Sperling, G. (1990). Comparison of perception in the moving and stationary eye. In E. Kowler (Ed.), *Eye movements and their role in visual and cognitive processes* (pp. 307-351). Amsterdam: Elsevier Biomedical Press.

First presented at OSA:

Sperling, G., & Speelman, R.G. (1965). Visual spatial localization during object motion, apparent object motion, and image motion produced by eye movements [Abstract]. *Journal of the Optical Society of America, 55*, 1576-1577.

TD11. Visual Spatial Localization during Object Motion, Apparent Object Motion, and Image Motion Produced by Eye Movements. George Sperling and Roseanne G. Speelman, *Bell Telephone Laboratories, Inc., Murray Hill, New Jersey 07971.*—Previously, we studied the apparent location (relative to a stationary background) of a test line illuminated instantaneously during an eye movement. We now report similar studies with a line flashed: (1) against moving backgrounds (particularly backgrounds whose motion across a stationary retina reproduces the image sweep caused by a typical eye movement), (2) against "apparently moving" backgrounds (i.e., backgrounds illuminated only in their initial and final positions—not between), and (3) after eye movements, when the background has been shifted during the movement. *Conclusions:* (a) Localization errors occur. Despite important differences, there are basic similarities among the various kinds of localization error. Thus localization during eye movement usually can be predicted from localization during object movement. (b) The appearances of rapid real motion and "apparent motion" are similar. This similarity, and the misconception that one does not see during saccades, are due to the unimportance in vision of stimulation produced during rapid image movement between fixed endpoints. (c) When backgrounds were shifted during eye movements, the shift was recognized if it exceeded about 2°. Although the eye may not know its absolute angular position (relative to the head), it obviously knows something about where it is going in a saccadic movement (relative to the environment) and what to expect when it gets there. (15 min.)

Sperling, G. (1966). Comparisons of real and apparent motion [Abstract]. *Journal of the Optical Society of America, 56*, 1442.

FA13. Comparisons of Real and Apparent Motion. George Sperling, *Bell Telephone Laboratories, Incorporated, Murray Hill, New Jersey.*—The present experiments compare real motion [a stimulus is (1) present for several seconds at a location A, (2) is translated continuously to a new location B (motion phase), and (3) remains at B for several seconds] with apparent motion [same as real motion except the motion phase is replaced by darkness]. The long stimulus presentations at A and B lead to a compelling illusion of motion for a far greater variety of conditions than the classical apparent-motion paradigm in which a stimulus was flashed only briefly at A and B. A more sensitive comparison method utilized the ability of an observer to judge the location—relative to the moving image—of a test line flashed instantaneously during the movement (location judgment). Location judgments are different for real and apparent motion when the motion is slow, of large amplitude, or the stimulus is intense, i.e., for those conditions which favor discrimination of the motion phase. Location judgments are identical for very small real and apparent motions (e.g., 10′) even when the dark interval exceeds 100 msec. For large, quick movements, at the high speeds which correspond to the speeds of image sweeps produced by saccadic eye movements, real and apparent motions also are perceived similarly, i.e., the motion phase is an ineffective stimulus. This implies that the failure to note the blur (motion phase) during saccadic eye movements is not caused by the eye movement *per se* but is a general characteristic of the perception of rapid image motion. (13 min.)

Eye movements and their role in visual and cognitive processes
E. Kowler, Editor
© 1990 Elsevier Science Publishers BV (Biomedical Division)

CHAPTER 7

Comparison of perception in the moving and stationary eye

George Sperling

Human Information Processing Laboratory, Department of Psychology and Center for Neural Sciences, New York University, New York, NY 10003, U.S.A.

1. Introduction

There are many different kinds of eye movement, each of which sweeps the image of the world across the retina in its distinctive way. Each kind of eye movement serves a unique function and in turn is served by a unique perceptual-motor process. Undoubtedly, the visual system has evolved special adaptations for this mode of operation. This chapter probes the question of to what extent these information-processing adaptations operate independently of the eye movements themselves.

Simulated eye movements: imposed motion. An important tool is the simulated eye movement: an image sequence which produces on a stationary retina precisely the same image motion that the moving eye would have produced. Comparing perception when image motion is produced by eye movements with perception under imposed motion offers substantial insights into both the mechanisms and the purposes of eye movements. To provide a frame of reference and to illustrate the general similarities between processing principles, all kinds of eye movements are considered briefly. The primary emphasis is on saccades because this is the domain the author has studied experimentally.

Restriction to eye-movement-induced image motion. Eye movements are usually measured in the laboratory with the body at rest and the head held stabilized by a 'biteboard' – an impression of the teeth of the observer which holds the observer's teeth, and thereby the head, in place. Of course, in normal viewing, the head and body move freely. The motion of images across the retina caused by uncompensated movements of the head and body is large compared to the image motion induced by some of the eye movements considered here. The nature and consequences of image motion produced by eye, head and body movements are considered in Ch. 3 of this volume (Steinman and Levinson). In the present chapter, only image motion caused by eye movements, principally saccadic eye movements, with the head and body held stationary is considered and compared with image motion produced by corresponding object movements. The descriptions of the eye movements themselves are very brief here because they are taken up in great detail in other chapters of this book.

2. Tremor

High-frequency tremor is a generic term applied to eye movements that are typically about 30–70 Hz, with amplitudes less than the width of a single cone, approx 0.5 min (Ratliff and Riggs, 1950; Yarbus, 1957). The blur circle under normal vision is about 2 min or more (Krauskopf, 1962; Westheimer and

Campbell, 1962), so the effects of tremor on the retinal image would be obscured by the much greater blur produced by the eye's optical imperfections. High-frequency tremor is probably irrelevant for normal vision. Occasional attempts to attribute some useful purpose to tremor, such as Yellott's (1987) proposal that tremor may act to smooth over irregularities in receptor spacing, have the aforementioned problem that the tremor is negligible compared to the much larger optical aberration.* Indeed, Krauskopf (1957, 1960) imposed tremor frequencies on retinally stabilized images and found that they did not improve the visibility of his test stimulus (a single line); in some instances imposed high-frequency motions were detrimental. Based on these measurements, I would predict that if normal tremor could suddenly be removed from vision, the change could probably not be noticed even in the fovea under psychophysical viewing conditions. Elsewhere in the visual field, or in the fovea under natural viewing with unrestrained head and body movements adding to retinal image motion, high-frequency tremor would seem to be far below the threshold of visibility.

3. Slow control movements

Slow control refers to the involuntary smooth motions of the eye that occur during steady fixation on a stationary target. A typical velocity for slow control movements, when the head is stabilized, is about 5–10 arc min per s (Ratliff and Riggs, 1950; Steinman et al., 1973), and a typical oscillatory frequency is about 2–3 Hz. Slow control movements may or may not be interrupted by small saccades, and the saccades may move the eye nearer or further from its intended fixation (see Ch. 1 of this volume for a more detailed review).

Are slow drift movements important for vision? When slow control movements and saccades are removed in stabilized vision, the image fades within several seconds. Visibility is restored to a stabilized image by imposing slow image oscillations. For optimal restoration of visibility, velocities higher than those typically observed in biteboard viewing are required (see Ch. 3 of this volume).

There are two issues here: (1) the role of drift image-motion in visibility, and (2) the appearance of movement in drifting images. I will consider first the appearance of movement in drifting images. Suppose that image drift were due to imperfect oculomotor control. Then, retinal drift would not be accompanied by signals of intentional motor movement; it would be residual image instability that was uncompensated by motor movement. Suppose also that proprioceptive information is unimportant when the eye is maintaining stable fixation. Then, if image drift were to be recorded from a subject and later produced as an imposed signal on a stabilized retina, the subject would have no way of discriminating the original drift due to image instability from the imposed motion. That is, image drift resulting from resolution failures of the oculomotor system logically cannot be discriminated from the same image drift imposed on a stabilized retina. Imposed drift will be discriminably different from natural drift when the amplitude of the imposed drift is artificially increased to be greater than natural drift. Just how much increase of artificial over natural drift is necessary for discrimination is not known. And we do not know to what extent typical drift movements, natural or imposed, produce apparent motion. This problem needs experimental study.

4. Slow drift with head free-moving

Not all head movements are intentional. Even when trying to hold the head as still as possible, as for example in walking, the head inevitably oscillates. The best possible compensation for retinal image slip with small head movements leaves a

---

* The suggestion that small eye movements might somehow overcome image perturbations induced by receptor irregularity, i.e., by higher visual centers assuming that the retinal receptors are embedded in a regular grid when they are not, encounters, additionally, a profound logical problem because receptors are typically as informative when they are spaced irregularly as regularly (Maloney, 1988, 1990; Yellott, 1987). The role of eye movements in correcting perception at a larger scale is considered later.

residual, uncompensated image slip of about 0.5 deg per s (Skavenski et al., 1979); with modest voluntary head rotation the image slip increases 10-fold to 5 deg per s (Steinman and Collewijn, 1980; Steinman and Levinson, Ch. 3 of this volume). In carefully controlled experimental situations, when motion of the head is induced by rotating the subject in a chair, the eye movements are invariably imperfect, and the proportion of compensation for head movement depends on the amplitude and frequency of the head movement (Skavenski et al., 1979). These authors found that the gain of compensatory movement decreased as the amplitude of oscillation decreased, and suggested an automatic adjustment of gain sufficient to maintain clear vision.

Despite the large image slip as the head moves around, the world does not appear to move, except in extreme situations. Remarkably, acuity for gratings hardly suffers: there is a slight decline in contrast sensitivy at high spatial frequencies and a slight improvement at spatial frequencies below 5 cycles/deg (Steinman et al., 1985).

When an image on the eye is stabilized, and image motions which mimic the large motions of normal unstabilized viewing are then imposed on this image, what does it look like? And how does the image movement affect acuity? Again, this experiment has not been carried out, although it seems obvious that the image would appear to move around. The effect of imposed motion on acuity has been studied only with very simple procedures. Kelly (1979) tested contrast sensitivity for sine gratings in stabilized vision with imposed constant image velocities, and found large acuity changes dependent on imposed velocity: a great decline in acuity at high frequency of imposed image movement, a small improvement at low frequencies. Steinman et al. (1985) tested acuity under comparable conditions of natural image motion in the same range of velocities and found smaller acuity losses. In Steinman et al.'s procedure, the image moved back and forth as the subjects moved their heads. In Kelly's procedure, the image moved at a constant velocity for several seconds before the subject responded. If Kelly's results with prolonged viewing of constant image velocities generalized to back-and-forth image motions, then we would have to conclude that imposed image motion is harmful to grating acuity over a range of image velocities that does not lead to acuity loss in natural viewing (see Ch. 3).

5. Smooth pursuit

Smooth pursuit refers to the smooth following of external image movement. Whether there is a significant distinction between the oculomotor subsystem responsible for following external image motion and the oculomotor subsystem that follows intrinsically caused image motion (produced, for example, by head or body movements) has been debated for many years. The velocity of smooth pursuit can be remarkably high, up to or exceeding 100 deg/s for large-amplitude motions (Collewijn et al., 1985; Meyer et al., 1985). The gain of smooth pursuit depends on many factors: notably the pattern of motion (waveform, frequency, amplitude, velocity of constant velocity motion, etc.) and on past history. The luminance contrast of the moving stimulus pattern seems not to be critical (Haegerstrom-Portnoy and Brown, 1979; Winterson and Steinman, 1978).

5.1. Localization in smooth pursuit

Flashed targets. A flashed target seen during smooth pursuit is very accurately localized relative to the body (Hansen, 1979). Untracked objects seen during pursuit are also accurately localized. Taken together, Hansen's results establish that eye position is accurately known during smooth pursuit, and the knowledge of eye position is available to perceptual judgements relative to body position. However, the extent to which this extra-retinal knowledge is available to visual judgements of the relative positions of targets flashed during smooth pursuit is less clear (see Ch. 5 of this volume). The extent to which flash localization during real pursuit differs from localization during simulated pursuit is not known (cf. sections on spatial localization during saccades and simulated saccades.)

Reconstruction of the trajectories of moving objects. Suppose that a moving dot describes a perfect circle. When the eye is fixated, the circular trajectory is perceived veridically (correctly). During linear smooth pursuit of another target, the retinal projection of the circle becomes distorted. The perceptual system for computing localization of the eye relative to the body only partially solves this distortion problem. That is, the perceived path is a composite of the distorted retinal path and the true circular path in external space. (See the review by Mack, 1986, and Chs. 5 and 6 for further discussions of these illusions.) The issue of how spatiotemporal relations between stimuli that occur during eye movements might be reconstructed will be reconsidered in the section on saccades.

5.2. Simulated pursuit movements

Acuity. Brian Murphy (1978) produced, in stationary eyes, image velocities that were the same as the image slip velocities previously measured during pursuit movements. He measured contrast sensitivity for a 5 cycles/deg grating in both conditions and found no difference. Velocities above 2 deg/s produced equivalent acuity losses in both viewing conditions. Kelly's (1979) data cited above appear also to be related here, and to yield a conflicting conclusion.

5.3. Attention during smooth pursuit: search task

From many experiments (e.g. Dodge and Fox, 1928; Dubois and Collewijn, 1979; Kowler et al., 1984) we know that subjects can selectively choose which one of several retinal stimuli to track. Even when retinal position is controlled, the tracking instruction determines what is tracked. The question Khurana and Kowler (1987) sought to answer was: can a subject track one stimulus while attending to another?

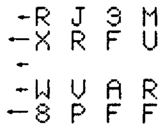


Fig. 1. Example of a display used by Khurana and Kowler (1987) Four rows of characters are visible at once. The arrows indicate the relative speeds of motion to the left. The subject is instructed to track an (invisible) point between the rows at the speed of one of the rows. The array contains two numerals among the letters: one in a fast row and one in a slow row. The subject's task is to report both numerals.

The subjects in Khurana and Kowler's (1987) experiments tracked a moving 4×4 letter array with smooth-pursuit eye movements. During the movement interval, all the characters of the array were briefly changed, with two of the former letters being replaced by numerals; the subjects' task was to detect these target numerals. In various procedures, the odd rows (1 and 3) were moved at twice or at 1/2 the velocity of the even rows (Fig. 1). Two targets occurred: one target in the even rows, another in the odd rows. The subject was instructed to report both targets on every trial. On different trials, the subject was instructed to smoothly pusue either the even or the odd rows, always with fixation in the middle of the array.

The results of this procedure showed that the subject reported the letters in the tracked rows better than the untracked rows regardless of the actual retinal slip (because the retinal velocities were too low to degrade performance). That is, visual attention was naturally linked to the pursuit attempt.

In a control experiment, tracking and attention instructions were manipulated separately. Subjects were asked to smoothly pursue one set of rows while attending to the other. All the conditions taken together provide a cross-design in which the positively correlated factors of the main experimental condition (row-to-be-attended and row-to-be-tracked) are negatively correlated in the control condition. Thus, we can estimate the effect of the two separable independent variables (tracking instruction, attention instruction) upon the two dependent variables (tracking accuracy, search accuracy).

The results showed that tracking of pursued but unattended rows was slightly worse than tracking of these same rows when they were attended (attention instructions only slightly affect tracking). Search performance on the attended but untracked rows was slightly better than search in the unattended untracked rows, but never approached the performance on tracked, unattended rows, again, regardless of retinal slip (attention instructions only slightly affect search). In other words, the tracking instruction, not the attention instruction, controls the accuracy of visual search.

Attention is inextricably linked to tracking. The following picture emerges of the role of attention in tracking: tracking instructions have big effects, attention instructions have only small additional effects. For a given rate of retinal slip, the only way that tracking per se can influence search accuracy is indirectly through attention. That an attention-instruction has almost no effect independently of tracking-instruction implies that attention is inextricably linked to smooth pursuit.* Tracking a row depends on attentional selection and only an insignificant attentional residue remains to be assigned elsewhere.

