow control system.
43. Large saccades have figured prominently in theories of form perception and also as explanations for a variety of visual illusions. See, for example, D. O. Hebb, *Organization of Behavior* (Wiley, New York, 1949). The possibility of large saccades causing or contributing to these phenomena has gained acceptance in some quarters recently, particularly since the intentions to make large saccades rather than the saccades themselves have been proposed as the causal perceptual mechanism. See L. Festinger, C. White, M. Allyn, *Percept. Psychophys.* **3**, 376 (1968); V. Virsu, *ibid.* **9**, 65 (1971). We cannot reject a similar purpose for miniature saccades, but prefer to believe that miniature saccades are not made for the purpose of perceiving form because the form of a target object that falls completely within the foveal floor (less than 90 minutes of arc) does not change when we suppress miniature saccades (B. Murphy, paper presented at the Association for Research in Vision and Ophthalmology Meeting, Sarasota, 1973). Of course, the intention not to make a miniature saccade of a certain size and direction may be functionally equivalent to the intention of making the same saccade.
44. We thank Profs. Nancy Anderson, Tom N. Cornsweet, Willard Larkin, John Z. Levinson, Jacob Nachmias, David A. Robinson, and Fredda Steinman for suggestions about and criticisms of various phases of the research described in this article. Also, we thank Joseph Kelly of Philcon Laboratories for making and fitting our contact lenses, Joseph Matthews for designing and constructing our electronic equipment, and Irma Nicholson for patient and skillful secretarial help with this and other manuscripts. Many present and former graduate and undergraduate students have also made valuable technical and conceptual contributions to our research. We particularly thank Robert Cunitz, Carol Jablonski, Elizabeth Kocher, Eileen Kowler, Patsy McGrath, Brian Murphy, Larke Nahme, Jane Puckett, Lucinda Romberg, Richard Sansbury, George Timberlake, Nina Weber, and Barbara Winterson for their help. The human research was supported by grant EY 325 from the National Eye Institute to R.M.S.; and the primate research was supported by PHS training grant GM 576 to the Department of Biomedical Engineering, Johns Hopkins University, and by grants EY 598 to David A. Robinson and EY 1049 to A.A.S. from the National Eye Institute.

Environmental Impact: Controlling the Overall Level

A rationing system may control environmental impact, while maximizing personal choice.

Walter E. Westman and Roger M. Gifford

Recent observations on the genesis of current environmental problems suggest that they stem from the interaction of three elements: the size and rate of growth of the human population (*1*), the growing per capita consumption of products (*2*), and the increasing use of products and technologies that are more pollution-generating and wasteful of resources (*3*). While people have disagreed on the relative contributions of each of these factors toward the overall impact of man's activities on his environment (*4*), there seems little doubt that the combined effect gives reason for concern. The Club of Rome report (*5*) is one of several (*6, 7*) which puts the case vividly that unchecked growth of each of these elements of environmental impact is incompatible with the perpetuation of human civilization.

It seems to be true of all dynamic systems that negative feedbacks must come into play if a long-term steady-state is to be achieved. If natural environmental feedbacks in the system of the biosphere were to come to exert full force, resulting in some variant of the Malthusian crash, much hardship would no doubt occur. There is disagreement about the extent to which improvements in technology can mitigate the crises predicted by a Malthusian analysis of the limits to growth (*8*). Quite apart from the question of the degree to which technological improvements can postpone behavioral changes, however, there seems to be general agreement that negative environmental feedbacks in some form will be necessary. To minimize the social hardships that will otherwise occur, and to spread them as evenly as possible across the populace, while giving each person the maximum freedom of choice of activity

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