In the imposed-motion control procedure for Khurana and Kowler's experiment, the eye remains stationary as the letter rows drift arross the field. The subject's attempt to fixate a stationary point while attending to one pair of moving rows leads either to a loss of fixation as the eye drifts in the movement direction or to a loss of search accuracy in the moving rows. Thus, the data obtained with eye movements and imposed movements are essentially equivalent. It follows that the attentional resources needed to maintain the eye fixated on a stationary point are not essentially different from those needed to maintain smooth pursuit at the image velocities Khurana and Kowler used. This result lends support to the view that fixation and smooth pursuit are governed by the same mechanisms (Nachmias, 1961).

6. Saccades

Saccades are voluntary, quick, ballistic eye movements that take the eye from one fixation point to the next. Saccades range in extent from several minutes of arc to more than 70 degrees. A typical saccade of 4 degrees is well described as a ramp function of time in which the eye travels from its initial to its final position in about 15–20 ms, and then remains relatively still in the final position for 200 ms or longer. During active search of a display or scene, saccades may occur at a rate of 4 per second, but slower saccade rates are more typical. The effect of saccades is to convert the input to the visual system into a sequence of up to 3 or 4 relatively stationary images per second, with rapid transitions between the images.

There are many provocative issues concerning saccades. How is it that the world seems to remain stationary during a saccade even though the saccade-like image sequence would be perceived as a vigorous jump if it were imposed on a stationary retina. The visual image of the world is smeared across the retina during saccades yet, on the whole, we are unaware of seeing such a smear. Is this because visual sensitivity is reduced during saccades? Are there special perceptual mechanisms designed to utilize and link information acquired during successive saccades? For example, do saccades initiate visual processing episodes? And are relative spatial coordinates defined by saccadic eye movements or by head movements inherently more useful than coordinates defined equally accurately by image movements or by other more indirect means? Is attention inextricably linked to saccades (as it is to smooth movements) or can attention move oppositely to a saccade? In what sense are saccades an optimal solution to the ecological problem confronting a visual system?

Some of these issues have been with us almost since saccades were first described by Javal in 1878. For example, with respect to the issue of vision

---

* To have reached the conclusion that subjects *could not* disassociate attention from tracking (versus simply that they *habitually did not* disassociate attention from tracking) it was essential that Khurana and Kowler's subjects actually received training – feedback as to the correctness of the responses – and despite the training failed to learn to perform both tasks.

during saccades, an early demonstration is due to Woodworth (1906). He executed a saccade from one side of a rotating wheel to the other and observed that he was able to see clearly the spokes that happened to be traveling at the same rate as his eye. Thereby Woodworth demonstrated his capacity for sharp vision during a saccade. After a review of similar experiments in his textbook Experimental Psychology, he wrote *"given the same retinal stimulation, it makes no difference whether it is the eyes or the external field that moves"* (Woodworth, 1938, p. 593, italics in the original). Woodworth's conclusion was so intuitively unsatisfactory that the issue of visual suppression during saccades has been reexamined many times, and we examine it once again.

6.1. Is vision turned off during saccades?

The rumor that vision is dead during saccades is grossly exaggerated. Some time ago, eager to observe such an effect, I put together an apparatus for studies of vision during saccades. A gas discharge lamp illuminated a thin slit before, during, or just after saccades. The illumination flash was very brief, contained within 40 microseconds, so there would be no significant retinal smear of the slit during a saccade. Before conducting formal experiments, I wanted to check whether the apparatus actually triggered flashes during saccades. I quickly discovered that, in viewing the slit against a dark background, it was not possible to ascertain whether a flash had occurred during a saccade simply by noting the appearance of the flash. A flash that occurred during a saccade did not look any different from a flash that occurred before or after. Obviously, if there were a change in visual sensitivity during saccades, it was too small and too subtle to make an obvious difference in the appearance of a suprathreshold flash. Nevertheless, there have been many reports of raised thresholds for stimuli presented during saccades (for a review, see Volkmann, 1986). How can this be?

The question of whether visibility is altered during a saccadic movement must be resolved by the proper control experiments. In the control experiment, it is essential to produce on the stationary eye precisely the same sequence of stimuli that the saccading eye produces for itself when its threshold is tested during saccades. There are two reasons for this requirement. First, the movement of fixation points and other fixed stimuli across the retina during a saccade can affect the threshold for a dim test field, and the amount of this visual masking must be measured in the control experiment. Second, the apparent location of a stimulus flashed during, or slightly before or after a saccade, will not generally correspond precisely to its objective location. From the observer's point of view, there are locational *uncertainties*, indeed, even locational illusions, in which the test flash appears to have occurred at an unexpected location. Because, as is demonstrated below, there are many similarities in spatial localization during saccades and during the equivalant imposed image motion, control experiments may provide reasonable estimates for locational uncertainty and locational illusions as well as for incidental masking. We defer the issue of altered visibility during saccades until after considering localization.

6.2. Spatial localization during saccades

There are now many studies of the localization (in which observers indicate the apparent location) of test stimuli that are flashed briefly during saccades. I describe studies (Sperling and Speelman, 1964, 1965; Sperling, 1966) that have not been fully reported before in which data from appropriate nonsaccade control stimuli are available. Subsequently, related experiments are considered in the light of these results.

6.2.1. Measuring and predicting localization errors

Objective and subjective foveal trajectories. In Sperling and Speelman's (1965) procedure, subjects view a display containing five marker spots (2×3 min), separated from each other by two degrees (Fig. 2a). These spots are called −2, −1, +1, +2. The observer is instructed to fixate spot −1, and then, upon an agreed-upon signal (a brief dimming of the spots), to fixate spot +1. About 200–250 ms after the signal, the observer's eye will execute a saccadic movement from position −1 to the neighborhood of position +1 (Fig. 2d). Observers' 4-degree saccades are quite individualistic; some observers have considerable overshoot; and all observers show corrective saccades after about 0.2 s (Fig. 2e). The objective trajectory of the fovea as a function of time $x_0(t)$ describes an observer's objective eye movement – the physical position of the fovea as a function of time referred to an external coordinate system.

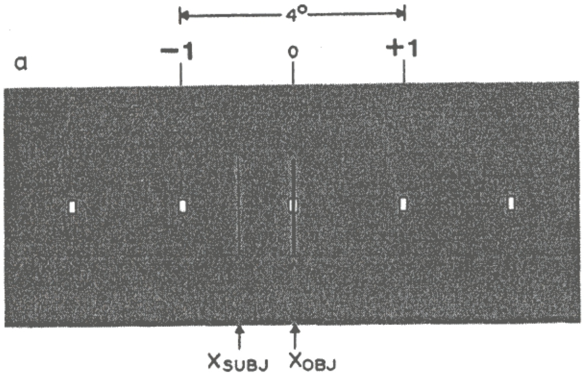
Suppose that at some time during the saccade, a flash of light occurs and that it falls directly on the fovea. We ask the observer where this flash appears to fall relative to the external −2 to +2 coordinate system defined by the five spots of light. Obviously, when the flash occurs long before initiation of the movement, it is subjectively localized at location −1 (the initial fixation point); when it occurs long after the movement, it is localized at position +1 (the post-movement fixation). The subjective location assigned to a flash of light that strikes the fovea changes as a function of time; this function is called the subjective foveal trajectory $x_s(t)$, and it is measured in the same coordinates as the objective trajectory.

If it happened that the objective and subjective foveal trajectories were exactly equal $[x_0(t) = x_s(t)]$ then an observer would never mislocalize a foveal flash – the observer would always report its position correctly. In general, however, the observer makes localization errors for flashes that occur during, or shortly before and after saccades. This indicates that the objective and subjective foveal trajectories are not identical. For 4-deg eye movements, the subjective trajectory is usually not quite as quick as the objective trajectory.

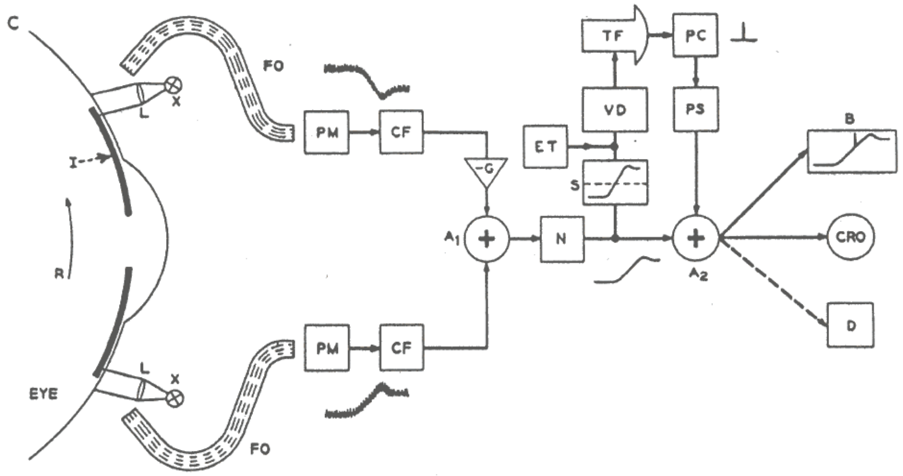
Procedure. Some further details of the procedure are relevant. Subjects viewed the display with their heads fixed to a dental impression. Horizontal eye position was monitored by a limbus monitor (Fig. 2b,c). Initially, the monitor was dynamically calibrated with an artificial eye. During the experiment, it was calibrated between successive eye-movement trials. Dynamic eye position was resolvable to an accuracy of about 3 min (for 4-degree saccades) but was recorded for subsequent analysis only to an accuracy of 12 min because, in the limbus monitor, DC accuracy is not as good as dynamic accuracy. Upon a 10-ms interruption of the display (which appeared as a dark flash), subjects were instructed to shift their fixation as quickly as possible from spot −1 to spot +1 (Fig. 2d). A thin vertical test line was flashed during the display and subjects were instructed to report its position to an accuracy of 0.1 unit of the display distance. For example, if the test line appeared to strike midway between spots 0 and 1, subjects were to report '0.5'. Preliminary experiments to teach and test the use of this method of report (during fixation) had shown that subjects could report positions to within ± 0.1 unit. The apparatus could trigger a flash when the eyes crossed the midpoint of the display or at any later time. To obtain test flashes that occur before eye movements, the apparatus is set to trigger a flash at a predetermined delay from the warning stimulus. Trial-to-trial variations in this delay, together with subject variability in saccadic reaction time, yield a distribution of trials with times of occurrence before, during, and after the midpoint of the eye movement is obtained.

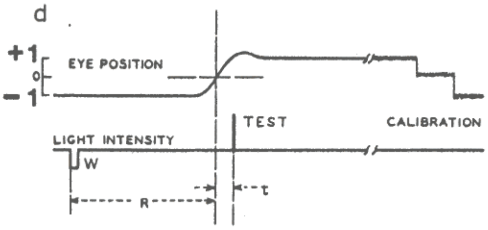
As a practical matter, in these experiments, all flashes occurred at precisely the same physical location, and hence at different retinal locations. The subjective foveal localization was computed from nonfoveal flashes on the assumption of a rigid translation of the central 4 deg of the perceptual coordinate system. (This assumption, and experiments by O'Regan (1984) testing it, are considered in detail later.) As a matter of convention, time is indicated relative to the moment at which the eye crosses the midpoint of the display. Four-degree eye movements typically take less than 20 ms; therefore the movement times are within ± 10 ms of zero (Fig. 2e).

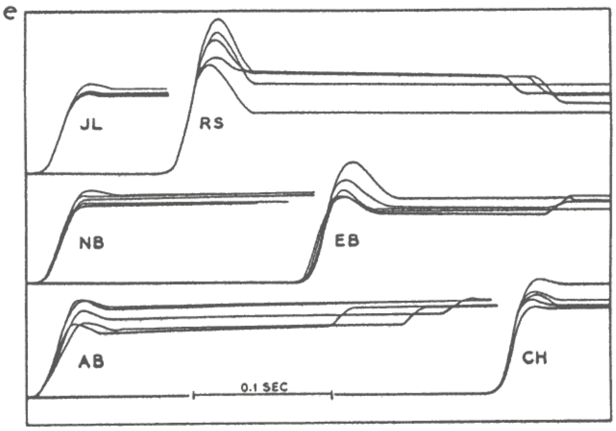
Localization errors. Some data from an eye movement experiment in which the test flash was posi-


a
4°
−1
0
+1
X_SUBJ
X_OBJ


b


C
FO
L
X
I
R
EYE
L
X
FO
PM
CF
PM
CF
−G
A1
N
ET
S
TF
PC
VD
PS
B
A2
CRO
D


d
+1
0
−1
EYE POSITION
TEST
CALIBRATION
LIGHT INTENSITY
W
R
τ


e
JL
RS
NB
EB
AB
CH
0.1 SEC

tioned always to occur directly superimposed on the middle marker are shown in the leftmost column of Fig. 3. In this procedure, a correct report by the subject would always be '0.0' and would be indicated as 0 in the graph. This setup was chosen so that correct localization would be obvious – the test flash would appear directly superimposed on the center marker; its illusory appearance anywhere else clearly represented an error of localization. The abscissa of Fig. 3 indicates the time relative to the instant at which the eye crossed the middle marker. When the subject reports that the test flash appears displaced towards the final marker position, the error is indicated by an ordinate value greater than zero. For example, the greater-than-zero errors by subject 3 indicate that the perceptual spatial coordinates of the retina had already started to change to their new values, even before the eye had begun to move. Values below zero indicate that the retinal coordinates lag behind the physical movement.

Not all eye movements are precisely correct; some fall short of the intended mark and are corrected by a subsequent saccade. The data in the left column of Fig. 3 include all eye movements, those which reached their intended mark and those which did not. The advantage of mislocation errors as a dependent variable is that mislocation errors do not depend critically on the extent of the movement. It is reasonable to aggregate mislocation data from movements of somewhat different extents.

In terms of a computational theory to account for mislocation errors, the extent of the movement becomes a parameter, and for this purpose it is useful to restrict consideration to 4-deg eye movements which begin and end within 0.5 deg of the initial and final fixation markers. The data for each subject that describe the recorded eye positions as a function of time $x_o(t)$ can be reasonably well characterized by a 3-segment straight line: horizontal at position −1 until the start of the movement, linear slope (constant velocity) during the eye movement, and again horizontal with constant slope at the conclusion of the movement. Thereby, only two parameters are estimated, e.g., the starting time and the duration of a trajectory. These data are illustrated in the right column of Fig. 3.

The subjective foveal location (the location in space to which a test flash striking the fovea would be referred) is derived by adding the localization error $e(t)$ recorded in the experiment to the objective foveal location:

$$x_s(t) - x_o(t) + e(t)$$

Like objective foveal locations, subjective foveal locations $x_s(t)$ can be characterized by a 3-segment function. Fig. 3, right column, shows the observed objective and subjective eye position data for six subjects together with the 3-segment trajectories that maximize temporal prediction (minimize the

Fig. 2. (a) The display viewed by Sperling and Speelman's subjects in the saccadic movement experiments. Five bright spots of light were visible in a dark field. Initially, subjects fixed the spot labeled −1; upon a signal, they saccaded to the spot labeled +1. (Left/right was reversed from session to session.) Sometime before, during, or after the saccade, a thin bar centered on 'O' was illuminated by a stroboscopic flash. The subject's task was to report the apparent location of the bar relative to coordinates defined by the illuminated spots. (b) A limbus monitor illuminated rectangular spots at the iris/sclera border, and measured the amount of reflected light to indicate the eye's horizontal position. (c) The limbus monitor and the linked display system. R indicates the direction of saccadic rotation; I is the iris; X is a light source focussed on the iris/sclera border by a lens L; FO is a fiber-optic bundle that collects the reflected light and carries it to a photomultiplier detector PM; CF is an electronic (cathode follower) amplifier; G is a variable gain chosen to equate the amplitude of the left and right signals; A1 adds the right and the inverted left signals to yield an estimate of horizontal eye position; N is a low-pass linear filter which removes high-frequency noise; S is the threshold location in the saccade at which trigger is initiated; VD is a variable delay; TF is the stroboscopic flash gun that illuminates the target; PC and PS, respectively, are photodetectors which monitor the target and stimulus displays; A2 adds the display information to the position information to produce three records of the events of the trial; B, an ink-on-paper record; CRO, a CRT display; and D, a digital record on magnetic tape. (d) The sequence of events on a trial. A momentary darkening of the background spots is the signal to initiate the saccade; the test flash occurs at time t; and a calibration sequence of fixations on spots +1, 0 and −1 occurs between consecutive trials. The midpoint of the intended saccade is the point $x=0$, $y=0$, $t=0$. (e) Eye movement records obtained for six subjects. Five traces are superimposed in each record.

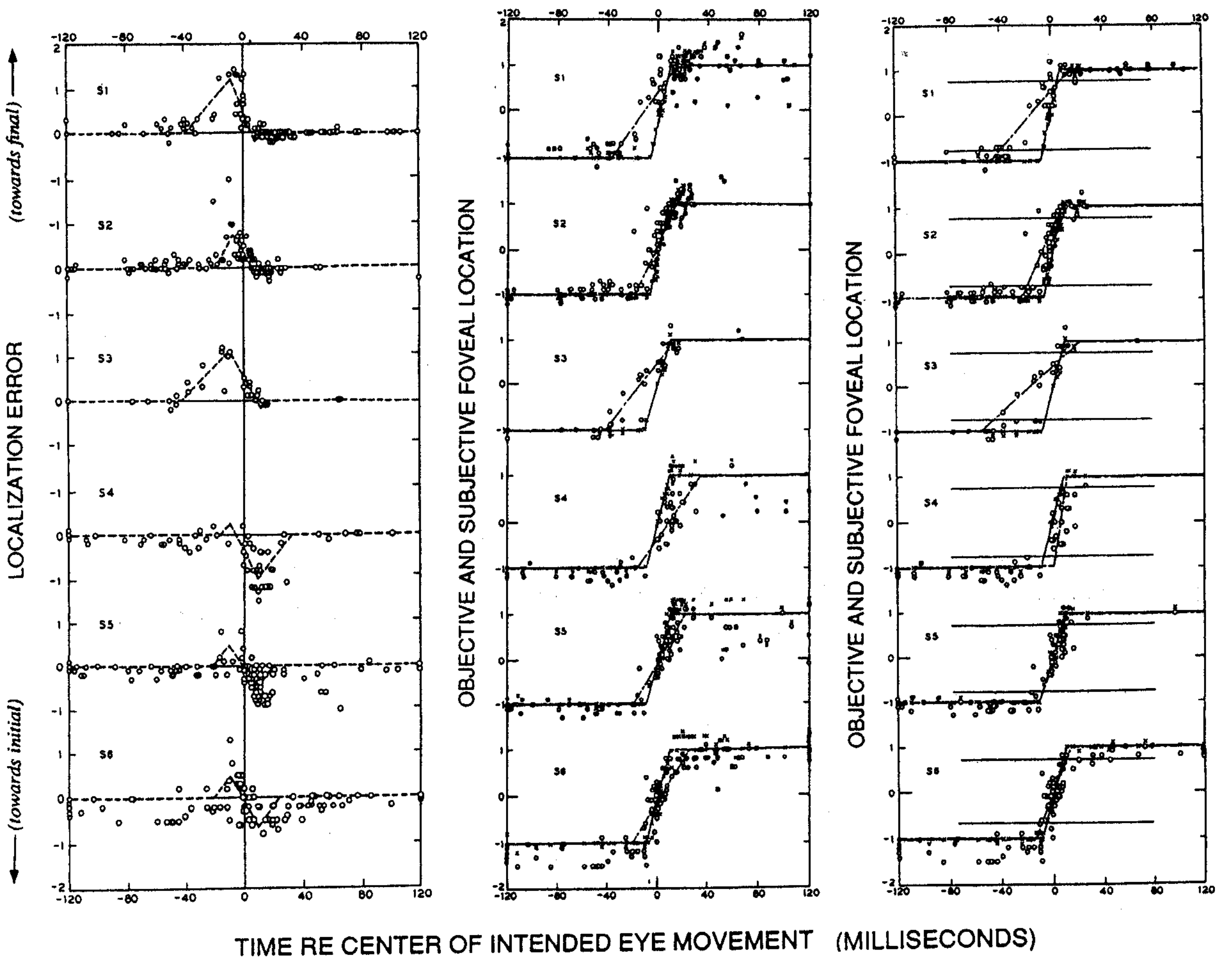


Fig. 3. Left. Errors in localization of a flash that occurs at location 0 as a function of its time of occurrence relative to the midpoint of the saccade. The ordinate is in display units: +1 represents a mislocalization of the target at the intended final location; −1 represents a mislocalization at the initial location. Each point represents one localization judgement. The dashed lines are the difference between the best-fitting objective and subjective eye trajectories shown in center. Right. Objective and subjective foveal location as a function of time relative to the midpoint of an intended 4-degree saccade. Data from all 'good' saccades that began and ended within 0.5 deg of the intended starting and final fixations are shown for six subjects. Each trial yields a paired objective foveal location (*) and subjective foveal location (open circle). The solid lines and dashed sloping lines minimize the squared horizontal distance from the objective and subjective location data, respectively, to the line within the middle three degrees of movement. Center. Same as right column except that all eye movements are included, and the three-segment functions minimize the vertical distance of the date to the function.

root mean square (rms) horizontal distances of the data to the trajectory) in the middle 3 degrees of the 4-degree movements. This treatment of the data is appropriate for the next section, 'A purely temporal analysis of saccadic localization'.

The center column of Fig. 3 illustrates objective and subjective foveal locations for all the attempted 4-degree saccades. These data include quite a few saccades that were substantially shorter and some that were longer than four degrees. The 3-segment functions which minimize the vertical rms distance of the data to the function are shown for both objective and subjective foveal locations. Strictly speaking, these objective (and subjective) foveal trajectories apply only to a homogeneous set of eye movements (e.g., movements between 3.9 and 4.1 degrees). However, the differences between objective and subjective trajectories, shown as dashed lines in the left column of Fig. 3, can be used to estimate mislocation errors even for a more heterogeneous collection of eye movements because saccadic extent cancels in the process of subtracting the objective from the subjective trajectory.

The estimated durations of the subjects' eye movements (objective foveal trajectories) vary from 16.4 to 20.8 ms. The durations of the optimized subjective foveal trajectories (those which best predict localization) vary from 29 to 56 ms (mean = 45 ms). There are considerable differences in the invidividual subjective trajectories; five subjects start the subjective movement before the objective movement, and one begins later.

The difference between the straight-line trajectory estimations of the observed objective and subjective foveal trajectories is the predicted localization error. These predictions are indicated by the dashed lines in the left column of Fig. 3. The objective-subjective trajectory difference gives a reasonable account of localization errors. Section 6.3 describes a saccade simulator: the data of Fig. 3 obtained with actual eye movements will be compared to data obtained with simulated eye movements. First, however, we consider an alternative analysis of the localization judgements.

6.2.2. A purely temporal analysis of saccadic localization

In the preceding section, errors in spatial localization were analysed in terms of the difference between the objective and subjective trajectories of the eye. Because localization errors are naturally measured as spatial localization errors, the spatial analysis was appropriate as an initial analysis. In this section, localization errors are considered not as spatial errors but as purely temporal errors. The reason is that spatial localization with stationary stimuli is extremely good, but, during rapid movements, small temporal errors would produce large spatial errors. Therefore, it seems most likely that the errors in spatial localization during saccades result indirectly from small temporal errors in when the saccade is estimated to have occurred relative to the test flash. Again, the temporal analysis is in terms of a mismatch between the objective and subjective trajectories of the eye but, in the purely temporal analysis, the trajectories are chosen to minimize the temporal prediction error (horizontal dimension in Fig. 3), not the spatial prediction error (vertical dimension in Fig. 3).

Temporally optimized trajectories. As was described above, ignoring overshoot, 4-deg saccadic eye movements are well described by a 3-segment function, a constant initial segment, a linear ramp, and a constant final segment. The duration of the movement, the ramp segment, is 18 ± 2 ms, and is constant for a particular subject.

The subjective foveal trajectories (derived from localization judgements) also are well fitted by three-segment functions. Earlier, in the left and center columns of Fig. 3, these functions were chosen to minimize the localization error – i.e., to minimize the vertical distance between the data points and the function on a graph of foveal trajectory versus time such as Fig. 3, center. Here, we are concerned with the hypothesis that all aspects of localization can be interpreted in terms of (a) temporal distortion of the movement trajectory and (b) irreducible temporal uncertainty (residual error). This requires estimating functions to maximize the goodness of temporal predictions, i.e., to minimize the horizontal distance between predictions and data.

Making horizontal (temporal) predictions is technically more difficult than vertical (spatial) predictions. Horizontal estimations can only be made in the middle sections of plots such as Fig. 3 (right). Basically, this requires selecting only good eye movements, those which finish within ± 12 min of the intended location, and making the estimates only at points between 0.25 and 0.75 of total traverse. This procedure considerably restricts the amount of data available; however, the statistics about objective and subjective location that we (Sperling and Speelman, 1965) computed for this subset of 'good movements' were, in fact, representative of the whole.

For three of six subjects (S4–6, Fig. 3, right), the duration of temporally optimized subjective trajectories was statistically within the range of objective saccade trajectory durations (11, 20, 27 ms). For the other three subjects (S1–3), the durations of subjective saccades (33, 60, 76 ms) were incontestably longer than objective saccades. Additionally, for these subjects, the midpoint of the subjective movement preceded the midpoint of the objective movement by 6–17 ms. Because of the overall similarity of localization judgements for real and simulated saccades for all subjects, the conclusion is that different subjects perceive rapid *visual* motion somewhat differently, and consequently make somewhat different localization judgements. (See, for comparison, the different time courses of visual persistence measured in different subjects by Weichselgartner and Sperling, 1985).

In addition to characterizing a subjective movement trajectory in terms of its duration, there is trial-to-trial variability in localization judgements. This variability can be conceptualized as resulting either from positional uncertainty or from temporal uncertainty. Positional resolution, as measured in control experiments, was extremely good in flash localization, with errors seldom exceeding ± 0.1 of the distance between markers. Therefore, we consider here to what extent localization errors can be modeled simply by temporal uncertainty in when the saccadic or simulated saccadic movement occurred.

Each objective eye position (Fig. 3, right) in the midrange between 0.25 and 0.75 of the total saccadic extent was interpreted in terms of the temporal (horizontal) deviation of the data point from the best-fitting trajectory. The root mean square deviation (rms, σ) of objective eye positions from the best-fitting objective eye trajectories varied only from 0.93 to 1.42 ms (for six subjects). Such small variations indicate that real eye movements follow a remarkably stereotypical time course. For the subjective foveal trajectories, the corresponding rms errors ranged from 4.0 to 8.2 ms, again a surprisingly small error and a small range of intersubject variation. There was no tendency for errors to vary with the duration of the subjective trajectory.

The purely temporal theory derived from the assumption that spatial localization errors in saccades are ultimately caused by temporal errors in the representation of the saccade relative to the test flash. This general principle led to the following specific conclusions concerning localization errors of a brief flash that occurred during a 4-deg saccadic eye movement with the visual reference stimuli continuously present:

(1) Flash-localization judgements in the presence of continuously present visual reference stimuli are determined primarily by visual factors.

(2) Half the subjects perceive the saccadic movement approximately correctly, and half perceive the movement to occur slightly too soon, and to be significantly longer than it actually is.

(3) Additionally, there is random temporal uncertainty with an rms value ranging from 4 to 8 ms (over subjects).

The irreducible *random* temporal errors in visual localization are somewhat greater than the temporal errors that can be estimated from Hansen and Skavenski's (1977 and 1985) motor localization tasks, which have the best experimentally observed temporal resolution. The main difference, however, is that the visual/perceptual representation of the movement is elongated relative to the objective eye movement for half the subjects in the present experiments, whereas Hansen and Skavenski (1977) found that the nonvisual (motoric) representation of the saccade in their motor task was uniformly accurate.

6.3. Simulated saccades

6.3.1. Saccadic motion smear

An eye movement simulator. To examine to what extent the visual stimulus, independent of the motor system, determined the observed localization judgements, we have to produce on the stationary eye precisely the same visual stimulus that the sac-

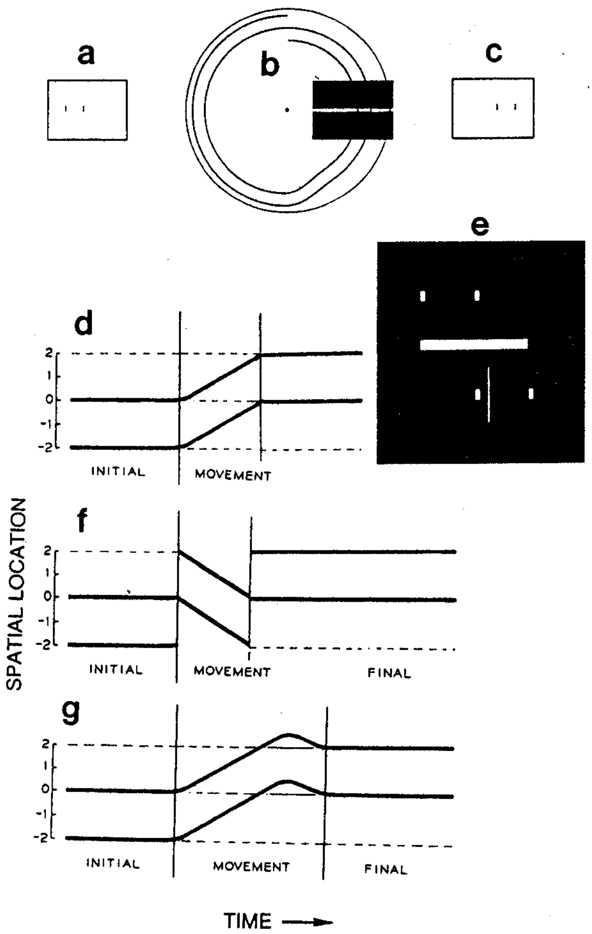


Fig. 4. Eye movement simulator: a mechanical device for generating saccadic images on a stationary eye. (a) The initial field. (b) The movement field. A large disk, rotating in the direction of the arrow, generates the moving component of the simulated saccade. The dark lines y1, y2 indicate translucent sections in the otherwise opaque disk, illuminated from behind. A masking partition M reveals only a narrow slit S to the observer. (c) The final field. (d) Representation of the position of spots y1 and y2 as a function of time for a linear saccade. The disk provides the moving field. A mirror tachistoscope, which illuminates only one field at a time, coordinates illumination of the movement field with the stationary initial and final fields. (e) The motion smear: a time-exposure photograph of the stimulus generated by the movement field. Also shown, markers in their initial and final positions, and the test flash. (f) A reversed eye movement. The direction of the motion segment is reversed relative to the initial and final fields. (g) A simulated saccadic trajectory with overshoot.

cadically moving eye produces. In the case of saccades, this is a formidable technical problem which was resolved as illustrated in Fig. 4. Again, the eye movement trajectory is composed of three parts: initial fixation, movement, and final fixation, produced in three fields of a tachistoscope. The initial stimulus is shown in Fig. 4a, the final fixation in Fig. 4c.

The moving stimulus was produced by a rotating a disk as shown in Fig. 4b. On an otherwise opaque disk, two transparent, approximately concentric, curves $c_1(\rho, \theta)$ and $c_2(\rho, \theta)$ are drawn. The disk spins continuously, is illuminated from behind, and is viewed through a narrow slit arranged along a horizontal radius. The observer sees two spots of light which move left or right as the radial distance ρ varies with θ. Almost any movement trajectory of the spots can be produced by appropriate choice of $c(\rho, \theta)$. When the disk spins at 6.3 rotations per second, the trajectory occupies 20 ms. Therefore, illumination of the moving field (Fig. 4b) has to be coordinated by elaborate temporal synchronization and optical superposition with illumination of the stationary initial and final fields (Fig. 4a and c).

A trial begins with the initial field displayed continuously. When the subject presses a key, at the first available rotation after 0.5 s, the initial field shuts off and the moving display turns on for 20 ms. After the movement section has passed, its illumination is shut off and the final field 3 is illuminated. In this setup, it was feasible to present only 2 of the 5 marker spots of the previous experiment, the −1 and +1 markers, corresponding to the initial and final fixations. A time-exposure photograph of the moving portion of the display is shown in Fig. 4e, as well as the initial and final fields. It illustrates the quite uniform motion smear produced by the simulated eye movement.

Finally, a Risley prism was inserted into the view path. By rotating the prism, the left/right orientation of the entire display could be reversed. By reversing the static initial and final positions and also reversing the entire display orientation (Fig. 4c), only the direction of movement remained reversed. Four conditions of movement trajectory were investigated: (a) normal motion trajectory (Fig. 4d), (b) reversed motion trajectory (Fig. 4f), (c) sampled motion trajectory – illumination of the moving field is turned off during the interval between initial and final fields – and (d) double reversed-direction sampled motion trajectory, i.e., this looks the same to the observer as the normal sampled motion trajectory. The temporal sequence of the normal initial and final fields is reversed, and the display is then reversed spatially with a Risley prism. This is a check for any undetected difference between initial and final fields that might affect the reversed motion trajectory. This apparatus was used to study continuous and sampled movements of various lengths and durations.

6.3.2. *The appearance of motion smear*

While the main purpose of the apparatus was to study spatial localization, I digress for a moment to consider the subjective appearance of the saccadically moving stimuli. The most surprising observation was that, even though the stimulus consisted of bright spots viewed against darkness, observers did not spontaneously discriminate the correct from the reversed movement trajectory when the imposed movements occupied 20 ms and the total distance traversed ranged from one to four degrees, according to the viewing distance. With the eye movement simulator, visual sensitivity to the various aspects of the retinal movement trajectory could be isolated. On alternate presentations, the illumination of the movement field was turned off, thereby eliminating the movement smear entirely and substituting 20 ms of darkness. Naive viewers did not spontaneously notice any difference between consecutive displays of continuous motion and sampled movement. Indeed, observers did not report a difference in the appearance of motion smear even when they were pressed, although many irrelevant aspects of the displays caught their attention.

When the difference between the normal-, reversed- and no-smear (sampled) displays is pointed out to viewers, they can notice a barely discriminable difference in the motion smear between continuous-movement and the sampled-movement trials but the direction-of-movement discrimination appears to be impossible. Of course, when the speed of the motion trajectory is slowed down by a factor of 10 or so, all the appropriate relations can easily be perceived.

Visual masking of motion smear. When the motion smear occurs alone (i.e., only Fig. 4b is shown and the initial and final fields (Fig. 4a and c) are turned off), the smear itself (Fig. 4e) is quite easy to detect. But the discrimination of motion direction in the smear remains difficult. MacKay (1970a), Campbell and Wurtz (1978) and Corfield et al. (1978) propose that the difficulty of detecting motion smear is due to visual masking by the visual stimulation that immediately precedes and follows the smear. In one experiment (Campbell and Wurtz, 1978), subjects initiated eye movements in the dark. During the eye movement, a light was turned on. When the light remained on only very briefly, subjects reported that the scene illuminated by the light was clearly visible and sharp (thereby reproducing once again the observation of clear vision during saccades). As the light remained on for 20 ms and longer during a long saccade, the scene appeared to become extremely blurred, much like the motion smear represented in Fig. 4e. On the other hand, if the light remained on for more than 40 ms *after* the saccade ended, the previous saccadic motion smear became invisible. Thus 40 ms of post-saccadic stimulation masked saccadic motion smear.

To study motion smear in the stationary eye, Corfield et al. (1978) represented saccadic motion smear by a stationary blank field, like that of Fig. 4e. They preceded and followed the blank field by different textured fields, principally sinusoid gratings and combinations of sinusoids. When the blank field was as brief as it would have been during normal saccadic eye movements, the blank field was not visible – it was completely masked by the preceding and following stimuli. While various parameters of masking were investigated, the process of visual masking itself was not elucidated in these experiments. However, whatever the masking process in the stationary eye may be, the experiments demonstrate that it is also sufficient to account for the invisibility of motion smear in the saccadically moving eye.

6.3.3. The effect of motion smear on spatial localization

Spatial localization during imposed saccade-like movements. The difficulty of observing motion smear during real and simulated saccades even under optimal conditions for its appearance (i.e., a scene consisting of bright spots on a dark background) suggests that motion smear would not contribute to other kinds of psychophysical judgements. Nevertheless, I (Sperling, 1966) used the saccadic motion simulator shown in Fig. 4 to investigate spatial localization. The motion trajectory on the retina and the psychophysical procedure were analogous to those of the saccadic spatial localization task described above in section 6.2.

The saccadic movement simulator was arranged to provide the linear saccadic movement stimulus illustrated in Fig. 4d. During the movement trajectory, a thin test line was flashed briefly, and the subject was asked to localize the flash relative to the position of moving spots at the instant of the flash. The localization judgement was similar to that illustrated in Fig. 2a, with the subject initially fixated on the spot labeled −1, except that the only other spot visibe was +1. The subject maintained fixation rather than moving his eyes, and the display moved quickly so that, after the movement, the spot +1 was at the fixation point.

The movement trajectory was a linear translation between initial and final positions which traversed the distance in 20 ms (Fig. 2d). In this experiment, the viewing distance was increased so that the total length of the movement trajectory was 95 min of visual angle. The movement was somewhat slower than a natural saccade and somewhat shorter than the saccades studied in the previous section. These experimental parameters were chosen to maximize the number of localization judgements between – rather than at – the end points in order to give the imposed trajectories the maximum opportunity to exert differential effects. Normal continuous movements, reversed movements (Fig. 4f) and sampled (no smear) movements were tested. The test line, rather than flashing at different retinal locations, as in the saccadic movement experiment, always occurred displaced slightly from the fixation point (the fovea) in the direction of the simulated movement (0.2 of the movement distance as shown in Fig. 4e).

The results can be described succinctly. No subject showed any significant difference between the normal and reversed movement conditions with respect to spatial localization of the test flash. In other words, the direction of the saccade-like image smear did not influence spatial localization judgements – they were determined by the pre- and post-movement fields.

There were minor localization differences between continuous-movement (normal or reversed) and sampled movement for some subjects and not for others. When there was a difference, it was a greater tendency in the sampled movement displays for the test flash to be localized at the initial or final positions, not in between. Data representing each type of performance are shown in Fig. 5. For example, S4 hardly ever localizes a flash at locations between −1 and 0 in the sampled control (top and bottom panels, Fig. 5), but does so frequently in both smear conditions (middle panels, Fig. 5).

Spatial localization during much slower-than-saccadic simulated movements. The saccadic simulator can be used to impose retinal motion at velocities that are higher or lower than saccadic velocities. Subjects viewed the moving stimuli while maintaining fixation on a stationary fixation point. In order that subjects did not correctly anticipate the image motion and move their eyes, the direction of motion was random from trial to trial. As in the case of movements at saccadic speeds, subjects were asked to judge the location of a brief flash relative to the moving coordinate system defined by the dots.

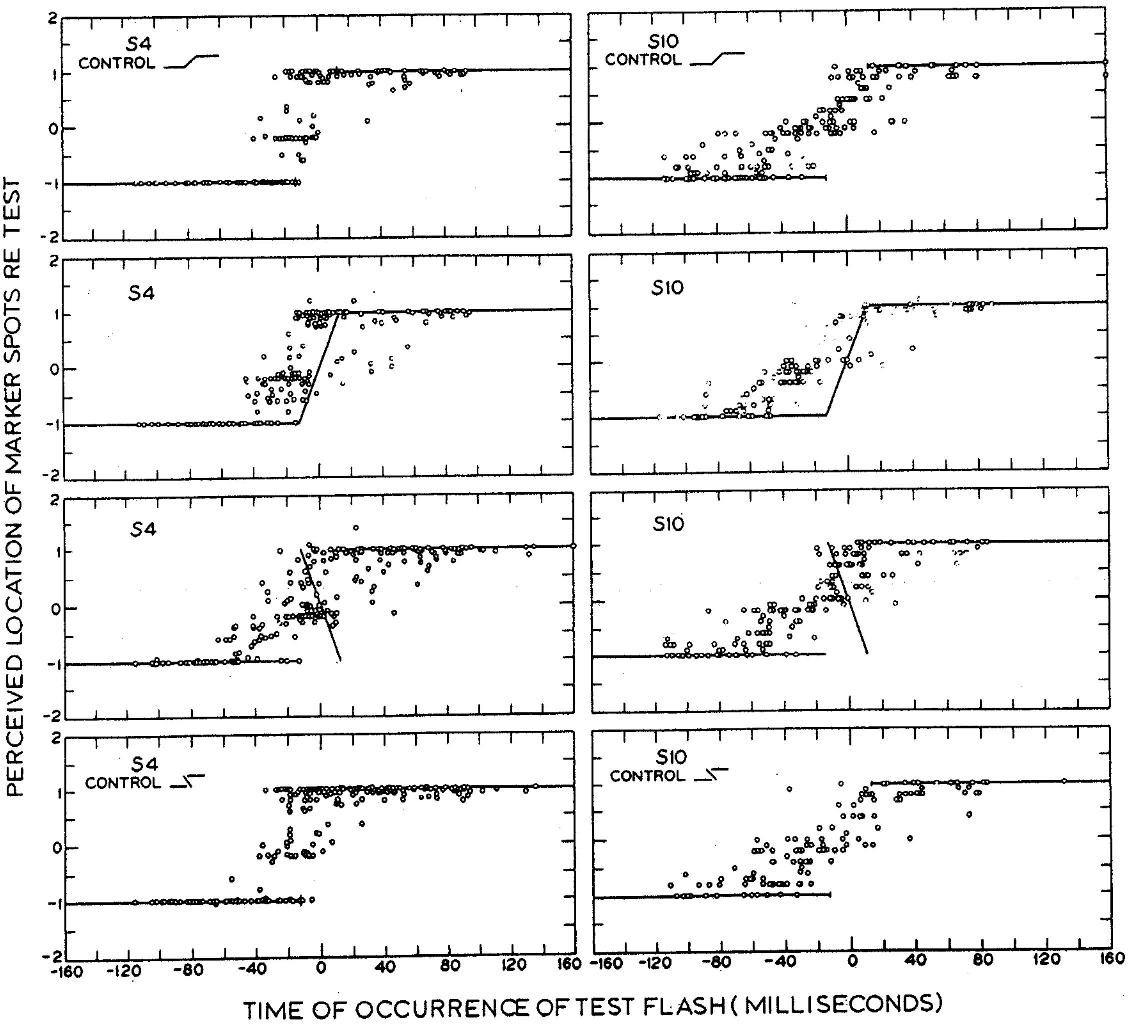


Fig. 5. Localization data from an experiment comparing simulated normal, reversed and sampled eye movements. The abscissa is time relative to the midpoint of the movement trajectory; the ordinate is the perceived location of the marker spots as computed from the judged relative location of a brief test flash. Solid lines indicate the actual location of the marker spots. Data from two subjects are shown; each point represents a single judgement. In the sampled movement conditions ('controls'), all illumination was turned off during the 'movement' section of the display. In the top control condition, the initial and final marker spots were those used for the sampled motion condition; in the bottom control condition, the initial and final marker spots were those used for the reversed motion condition; the actual direction of motion was the same in all conditions (see text).

The left half of Fig. 6 shows the localization of the test flash relative to the moving coordinate frame during 4-deg continuous movements, with durations of 50, 125, 250 and 500 ms. The right half of Fig. 6 shows localization during no-smear (sampled) movements. As in the previous experiment, the test line occurred slightly displaced from fixation in the direction of movement (Fig. 4e).

As the duration of the movement component of a trajectory is stretched out in time so that it is much slower than saccadic eye movements, there eventually come to be quite obvious differences in appearance between a display with a normal movement trajectory and one with the movement trajec-

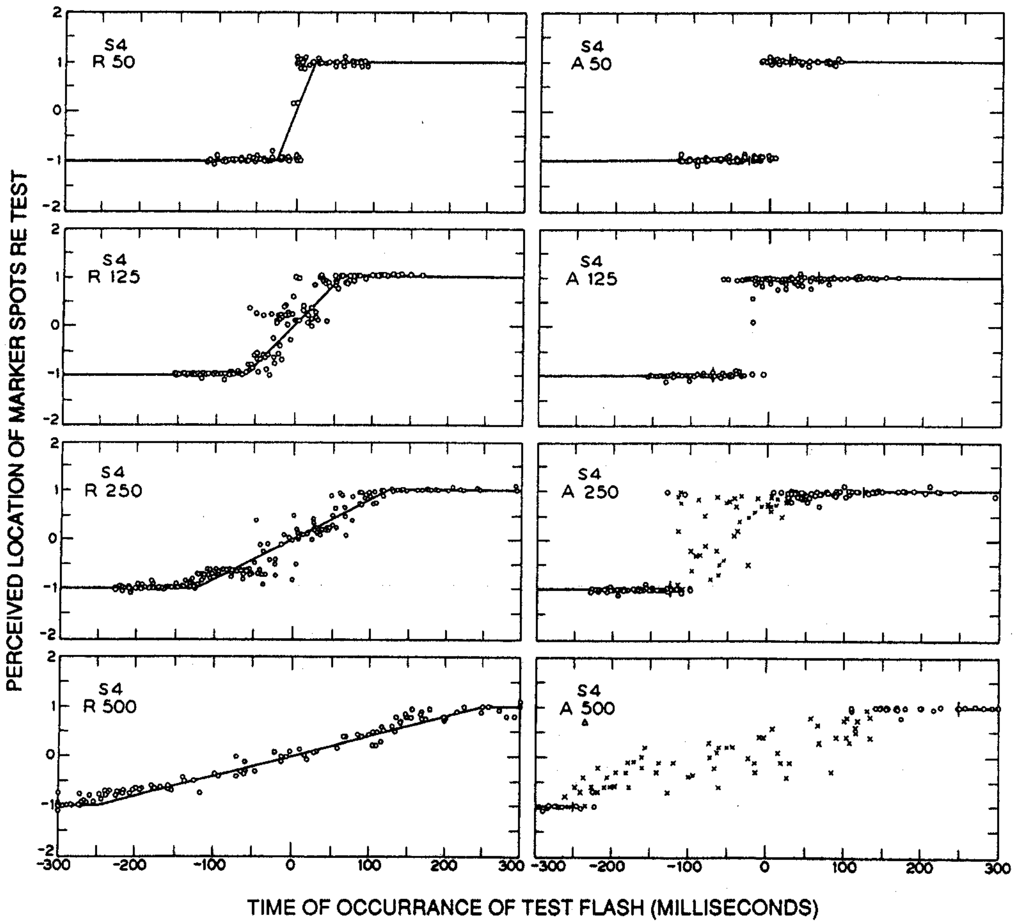


Fig. 6. Spatial localization compared in continuous and sampled motion stimuli of various speeds. The solid lines indicate the actual motion trajectory; the coordinates are as in Fig. 5. Left panels show continuous motion stimuli, right panels show sampled (sometimes called *apparent*) motion stimuli. Open circles indicate the perceived location of the moving marker spots as computed from the judged location of a brief test flash; x's indicate that the marker spots were temporarily eclipsed at the instant of the test flash and the location judgement was made relative to an *inferred* trajectory.

tory turned off. The trajectory between the initial and final position is correctly perceived as a slow translation; when it is absent, a blank period is perceived (e.g., blank times of 250 and 500 ms are quite obvious). With long blank times, the localization task for sampled-motion (interrupted) stimuli is ambiguous. When the localization task is redefined as 'judge the flash relative to where you believe the markers would be if they were visible,' the results of localization experiments with continuous-movement and with sampled-movement stimuli are quite similar. (Localization judgements made when the coordinate frame appeared to be invisible at the instant the test flash occurred are indicated by x in Fig. 6.) Because the linear interpolation of visual motion is so natural, even when there is an obvious blank period between initial and final positions, the localization task is not appropriate for revealing the differences in appearance.

Localization judgements during movements of various speeds yield some obvious and predictable results and some surprising ones. (1) For practical purposes, flash localization judgements do not distinguish between continuous and sampled motion at saccadic and near-saccadic velocities, i.e., 1.6 deg, 20 ms imposed movement (Fig. 5) and the 4.0 deg, 50 ms imposed movement (Fig. 6). (2) When markers spaced by 4 degrees traverse the intermarker space in 50 ms, flashes are nearly always localized only at their initial and final locations. This strictly bimodal distribution of localization judgements obtains for greater spaces or quicker traverses. (3) For motions of 125 ms (less than 1/6 of saccadic velocity), the localization judgements for continuous and sampled movements are profoundly different. For continuous movements, test flashes are localized quite accurately along the continuous motion trajectory. For sampled movements, test flashes are localized only at the endpoints of the trajectory. Bimodal localization judgements accurately reflect the fact that the motion trajectory is bimodal. However, bimodal localization judgements fail to reflect the phenomenology: the 125-ms sampled motion stimulus appears to jump across the space and to take a non-zero interval of time doing so. (3) With long blank times, localization judgements made during the interval in which the moving reference stimulus was turned off indicate remarkably accurate predictions of position. While these 'cognitive' localization judgements based on an invisible stimulus are somewhat more variable than 'perceptual' judgements based on an actual moving stimulus, they are nevertheless remarkably similar.

Spatial localization with overshoot trajectories. Saccadic trajectories typically have brief overshoots at the end of the movement in which the line of sight briefly extends beyond the intended endpoint and then returns back to the steady intersaccadic position. One of our subjects typically showed overshoots as large as 50 percent of the movement. To determine whether such a trajectory might influence perception, we (Sperling and Speelman, 1965) simulated a trajectory with 33% overshoot on the movement apparatus (Fig. 4g). In order to give the unusual trajectory the maximal opportunity to affect localization, it was run much slower than real time: the linear component from start to first arrival at the final location was 80 ms, and the overshoot duration was an additional 40 ms (see Fig. 4g). Stimulus conditions were similar to the previous simulated-motion experiments. As before, the subjects' task was to judge the location, relative to the moving coordinate frame, of a test flash that occurred during the movement.

Two motion extents (from initial to final) were investigated: (1) 95 arc min, and (2) 9.4 arc min. This small extent of movement was produced by means of an inverting telescope which reduced the 95 arc min by a factor of 10. Data for one typical subject are shown in Fig. 7. Two aspects of the data are noteworthy. Test flashes are never localized outside the initial-to-final interval in spite of the large, simulated saccadic overshoot. Indeed, even with these slow simulated movements (which are at least 3 times slower than real time) there is no evidence that the overshoot has any effect on perception.

The stimulus to study overshoots also revealed another important characteristic of localization. With the small displays (and correspondingly slow, small movements), there was no difference between localization in continuous-movement displays and in sampled movement displays with the motion segment turned off. However, with the 1.6-deg movement, the difference between continuous and sampled motion is overwhelming: test flashes during continuous movements nearly always appear at locations between the initial and final markers; with sampled movements, the test flashes are localized only at the endpoints. These data extend the top panels of Fig. 6, showing that the continuous–sampled motion difference can be made to vanish with sufficiently small displays, just as Fig. 4 showed that the continuous–sampled motion difference vanished with sufficiently brief (20 ms) motion periods (Fig. 6). All these differences between continuous and sampled motion follow immediately from a Fourier frequency analysis of the stimuli (Watson et al., 1986). Obviously, the parameters of visual motion exert a controlling influence on how test flashes are localized relative to a saccadic-like moving reference stimulus. This will be important in interpreting test flash localization during real saccades.

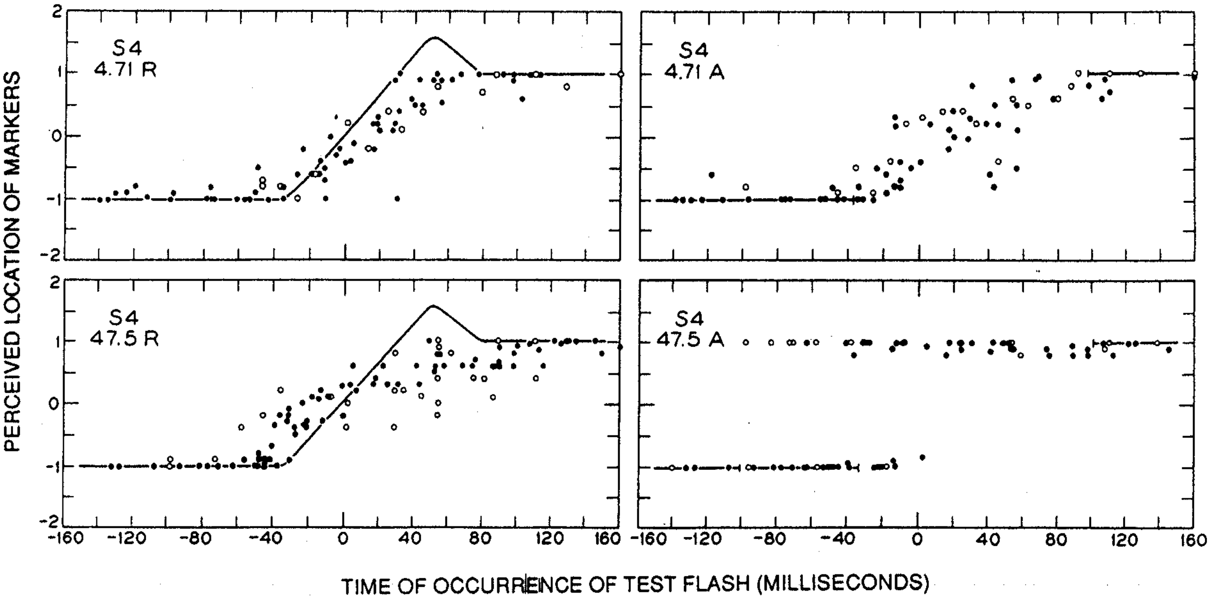


Fig. 7. Location judgements with continuous and sampled motions of two sizes. In the lower panels, the moving markers traversed from 47.5 min on one side of fixation to 47.5 min on the other side. In the upper panels, the display size was reduced by a factor of 10. The movement was a much-slower-than-real-time simulated saccade-with-overshoot (see text). Overshoot appears not to matter at these motion speeds. Turning off the movement field (saccadic *smear*) matters only for the larger movement.

All these observations indicate that the invisibility of high-velocity motion smear, which is present naturally during saccades, and errors of test flash localization relative to continuously moving images are not unique to saccades, but reflect visual responses to moving retinal images. With respect to motion smear, the visual system may have developed insensitivity to rapid-motion smear as a way of dealing with saccadically induced stimulation. However it may have evolved and developed, the visual system that we now have seems to respond in the same way to the same retinal stimulation – whether the stimulation is saccade-produced or object-produced. The following sections investigate the extent to which the mechanisms of spatial localization, which include nonvisual mechanisms, operate similarly in real and simulated saccades.

6.3.4. *What determines the subjective foveal trajectory $x_s(t)$ during eye movements?*

Comparisons of spatial localization in real and simulated saccades. The saccadic simulator was designed to imitate the retinal stimulation produced by objective movements. While it is possible to reproduce the trajectory of any particular eye movement, it is not practical nor necessary to reproduce the normal variation of saccadic trajectories in this experiment. Since we now know that saccadic motion smear does not importantly affect visual localization judgements, it is sufficient to use one typical trajectory in the imposed-motion control experiment – a 20 ms, 4 deg, linear motion trajectory. How does spatial localization with this simulated eye-movement trajectory on the stationary retina compare to localization during real saccades?

To compare real and simulated saccades, a subset of all the saccades was selected for which the simulated trajectory was a good approximation, i.e., saccades that began and ended within 12 min of their intended locations. For each saccade in this subset of 'good' saccades, the retinal location of the test flash relative to the saccade was noted. In the simulated saccade condition, the test flash was produced at precisely the same retinal location relative to the moving reference points, and the observer made the corresponding location judgement of the test flash relative to the marker spots.

In the simulated saccade experiment, the subject sees two stationary spots (−1, +1, Fig. 2a) with a 2-degree separation between adjacent spots. When the subject is ready, the subject initiates a trial by pressing a button. After a variable delay, the lines quickly move to replicate the saccade-induced sweep of the grid across the retina. During this sequence of events, the brief test flash occurs, and the subject's task is to report the location of the flash relative to the moving coordinate system.

Twin procedure. Each trial in the simulated saccade experiment is the twin of an earlier saccadic trial. The stroboscopic flash in the simulated movement trial always occurs at the same coordinate point relative to the moving reference stimulus (0.0) and the same time relative to the movement as did the original flash in the saccadic trial. The order of the simulated trials duplicates the order of the original 'good' saccadic trials. The perceived location of the brief flash relative to the saccadically simulated moving coordinate system on the stationary eye is precisely analogous to the flash location relative to the real saccade-induced moving coordinate system. That is, if localization with eye movement and simulated movement trajectories were entirely equivalent, observers would make precisely the same localization judgements in the two conditions.

Five of the six subjects whose saccadic localization data were shown in Fig. 3 served in the simulated saccade experiment. On the whole, the localization data from the simulated eye movement condition were similar to the data from real saccades. The main significant differences were a few instances in which observers judged a test flash in the simulated display at an endpoint when they had previously, in the real saccade, judged the flash at an intermediate position. Were these differences due to residual physical differences between the real- and simulated-movement images? For example, the display for the real saccadic movements (Fig. 2) showed five marker spots, whereas the simulated saccadic movement image showed only the −1 and +1 marker spots (Fig. 5).

Whether the slight differences in localization judgements between these real and simulated movements were due to residual differences between the displays in saccadic and simulated conditions or to differences in the process of localization between real saccades and simulated saccades was not determined for 4-degree saccades. However, if there are differences in localization between real and simulated 4-deg saccades, they are certainly not much larger than the trial-to-trial and subject-to-subject variability for the displays studied here.

To help resolve the issue of saccadic versus simulated saccadic localization differences, data were obtained with one subject using 8 (rather than 4) degree real and simulated saccades. With the larger motion extent, the localization differences between real and simulated saccades increased strikingly: there was much more localization of the test *between* endpoints for the 8-deg real saccade, and more localization *at* the endpoint for the simulated saccade. The change in simulated saccadic localization with scale followed basically the pattern illustrated in the sampled motion conditions of Fig. 7. Another indicator of a change in the localization process with saccadic size was that the duration of the 8-deg subjective trajectory $x_{s,8}(t)$ was briefer than the duration of the 4-deg subjective trajectory $x_{s,4}(t)$, although the objective 8-deg saccade took about twice as long as the 4-deg saccade. While such data were obtained with only one subject, they suggest that, even when visual information is prominent in the visual field, in larger saccades the motor movement itself importantly influences localization judgements in larger saccades. This issue is considered in the next section.

Visual versus nonvisual factors. As noted above, dynamic visual stimulation during saccades – certainly during brief saccades – is unimportant because it is effectively masked by stimulation arising from the static pre- and post-saccadic fields. Therefore, the static pre- and post-saccadic stimuli are the primary contributors to dynamic visual localization judgements, a matter illustrated in Fig. 5 (insensitivity to trajectory) and whose consequences will be taken up in more detail later. By contrast, nonvisual (motor system) factors might become more prominent in localization for large eye movements (e.g., 8 deg for the kinds of displays considered above; see also Pola, 1972). In addition to size of a saccade, the most obvious factor that determines the role of nonvisual factors is the visibility of the visual scene itself. As the scene becomes dimmer and thereby less visible, and ultimately invisible, spatial localization of a test flash will be determined more and more, and finally exclusively, by nonvisual knowledge of eye position.

A number of experimenters, among them Bischof and Kramer (1968), Mateeff (1978) and MacKay (1970b, 1973), have studied spatial localization during saccades in the presence of background stimuli. O'Regan (1984) points out, in effect, that the failure to use an adequate simulated saccadic control may invalidate conclusions about possible localization mechanisms from these earlier studies. In his own experiments, O'Regan (1984) did use a simulated saccadic control. While he found similarities between real and simulated saccades, his data were not collected in a twin procedure and they do not allow one to detect small differences that might exist. Even so, O'Regan's data, like the data reported in the previous section, show a tendency to localize test flashes at intermediate points more often for real than for simulated saccades.

The conclusion, based on the data described here and from published data in which judgements were made of the spatial location of a visual test flash against a structured visual background, is that, in normal viewing, visual factors predominantly determine test flash localization, whether the eye or only the image is moving. However, when visibility is reduced (darkness is an extreme case) or when nonvisual components are enhanced (as in large eye movements), or when the test flash is judged relative to the body rather than relative to another visual stimulus (Hansen and Skavenski, 1977, 1985) then nonvisual factors become more and more important.

6.3.5. *Visual localization in the dark*

Spatial localization after a visual frame of reference is extinguished. What is the perceived location of a test line flashed while the eye is executing a saccadic movement in the dark? For example, the observer views a fixation point *A*. It goes off and subsequently a point *B* appears which is the target of an intended saccade. The observer is instructed to saccade from *A* to *B*, but the *B* is turned off 100 ms after it appears, before the eye begins its movement. A stroboscopic flash is programmed to strike the fovea sometime before, during, or after the movement. The observer perceives this flash as originating from some point in the environment. Where? And how does the observer indicate where?

The test flash is judged relative to the memory of the extinguished markers, *A*, *B*. Obviously, just as in the light, a flash striking the fovea would be localized first at the initial location and then, sometime after the end of the saccade, at the final location. During, and shortly before and after the saccade, flashes are localized at intermediate points. For this experiment, there is no equivalent control experiment in the stationary eye. Spatial localization in the absence of visual stimuli must be controlled by nonvisual factors. The computation of the location of the fovea could rely on efferent outflow signals or upon proprioceptive feedback, but, in the absence of visual stimuli, it cannot rely on vision. This procedure allows one to measure the quality of visual localization information that is available via the motor system.

Experiments show that the perceived location of a foveal flash during a saccadic movement in the dark changes very slowly relative to the speed of perceived location of a foveal flash viewed against a visually structured environment. It takes hundreds of milliseconds for the perceived location of flashes in the dark to move from *A* to *B* compared to the few tens of milliseconds needed to execute the saccade (see Matin, 1986, for a review).

Hypothesis: feedback determines the frame of reference. In a closely related experiment in which the task of the observer is not to judge the test flash relative to a previously remembered location but to strike the flash directly with a hammer, Hansen and Skavenski (1977, 1985) find extraordinarily accurate localization. In their experiments, subjects have almost perfect, almost instantaneous, nonvisual knowledge of position relative to the body of the saccadically moving eye. Why does this knowledge not manifest itself when the subject is asked locate a visual flash relative to a remembered visual location? Skavenski (Ch. 5) proposes that the subject adopts a different frame of reference in the two tasks.

Adopting a task-dependent frame of reference means that the weight the subject assigns to different sources of information in arriving at a response depends on the task. This matter will be considered in the next section. Here we note that for the subject to achieve an optimal weighting of information sources in any of these complex tasks requires practice with feedback. All humans practice all their lives coordinating saccadic eye movements with body movements. Therefore, it is not surprising to discover that a subject is aware of the position of the eye relative to the body. However, people never practice making a purely visual judgement, which does not involve any body movement, in circumstances in which illumination is suddenly extinguished. The hypothesis put forward here is that, because all information necessary to perform this task is available to the subject, with practice a subject should be able to learn the purely visual task. The critical aspect for all the visual localization experiments considered here is that they measure what the subject habitually does, not the subject's capacity. To make an inference about capacity – an intrinsic *inability* to visually localize stimuli when a visual frame of reference is extinguished – requires that a subject *fails to learn* in an experiment with feedback (Sperling et al., 1990).

6.4. Models for spatial localization during eye movements

This section considers theories for the data that have been presented concerning the localization of flashes which occur during or proximal to eye movements. (The issue of how information from successive saccades is combined is considered in a later section.) Basically two kinds of information are involved; purely visual and visuo-motor. Visual information ('retinal factors' in the literature) refers exclusively to information carried by light, and it is the same in real and in simulated eye movements. Visuo-motor information includes efferent or afferent motor-system information ('extra-retinal factors') linked to vision. Here *visuo-motor* information is abbreviated to *nonvisual* although it makes no sense to consider nonvisual information alone – without vision – in a visual localization task.

Obviously, only nonvisual factors distinguish between real and simulated eye movements. (This requires that the simulated events are truly equivalent to the retinal images during eye movements, a technical requirement that has often been violated because it it difficult to achieve.) To evaluate the role of purely visual and visuo-motor factors in spatial localization, it is useful to have in mind at least one specific model for how each kind of information might be processed. We consider here a model for each process.

6.4.1. Model for purely visual localization during saccadic-like image sequences

Attention gating model: events, glimpses, episodes. The mechanism of the attention gating model of Reeves and Sperling (1986) and Sperling and Weichselgartner (1989) is the core building block of all the proposed models. The gating model deals with the mental representation of external stimulus events that occur in close temporal and spatial proximity to each other. According to the model, such closely contiguous events are not stored or accessed individually in memory; they are packed into an attentional *glimpse*. The glimpse is the smallest attentional unit. Its contents result from a single opening and closing of an attentional gate. The events that comprise a glimpse define its space-time window, much as the location where a camera is pointed and the time its shutter is open determine the space-time window of a photograph. A glimpse may incorporate events that span from about 1/4 s up to about 1 s. One or more glimpses may be bundled into an episode. The episode is the unit that is accessed when information is retrieved from long-term memory.

The gating model (Reeves and Sperling, 1986) describes the computational mechanism that creates attentional glimpses. In the environment in which it was developed and tested (highly controlled stimulus sequences which give the experimenter full control over the sequence of events) the gating model has great predictive power. The time course of attentional glimpses was found to be highly constrained and constant for an individual. The basic premise of the attention gate is that the *amount* of information recorded internally about an external stimulus event is proportional to the amount of attention received by the stimulus event at its time of occurrence, which, in turn, is determined by where within the glimpse the event occurs. The amount of information recorded about an event is characterized by a positive real number, its *strength*. The computational concept of *strength* represents the structural concept of the *strength of a link* which connects an event to the node designating the episode to which the event is attached.

To arrive at an observable response, information recorded in a glimpse must be interpreted. Here, the following assumptions are made. In the decision algorithm, information is weighted according to its strength. In arriving at a decision, it is not critical whether information is acquired from one or from several glimpses.

According to Weichselgartner and Sperling (1987), there are two kinds of glimpse, automatic and voluntary. In automatic glimpses the opening of the attentional gate is determined by the contents of the glimpse itself. For example, in the glimpse that records the test flash in a localization experiment, the attentional gate admits information about the test flash itself, about the visual field in proximity to the test flash, and about other events that may have occurred in close temporal proximity to the test flash.

In a voluntary attentional glimpse, information is admitted according to an attentional gate which is triggered by events external to the glimpse itself. For example, if the occurrence of a test flash were a cue to the observer to begin remembering the configuration of a complex background, the test flash would be remembered in the first glimpse and background information would be recorded in a subsequent glimpse.

Attentional gating functions are derived empirically from experiments in which a subject is asked to remember a single test event embedded in a visual field populated with other events (Reeves and Sperling, 1986; Weichselgartner and Sperling, 1987). The spatial and temporal location of events that the subject extracts along with the test can be used to derive the spatio-temporal gating function. Fig. 8 illustrates the time courses of an automatic and voluntary glimpse derived from such an experiment. The trigger event was the brief flash of an outline square, much like the test flash in the spatial localization experiments. The other events that the observer attempted to remember along with the outline square were flashes of letters, superimposed in a rapid stream inside the square. The voluntary attentional glimpse was quite slow compared to an automatic attentional glimpse – just as slow as if it had required a spatial shift of attention. Such voluntary attentional glimpses have been studied in a great variety of contexts (Reeves, 1977; Sperling and Reeves, 1980; Reeves and Sperling, 1986) and been found to be remarkably constant for a particular individual over a variety of conditions. The properties of the automatic attentional glimpses have not yet been quite as well defined.

Sources of information for localizing test flashes during saccade-like image movements. In a localization experiment, there are four stimulus events: (i)

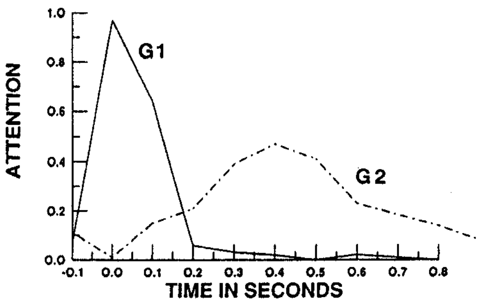


Fig. 8. Time course of attention triggered by the occurrence of a brief flash of an outline square. Two glimpses are distinguishable: G1, an automatic glimpse which records the flash and closely neighboring events, and G2, a controlled glimpse which mainly records events 200–600 ms later. The abscissa is time relative to the trigger event which occurred at time 0.0; the ordinate is the instantaneous amount of attention. (After Weichselgartner, 1984, Fig. 4.19a.)

the premovement field (a visual image of the retinal stimulus as it existed before the movement); (ii) the movement flowfield (a representation of the movement and, possibly, a visual respresentation of motion smear caused by the retinal sweep of the background), (iii) the post-movement field (an image of the retinal stimulus after the movement), and (iv) the test flash to be localized. When the test flash occurs during or in close temporal proximity to the movement, these events are represented in three glimpses: (1) a controlled glimpse which contains the premovement field plus weak representations of subsequent events, (2) an automatic glimpse triggered by the test flash which contains the test flash and possibly all the other events, pre-field, movement, and post-field, and (3) a controlled glimpse which contains primarily the post-field. It is assumed that, at the level of processing where a localization judgement is made, the automatic episode in which the test flash is recorded will be given the primary weight in determining the localization judgment.

Content analysis of the visual component events. There are two separate kinds of motion information: motion smear (a static retinal image) and the *motion flowfield.* In the case of saccadic movements, because of masking by pre- and post-saccadic fixation fields, motion smear is usually invisible and therefore unavailable for any subsequent processing (see section 6.3.2.). Therefore, motion smear is retained explicitly as 'null' in Glimpse ii. In the case of test flash localization in much-slower-than-saccadic movement, the motion smear takes on non-zero values.

The motion perception system calculates the motion flowfield, an assignment of motion velocity (a vector) to each point in two-dimensional space (Clocksin, 1980; Hoffman, 1982; Koenderink and van Doorn, 1986; Longuet-Higgins and Prazdny, 1980; Sperling et al., and Perkins, 1989). The neural computations of image motion are assumed to be the same whether the flowfield is produced by saccades or by image movements and whether the motion is continuous or sampled (e.g., Adelson and Bergen, 1985; Heeger, 1987; van Santen and Sperling, 1984, 1985; Watson and Ahumada, 1983; Watson et al., 1986). In the automatic glimpse containing the test flash, the temporal and spatial proximity of the saccadic image-velocity vectors to the test flash determine the weight of image motion in the localization judgment. This weight, expressed by the area (w_2 in Fig. 9a) under the test flash's attention glimpse function, represents the belief: 'The test flash occurred during the movement'. The computation of the weights of the various events that comprise the test-flash glimpse is illustrated in Fig. 9.

Visual persistence and test flash localization. While pre- and post-saccadic fields mask saccadic motion smear, the test flash in localization experiments is typically not masked. Therefore, because of its visual persistence (e.g., Efron 1970a,b; Sperling, 1960, 1967), the test flash becomes a de facto component of subsequent stimuli. Unless the test occurs long before the movement, it will persist into the post-saccadic background stimulus. In computing spatial relationships within an image, the persisting visual image of the test flash is treated in the same way as a physically present test image would be. Therefore, the persistence of a test flash

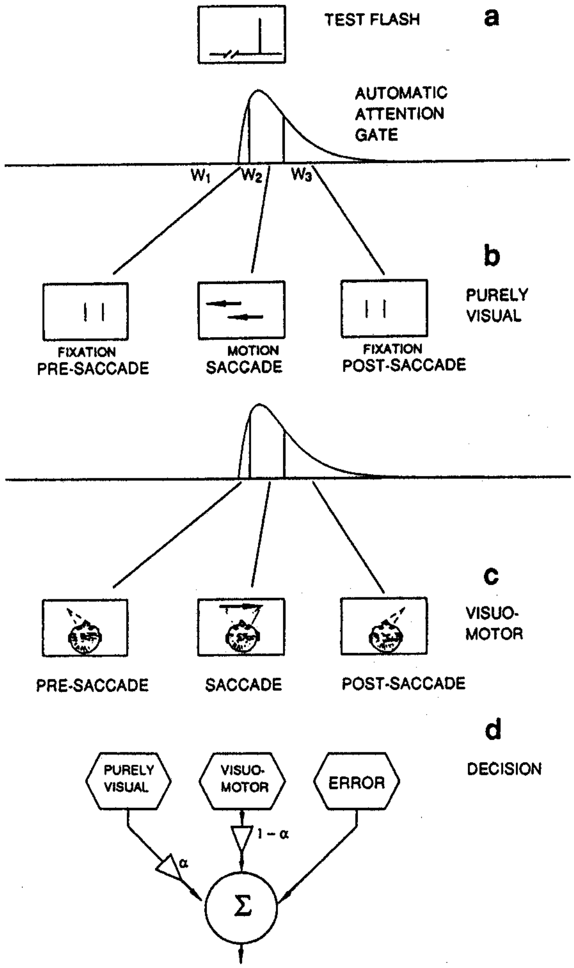


Fig. 9. Models for purely visual localization, visuo-motor localization, and for the combination of different sensory cues. (a) The intensity of a nearly instantaneous test flash as a function of time, and the attentional window of the episode in which the flash is recorded. (b) Representation of the retinal images of a stationary background before, during, and after a saccade. In purely visual localization, the images, weighted by their proximity to the test flash (w_1, w_2, w_3), are the only information available for the judgement/decision process. The particular weights shown here are appropriate for a test flash that occurs early in a saccade. (c) In visuo-motor localization, the representations of the pre-saccadic eye position, the moving eye positions and the post-saccadic eye position are weighted to derive the eye position to be linked with the test flash. (d) A simple model for the combination of cues from different sensory sources that has been found to accurately predict the data from multi-cue experiments. Data from various sources, weighted according to the task requirements ($0 \leq \alpha \leq 1$) are summed together with irreducible sensory noise (*ERROR*) to generate a response on each trial.

at particular location of the post-saccadic field is interpreted as very strong evidence (large weight) for occurrence of the test at that location. Visual persistence is probably the most important factor in the tendency of most observers to locate test flashes that occur shortly before saccades relative to the post- (rather than pre-)saccadic visual environment (O'Regan, 1984).

The entire rise and decay of visual persistence was mapped for individual subjects by Weichselgartner and Sperling (1985). Large individual variations in visual persistence functions were found. It would be of great interest to determine whether the duration of an individual's persistence function is correlated with the tendency toward localization errors in the post-saccadic direction.

When multiple tests are flashed during a saccade, their location is judged as though they all occurred at the same time (Mateeff, 1978; O'Regan, 1984).* That is, they are judged at their actual retinal positions without taking into account that the eye and the background retinal image were moving. This is explained by the persistence of all the flashes in the post-saccadic image. The simultaneous persistence of many flashes allows their retinal spatial relationships to be computed in the same way as if they had actually occurred at the same time. Such internal evidence of consistent spatial relationships is compelling, and overwhelms evidence of a differential time of occurrence during movement.

Nondistortion of images flashed during saccades. It was mentioned above that complex images briefly flashed during eye movements do not appear distorted. This observation has a long history (e.g., Woodworth, 1906, 1938; Campbell and Wurtz, 1978). One might expect images to appear distorted because the latency of visual responses varies with retinal location, as well as with stimulus contrast and with spatial frequency. In the stationary eye, this variation in the precise arrival time of sensory information at some more central process-

---

* Mateef has a different interpretation of his data.

ing center might be irrelevant. In the saccadically moving eye, small time differences represent large location differences. Again, it is not that time differences in sensory processing are somehow compensated for during saccades. When stimuli are flashed in isolation, retinal location and intensity influence perceived location (O'Regan, 1984). However, in the face of visual persistence that is long relative to the difference in onsets, there is a long period when all the stimulus information is simultaneously available. As with test flashes produced in rapid succession during saccades, the computation of spatial relationships between simultaneously available stimulus components provides evidence which is given overwhelming weight relative to evidence of difference in arrival times. Small differences in arrival times are used with extraordinary sensitivity in motion computations. During saccades, however, object motion is *masked* by saccadically produced image motion and perhaps also *suppressed* (see below, section 6.5). Small arrival time differences *un*associated with stimulus motion are not generally treated as significant data. It requires unusual stimulus conditions to demonstrate that uncompensated sensory processing times can enter into perceptual computations.

Saccadic versus simulated saccades. In the preceding discussion, it has been taken for granted that statements made about moving images in saccades would hold for simulated saccades in the stationary eye. For example, flashing a complex scene during a saccade from one marker spot to another is simulated by flashing a complex scene during the movement of two marker spots on a stationary retina. It seems so obvious that moving two marker spots would not alter the appearance of the flashed scene that it has not been explicitly tested. Similarly, it seems likely that two quickly consecutive flashes striking the fovea during the sweep of a moving background would both be localized at the same place. But this, too, still needs to be tested.

Computing visual evidence. Ultimately all sources of localization information are combined and a decision is reached. Of the various glimpses in which the test flash is represented, the automatic glimpse triggered by the test flash itself will be the main determiner of localization, and this is illustrated in Fig. 9. Fig. 9a and b illustrates the weights of the pre-saccadic, motion, and post-saccadic events in the automatic glimpse. The test flash also may occur in the pre- and post-saccadic glimpses. Their weights in the overall computation, which are disregarded in this illustration, would be determined by the attentional strength of the test flash within these events.

A full computational model requires specification of the following major component processes (as well as many subsidiary ones). (a) It must specify the gating function that computes the precise weighting of events in the temporal neighborhood of the test flash. It has been assumed here that the gating function is similar to the automatic attentional glimpse of Weichselgartner and Sperling (1987). In these experiments, a visual test flash of an outline square was linked primarily to visual events within ± 50 ms of its occurrence (Fig. 8). (b) A formal specification is needed of the decision rule – how the weighted mixture of events linked to the test flash is interpreted to generate a response. For example, if a test-flash glimpse assigned 20% of the weight to the prefixation field, 45% to the motion field, and 35% to the post-fixation field, what localization response would be generated?

The simplest decision rule occurs when the link of the test flash to the motion segment is very weak, i.e., when the motion segment in Fig. 9b is very brief and its weight w_2 is negligible. This usually occurs in displays in which the test flash is far away in space or time from the nearest test marker spot. A reasonable initial hypothesis for this decision rule is that such a location judgement is binary – appropriate either to the pre- or to the post-fixation background, depending on which has greater strength. With a significant motion weight, intermediate location responses become more plausible. An intermediate location response would be generated, reflecting the relative strengths of the pre- and post-fixation backgrounds. However, at saccadic velocities, the motion is so fast that even when motion enters into the localization computation, it enters only as a weight to determine whether an intermediate response is appropriate and not as a cue to localization.

Close proximity of the test flash to a background marker yields more convincing, and hence more persistent, spatial evidence of test location than when the test flash is far away from the nearest marker. (The definition of near/far depends on distance from the fovea.) While this can be formally modeled as a distortion of spatial localization in the neighborhood of spatial markers, it represents an inherent complexity of vision. The perceived spatial location of a test flash during image motion depends critically on the nature of the moving image itself.

6.4.2. Model for visuo-motor localization during saccadic eye movements

The model for visuo-motor (extra-retinal, nonvisual) localization during real, rather than simulated, saccades is basically analogous to the model for purely visual localization. Instead of linking the test flash to three visual events, it is linked to three corresponding nonvisual events: (1) a representation of eye position relative to the head position before the saccadic movement; (2) a representation of the saccadic movement command itself (outflow) or the saccadic movement itself (inflow); and (3) a representation of eye position relative to head position after the movement. As in the purely visual model, the glimpse in which the visual test flash is contained assigns weights to each of these nonvisual representations; the relative strength of the link is determined by the degree of temporal overlap of the test flash with the nonvisual event. Indeed, in the nonvisual as in the purely visual computation, a simple weighting function which uses overlap with the motion segment only to determine whether or not intermediate location judgements might be justified, and then uses the ratio of strengths of post- to pre-fixation links to determine the location, might suffice to account for the data. The advantage of this kind of computation is that it offers good resolution of position of test flashes which occur during saccades without requiring any correspondingly fast visual processing. We will return to the issue later.

6.4.3. A model for resolving conflicting cues

A natural question to ask is: when both purely visual and nonvisual information are available, how are these sources of information utilized in the performance of various tasks? A linear model based on Thurstone's Case V (Thurstone, 1927) for the combination of perceptual cues has been found to work remarkably well in a variety of tasks involving visual judgements (Dosher et al., 1986; Bruno and Cutting, 1988). Predictions work equally well when cues agree (add) and when they conflict (subtract).

Weighing the evidence. In the case of two perceptual alternatives (such as two different perceptual interpretations of a rotating Necker cube), each perceptual alternative is represented by a pan on balance scale. Each cue represents evidence, and a weight proportional to the weight of its evidence in favor of an alternative is placed on the balance pan of that alternative. The relative importance of a particular cue depends not only on the abstract quality of information provided by the cue itself but also on how each subject weights that quality in the particular task. The final perceptual decision is determined by the algebraic addition of the strengths of all the cues plus a random error that reflects the variability of judgement (Fig. 9d).

For localization judgements during real saccades, the present evidence suggests that visual information is given greatest, perhaps exclusive, weight in making visual judgements (Hansen, 1979). For example, in localizing one visual event (a flash) relative to other visual events (the saccadically moved background), visual information appears to dominate. With increasing saccade size the situation may be different because two factors come into play. First, if the background markers against which a test flash is localized are not size scaled, they become less effective stimuli as they become more peripheral. For this reason, saccade size would be best varied by varying the viewing distance and keeping the display constant. Otherwise, placing markers and test flashes more peripherally alters the early computations of visual spatial relations. Usually the alteration is in the direction of weakening the contribution of the spatial visual information. On the other hand, it seems obvious that nonvisual information would be stronger for larger saccades than for smaller saccades. Thus, even in purely visual localization judgements, nonvisual information may come to play a role in larger saccades. This relative increase in nonvisual influences on localization in large saccades does not involve a change in strategy (decision weights) but rather a change in the strengths of sensory inputs.

Motor localization reponses. In localizing targets by means of motor responses (versus making perceptual judgements) visuo-motor information is given greatest weight (versus purely visual information). For example, as was noted above, when an observer is asked to strike the location of a flash seen during a saccade with a hammer, the response is extremely accurate (Hansen and Skavenski, 1977, 1985). In this experiment, visual cues to flash localization were removed so that the observers were forced to rely on nonvisual information. Indeed, in localizing the flash relative to their body position, the observers did not succumb to the mislocalizations that they would have made if they were judging the flash's location relative to its visual environment. For further evidence that different sources of information are used in purely visual and visuo-motor saccadic localization tasks, see Ch. 5 of this volume.

6.5. Motion perception during saccadic eye movements

Suppose that, during a saccadic movement, the experimenter tricks the subject and shifts the visual field. To what extent can the subject detect such trickery? This question devolves into several component questions.

(1) When the retinal image sequence that would have been produced by a saccadic motion is artificially perturbed by extraneous motion, how detectable is the perturbation? (Motion masking.)
(2) How well can the observer detect that his eye has not landed where it intended? (Saccadic calibration.)
(3) Given that motion is a perceptual primitive, why is image motion not experienced during saccades? (Motion suppression.)

Motion detection and discrimination during saccades. Earlier, this chapter considered the detection of a simple flash during a saccade. Early investigators had claimed there was great loss of sensitivity during a saccade. Once the proper control experiments were conducted with simulated saccades, it became clear that the actual sequence of images on the retina produced visual masking and positional uncertainty of the test stimulus that was sufficient to account for threshold changes observed during saccades. There was no residual threshold change that could be attributed to the saccade per se. The problem of detecting and discriminating visual motion during saccades seems to be similar. There are several reports of an impaired ability to detect or discriminate motion during saccades (e.g. Bridgeman et al., 1975; Mack, 1970; Stark et al., 1976; Whipple and Wallach, 1978). However, when Brooks and her collaborators (Brooks and Fuchs, 1975; Brooks et al., 1980a,b; Brooks and Impelman, 1981) produced equivalent motion perturbations in real and in simulated saccades, they found them to be equally detectable.* Their answer to the motion masking question raised above is that any inability to detect motion perturbations during eye movements is explained entirely by the sequence of images on the retina. To this it must be added that in both real and simulated saccades, Brooks et al.'s subjects discriminated nor-

---

* While Brooks et al. (1980a) mostly found identical thresholds in real and simulated saccades, in a few of their conditions there were slight differences that could have been caused by residual, uncontrolled differences in procedure.

mal from perturbed motion on the basis of the shape of the perceived motion blur – not on the basis of perceived motion of the perturbation (Brooks, personal comunication).

In Brooks et al. (1980b) and in every other instance up to this point, when a psychophysical discrimination was based on retinal images, it has not mattered whether these images were viewed in a stationary or saccadically moving eye provided that the retinal images were equivalent. However, the problem of *motion* detection and discrimination during saccades is more complex than the problem of simple object detection because the *sensation of image motion obviously is suppressed during saccades.*

The sensation of motion: saccadic motion suppression. Consider Question 3: saccadic trajectories are excellent stimuli for the motion perception system. That is, moving an image in the trajectory of a simulated saccade on a stationary retina produces a strong sensation of apparent motion.* Why do we not experience visual apparent motion during the same retinal image movement when it is saccadically induced? Notice that the sensation question is a fundamentally different question from the discrimination question raised above. Sensation refers to how an observer describes his experience, and does not involve a right or wrong answer as does a discrimination task.

It is helpful to place the suppression of motion sensations during saccades into the broader context of other voluntary movements. For example, the otolith signals acceleration with respect to gravity: why don't we experience a sensation of falling whenever we voluntarily sit down? When we voluntarily turn our head, the vestibular and visual systems should signal vertigo, but we do not experience it. The other side of the coin is the shock we experience when we expect one sensory input, for example, strawberry mousse, and encounter another, sour cream with salmon roe. However, merely observing that the interpretation of sensory input quite generally depends on voluntary movements and on the corresponding sensory expectations does not answer any specific questions about the processes that are invoked. We first consider Question 2 (Saccadic calibration) and then the issues concerning the types and levels of sensory processing.

Saccadic calibration: piano analogy. The answer to Question 2 concerning sensitivity to environmental displacement during saccades depends on the size of the displacement as a fraction of intended eye movement, and on the suspicions of the observer. Sperling and Speelman (1965) observed that a stimulus displacement of 2 deg during a 4-deg saccade was reliably detected (cf. Bridgeman et al., 1975; Stark et al., 1976; Whipple and Wallach, 1978).

The issue of sensitivity to visual displacements can be easily understood by an analogy. Imagine a pianist performing a difficult piece on a piano. While his hands are in the air, we move the piano. Indeed, on grand pianos, the soft pedal accomplishes just such a movement, moving the keyboard by about a quarter the width of a key so that the hammers strike only two of three strings. Such small keyboard movements usually go unnoticed. Suppose, instead, that while the pianist's hands are in the air, we move the piano the width of a key. The unfortunate pianist would strike wrong notes and probably infer that he was out of practice. But, suppose we moved the piano a foot, so that the pianist's hands struck completely unbelievable notes. Not only would such trickery be shocking and instantly recognized, but the pianist would attribute every subsequent wrong note to external interference. In a psychophysical procedure, the pianist's ability to discriminate real mistakes from induced mistakes would follow roughly a Weber fraction of the lateral hand movement. The situa-

---

* The motion perception of objects moving at saccadic speeds has been studied almost exclusively with part-field stimuli. Saccades move the entire retinal field and, except in the laboratory, the entire retinal field is usually filled with stimuli. The author is not aware of any study that examines whether full-field stimuli moving at saccadic velocities produce as strong a perception of motion as part-field stimuli.

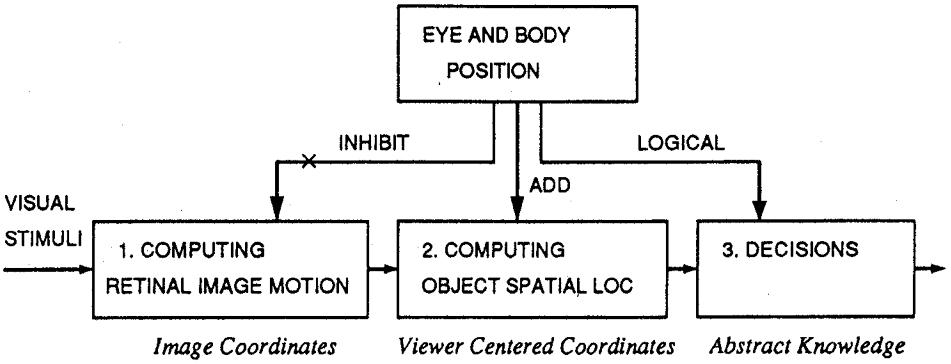


Fig. 10. Processing of visual and nonvisual information. Three stages at which nonvisual information interacts with visual information: the label on the arrows indicates the mode of interaction.

tion with saccadic eye movements is not essentially different. Whether we move the hand or the eye, we know what to expect when we arrive. The cognitive processes by which we build up representations of the external world and derive predictions from the representations are quite complex; they are considered briefly later in this chapter.

The experiments on the spatial localization of flashes during eye movements are analogous to the localization of tactual stimulation during ballistic hand movements. As with the eye, when the hand is stimulated as it is moved rapidly over a surface, the source of stimulation is projected onto a location on the surface. The subject's hand trajectory can be compared quantitatively to the objective trajectory, just as with eye trajectories, and it is undoubtedly subject to similar illusions. Indeed, comparisons of motor programming in vision with motor programming in other modalities promise to yield insights into both domains of study.

Determining the level of visual–nonvisual interaction in the perception of image motion. To analyse the processing of visual motion during saccades, we consider the visual and nonvisual inputs and the three levels at which they can interact. Specifically, the inputs are (1) the retinal images generated by the saccades and (2) the nonvisual eye movement and body position signals. The computational levels are (1) computing retinotopic image motion, (2) computing object spatial position, and (3) a decision level (Fig. 10). At each level, we consider computations that could inhibit the sensation of motion during saccades.

At the level of computing retinotopic motion, the effect of nonvisual input from a saccade would have to be inhibitory and nonspecific. That is, because all parts of the visual field may be stimulated by saccadic motion, motion signals would have to be suppressed throughout the visual field. The question of whether motion signals that represent directions of motion counter to or perpendicular to the saccade are also suppressed (Stark et al., 1976; Whipple and Wallach, 1978) is left open because, it will be argued, the retinotopic inhibitory mechanism is itself implausible.

A higher level of saccadic visual–nonvisual interaction is at the level of computing the position of a visual object relative to the head. (For specificity, we take head direction to be the direction the nose is pointing.) Computing object position requires adding two angles: (1) the retinal angle between the object and the fixation point – the line of regard – and (2) the angle between the line of regard and the nose. Saccadic motion suppression at this level implies that spatial position rather than the retinotopic motion is used to infer perceived motion.

At the decision level, a decision is made about whether or not object motion may have occurred during a saccade. Consider the piano analogy. The pianist's hands land on the piano but on a wrong note. Ordinarily, the pianist does not entertain the hypothesis that the piano has moved, and so the sensory signal is logically re-interpreted to indicate that the hands must have erred in executing their intended movement. The case of visual objects whose position is perturbed during a saccade is similar. All the systems up to the point of decision may be sending appropriate signals, but they are discarded at the point of decision. However, when the new game is pointed out to subject or pianist, the decision rule can be quickly revised.

Modifiability, the critical role of feedback. It is assumed here that the modifiability of processing is related to level: the higher the level, the more easily processing is modified.

Full-field inhibition of retinotopic motion computations during saccades would generally be assumed to be an unmodifiable genetically determined process. At the level of computing coordinates, the ability to calibrate eye movements is genetic, but saccadic extent (and many other motor components of eye movements) can be recalibrated in a few minutes to a few hours of observation time (Keller and Zee, 1986). The situation is not essentially different from the case of a pianist switching from a standard piano to a harpsichord which has narrower keys or, in the second case, having different dynamic properties so that key-press movements have to be recalibrated.

The issue of modifiability is critically related to experimental method. Feedback means that a subject is told and/or experiences the consequences of correct versus incorrect responses. When they are correctly carried out, experiments without feedback are essentially ecological investigations; they determine how sensory inputs are habitually computed. Experiments with full feedback can determine the computational limits. For example, to establish that there is retinotopic motion inhibition requires an experiment with feedback. From experiments without feedback one can learn only that subjects habitually ignore motion signals during saccades. To determine that the failure to perceive motion during saccades is not merely a habit but an unmodifiable deficiency would require the experiment with feedback to fail to train subjects to use retinotopic motion signals.

To understand the limits of motion perception during saccades requires at least two conditions: (1) comparing real saccades with simulated saccadic controls and (2) experiments with feedback. The numerous reports of saccadic motion suppression cited above fail one or both of these criteria. We consider saccadic motion perception below in the section on correlating successive saccadic images.

The issues suggested by the flow diagram in Fig. 10 are, in principle, resolvable. For example, a possible generalized loss of sensitivity to image motion during saccades can be investigated experimentally by presenting visual motion stimuli (motion probes) before, during, and after saccades. There are the masking and suppression questions: the ability to experience the perception of motion of the probe and the ability to discriminate different probe motions. Generality of suppression is studied by determining to what extent perception and discrimination of motion are inhibited by temporal proximity of the motion probe to a saccade, and determining whether the direction of motion matters. The problems in pursuing this research are great technical requirements in eye movement recording and even greater technical difficulties in producing the proper simulated-saccade controls.

One argument against motion suppression occurring early in visual processing is the autokinetic effect. Stationary points of light in the dark, even when fixated, appear to make small movements from time to time (see Mack, 1986, for references). Autokinesis seems like an obvious failure of motion suppression for small eye movements, although it is not unexpected, given that nonvisual information appears to be quite weak for small saccades. On the other hand, with normal full field stimulation in the light, the world as a whole does not appear to jump around, suggesting that more stringent perceptual criteria are applied to large-field than to small-field motions. In summary, the question of "At what processing level, and by what mechanisms are the sensations of motion re-interpreted during saccades?" remains unresolved.

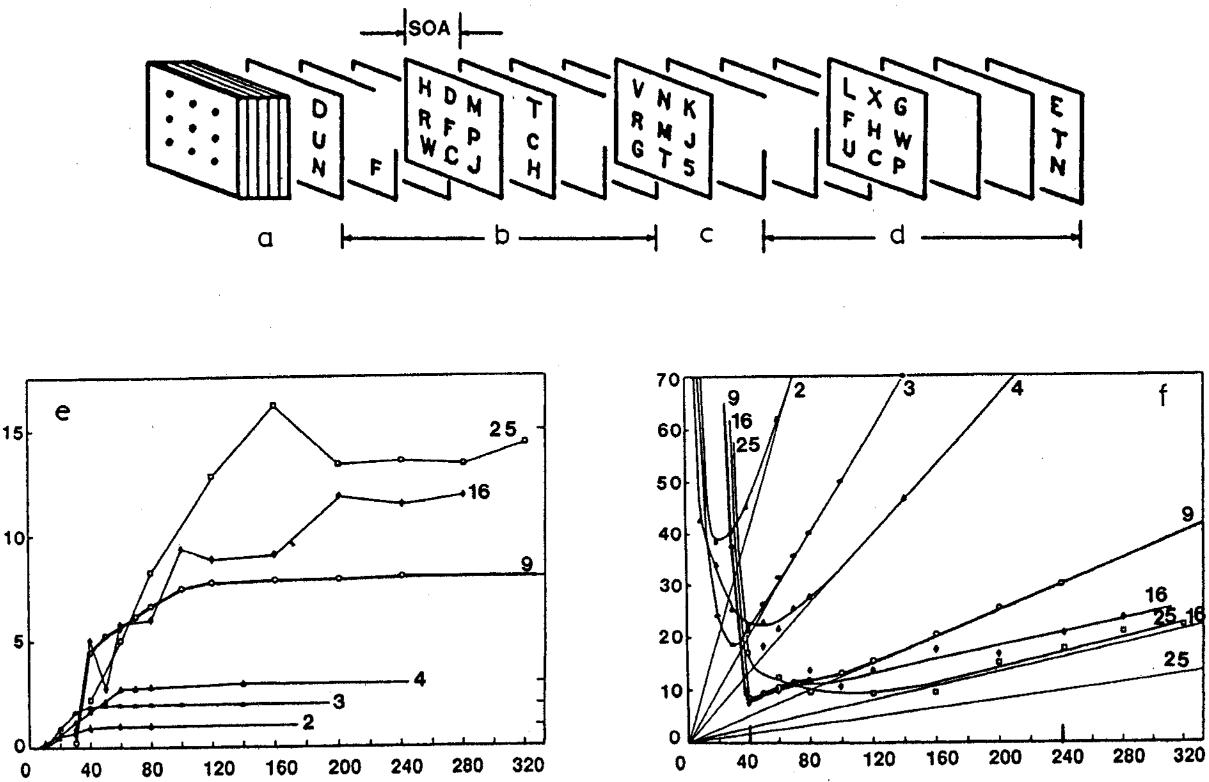


Fig. 11. Simulated saccadic search. A fixation field (a) is followed by a variable number (b) of arrays which contain letter distractors. The critical array (c) is embedded near the middle of the sequence. It contains a numeral target, and is followed by (d) letter arrays. The time between successive arrays is SOA (stimulus onset asynchrony). (e) The estimated number of characters in each array successfully searched by the subject as a function of the SOA. Data for the 9-character array illustrated above are emphasized by a heavy connecting line. The lack of improvement with SOAs longer than about 120 ms for arrays of 16 and 25 ms indicates that the second half of the exposure interval is wasted when the interval is as long as the intersaccadic interval. (f) The same data replotted to show the estimated scan time per character. 40 ms indicates the quickest scan times for 9- and 16-letter arrays; 240 ms indicates the minimum intersaccadic interval. (Redrawn from Sperling et al., 1971. Data from subject J.S.)

7. Sequences of saccades

7.1. Visual search

7.1.1. Simulated search: saccades are not always the optimum information-gathering strategy

By the definition of 'survival of the fittest', the visual system that we now have, which includes a high-resolution fovea, a low-resolution periphery and saccadic eye movements, is the optimum visual system under the set of constraints under which humans evolved. In this light, it is informative to consider a simple search task in which the saccadic mechanism is nonoptimal because it is too slow.

Consider a simple search task such as scanning a large array of letters (distractors) for an embedded numeral (the target). Normally, this search would be carried out by means of saccades, each saccade positioning the eye in a different region of the array. To simulate this search task in the stationary eye, the new information is presented to the stationary eye at regular intervals, as illustrated in Fig. 11. The subject views a long sequence of stimulus frames; all except the critical frame contain arrays of letters. In the critical frame, a number is embedded at an unknown position of the array. The subject's task is to detect the number. As a purely technical matter, the subject is also required to press a reaction-time key as quickly as possible upon detection, to give the position in the array at which the number occurred, and to state a confidence for the identification task. These additional bits of information are useful in discriminating true from accidentally correct detections.

The results of such an experiment are the percentages of correct detections as a function of the parameters of the experiment (Fig. 11e). The percentage of correct detections is most usefully transformed into a search rate – the number of distractors that must be searched each second in order to support the observed percent correct (Fig. 11f). The parameters include the time interval from one array to the next (stimulus onset asynchrony, SOA), the size of the arrays to be searched, the sets of items used as targets and distractors, the size and discriminability of the items, the advance knowledge that the subject may have about possible targets, and so on (Sperling and Dosher, 1986).

The parameter of interest with respect to simulated eye-movement search is the interval between arrays. Saccades do not occur faster than about 4/s; this corresponds to a presentation time of 250 ms per array in the simulated search procedure. Indeed, when arrays of characters are presented every 240 ms, the observed search rate is about 50 characters per second, which is equivalent to 20 ms per character (Sperling et al., 1971). About the same search rate is observed in natural search (Neisser, 1963, 1964; Neisser et al., 1963). However, when the interval between arrays is reduced, the search rate can be substantially higher. The highest rate of search, more than 100 characters per second (less than 10 ms per character), occurs when new arrays occur every 40–50 ms, a presentation rate five times faster than the rate of eye movements. The simple empirical conclusion is that eye movements, which limit the time between bursts of new information to one per 250 ms, limit the rate of search to half of what it can be when the presentation rate is increased.

Why is this particular search task (a numeral among letters) slower with natural eye movements than in the simulated search procedure? According to analyses by Fisher (1982) and Sperling and Dosher (1986) there are two interlocked reasons. First, the visual system seems to be able to execute the search in parallel in at least three of four locations of the visual field. Second, foveal search is faster than peripheral search. To some extent, foveal/peripheral search differences can be overcome by appropriate size scaling of stimuli to be searched. However, mixing character sizes in arrays to be searched slows search down rather than speeding it up (Sperling and Melchner, 1978). Therefore, the fastest search occurs when arrays of four or more characters are presented to the fovea at a rate consistent with its information-processing capacity. For highly legible characters, central vision can process 25 batches of four characters per second. This mode is two times more efficient (in terms of the number of characters searched) than saccadically driven search, which processes only 3 or 4 batches per second.

7.1.2. When is saccade rate a limiting factor in performance?

There is enormous flexibility in visual processing. The only task in which saccades have been a limiting factor was the simulated search for a relatively large, highly familiar target (a numeral) among letter distractors (Fig. 11). This is contrary to intuition, which suggests that saccades would limit performance when searching for tiny targets which could be discriminated only in the fovea. The problem is that, when a target is made so difficult to detect that it requires foveal acuity, the processing time to detect that target, even in the fovea, is likely to become so long that processing time itself, rather than intersaccade time, becomes the limiting factor. All this merely indicates that the capacities of the motor and processing components of the visual system are matched to each other, which is as it should be.

7.2. Do saccades initiate processing episodes? The optimal duration of inter-saccadic fixations

When the retinal image is artificially kept motion-less, independent of eye movements, it fades, and information-processing from that image ceases (Ditchburn and Ginsborg, 1952; Riggs et al., 1953; Yarbus, 1957). Saccades can maintain or restore an image to visibility; however, they are not necessary – smooth eye movements are perhaps even more effective (e.g., Gerrits and Vendrik, 1974; see Kowler and Steinman, 1980, for a review). These observations have induced vision scientists to speculate that smooth eye movements are especially associated with continuous information-processing whereas saccades are associated with discontinuous, episodic information-processing. Saccades are assumed to initiate processing episodes. The visual system is assumed to be especially adapted to process the kinds of image sequences that saccades provide: tens of milliseconds of smear followed by hundreds of milliseconds of steady image, repeated over and over. Undoubtedly the visual system is adapted to this saccadic mode of operation. This chapter continues, with more complex stimuli and tasks than before, to deal with the question raised at the onset: to what extent do the information-processing adaptations to saccadic vision operate independently of the saccades themselves? In particular, to what extent are adaptations to saccadic vision exhibited equally when the simulated saccadic sequence of images is presented to a stationary eye?

7.2.1. In natural saccadic viewing, are long-duration fixations 'better' than brief ones?

Loftus (1972) investigated this question experimentally using natural saccadic movements in a recognition memory experiment. In the learning phases of the experiments, subjects viewed a sequence of photographs of natural scenes; each scene was exposed for a fixed time interval. Later, subjects were tested for their ability to discriminate previously viewed scenes from new (distractor) scenes. Loftus found that the best predictor of later recall was the number of saccades that a subject made in the initial viewing. Exposure duration itself had an effect upon recall only in controlling the number of saccades: given the same number of saccades, the inter-saccadic durations themselves had no influence on recall.

Loftus's finding that increasing inter-saccadic duration has no effect on recognition accuracy invites the inference that each saccade initiates a processing episode which is completed in less time than the shortest inter-saccadic duration. The possible difficulties with this conclusion illustrate the problem of studying saccades naturally without also using an appropriate simulated-saccade control. The problem is that saccadic viewing strategies are determined by the subject, not the experimenter. Therefore the viewing strategy may be perfectly confounded with the intrinsic memorability of a picture. Easy-to-remember pictures induce short inter-saccadic durations. Without further embellishments, Loftus's procedure would admit no conclusions about the effectiveness of saccades as a function of the inter-saccadic durations. This kind of difficulty in studying natural saccadic viewing is very difficult to overcome because inter-saccadic duration is a dependent variable rather than an independent variable. Loftus himself ultimately found it necessary to study approximately-simulated saccades (Loftus, 1981). Sometimes, it is desirable, additionally, to use artificially constructed stimulus materials to give still better experimental control, as in the attempt to answer the following question.

7.2.2. In a search task, are two short saccades better than a long one?

The question of whether saccades initiate processing episodes that are quickly over – even before the onset of the next saccade – suggests several experiments with simulated saccades. For example, in a simulated search task, are two saccades better than one long saccade? And, if two short saccades are indeed better than one long one, must the information presented in the two successive exposures fall on different retinal coordinates?

Letter arrays. Kowler and Sperling (1980) studied simulated search for a numeral embedded in a 5×5 letter array viewed with either single or double exposures of various durations. Each stimulus sequence was terminated with exposure of a visual noise field. The stimulus array was either flashed once (a), or twice (b), or twice with a lateral translation between exposures (c), or the array was presented continuously (d), or continuously with a lateral translation in mid-exposure (e). Search accuracy depended little on the viewing condition when the total duration of visual availability (onset of the stimulus to onset of the noise field) was less than about 100 ms. For longer exposures,the order of conditions, from best to worst, was d > e > b > c > a. That is, displacements were not helpful, two flashes were better than one, but a single continuous exposure was always best. Even for the longest simulated fixations (800 ms), dividing the long fixation into two short ones was harmful under the parameters of this search task.

Natural scenes. To complement his study of natural scenes viewed by natural eye movements, Loftus (1981) studied natural scenes viewed by successive bursts of illumination, each burst followed by a visual noise field. His procedure was not a saccadic simulation because the time interval between successive exposures was long enough to permit real saccades to reposition the eyes. Like Kowler and Sperling (1980), Loftus (1981) found that breaking a long flash into several shorter ones did not improve recognition memory. However, when fixation changed voluntarily between flashes, performance did improve with the number of fixations. Loftus concluded that the critical component in later recognition is the number of picture-features that a subject remembers from a scene. For example, generally, performance improves with number of flashes. But, "when the number of places looked is held constant, the effect of number of flashes vanishes, thereby indicating that additional flashes are only useful insofar as they permit acquisition of information from additional portions of the picture" (Loftus, 1981, p. 373). Memorable features in Loftus's natural scenes were less dense and more widely spread out than were characters to be searched in Kowler and Sperling's 5×5 arrays, so subjects benefited from successive images that fell on different retinal locations in the scene experiment and not in the character search experiment.

7.2.3. Are sudden onsets (such as might be provided by saccadic eye movements) necessary or beneficial for information-processing?

To directly test the utility of abrupt stimulus onsets for information-processing, Kowler and Sperling (1983) used a simulated saccadic sequence of images in a search task for a numeral embedded in a sequence letter arrays, as shown in the top panel of Fig. 12. Additionally, in various conditions of their experiment, the temporal waveform of the successive images was varied. They measured search accuracy with both abrupt (step) and gradual (sawtooth) onsets and offsets of images in the sequence, at two presentation rates (Fig. 12).

Search accuracy was the same, independent of the waveforms shown in Fig. 12; search accuracy depended only on the time between successive arrays. That is, only the time available to process the stimulus items influenced performance, not how that time was apportioned into dark and light phases of the cycle. These results are quite different from those obtained with stimuli at the threshold of detection or discrimination. When visual process-

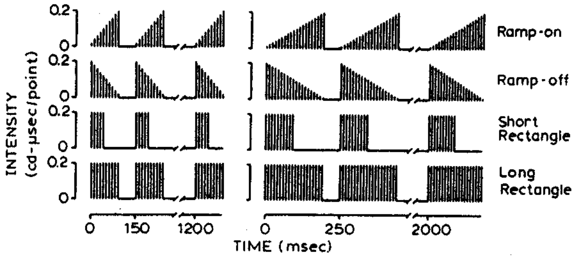


Fig. 12. Sequences of stimuli whose intensity waveform is varied according to four different functions at each of two presentation rates. Each triangular (or square) packet represents the exposure of a new array of characters in a search experiment. Because ramp-on stimuli do not have sudden onsets and all the other stimuli do, a theory which asserts that sudden onsets initiate periods of information-processing would predict (incorrectly) that search performance is inferior with ramp-on stimuli. (From Kowler and Sperling, 1983.)

ing is limited by the energy in the stimulus, the temporal waveform of the stimulus matters critically for performance (Watson and Nachmias, 1979). However, when stimuli contain sufficient energy to be easily discriminated processing is time-limited, not energy-limited, and the temporal waveform becomes relatively unimportant (Kowler and Sperling, 1983; Sperling, 1979).

The conclusions are that, under good visibility conditions, the physical parameters of image onsets imposed by saccades are relatively unimportant, presumably because of the great efficiency of visual preprocessing. For a particular stimulus and a particular task, high-level processes of feature encoding (in recognition memory experiments) and of feature matching (in search experiments) determine where the eye should be placed and when it should be moved for optimal performance.

7.3. Two-flash displays: masking, localization, movement, memory

The two-flash paradigm. Experiments with a two-flash stimulus have been particularly productive in the analysis of information-processing within and between fixations. The observer views two consecutive, brief flashes separated by a time interval δt. Either both flashes are confined to within a single fixation (the Within condition, Fig. 13) or a saccadic eye movement occurs between the flashes (the Between condition). Comparison of performance in Within and Between fixation conditions yields insight into saccadic information-processing. The ability of the observer to correlate the contents of the two images is tested by memory tests or by psychophysical tests that involve, for example, the ability to perceive motion between the images. The previous section considered search experiments in the within-fixation but not the between-fixation variant of the paradigm. The two-flash paradigm has also been used to study spatial localization and visual masking.

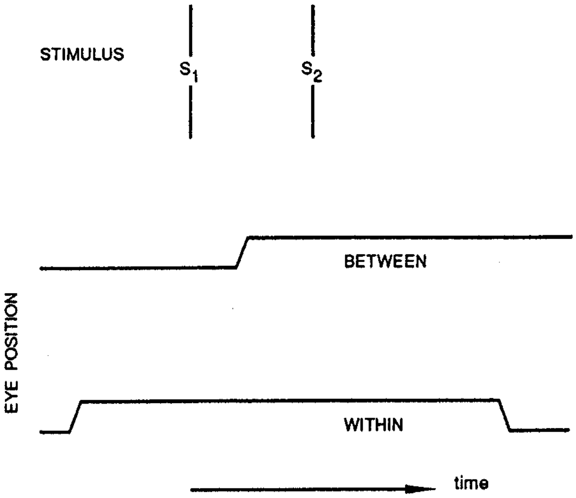


Fig. 13. The two-flash procedure. S_1 and S_2 represent stimuli illuminated by the first and second flashes, respectively, and the horizontal coordinate represents time. In the Between-fixation condition, a saccade occurs during the interval between the flashes; in the Within-fixation condition, both flashes occur within the same fixation.

The great technical advantage of the two-flash procedure is that the simulated eye movement control experiment does not require producing a complex eye movement streak on the retina, merely two flashes. As with other eye movement paradigms, there are two disadvantages of the two-flash paradigm. The exact time of occurrence of a saccadic eye movement cannot yet be perfectly predicted. Many trials must be conducted in order to obtain a few critical trials with the eye movement centered between the flashes. To control for possible effects of the context of imperfect trials on performance in the critical trials, an equivalent imperfect context has to be provided for the within-fixation control experiment. The second problem is that the eye position must be known exactly at the time of the two flashes in order to ensure that the control presentation in the within-fixation presentation is truly equivalent to the between-fixation presentation – for both the 'same-retinal-coordinates' and 'same-spatial-coordinates' variations. While the problem of positional accuracy is endemic to all eye movement recordings, the apparent simplicity of the two-flash paradigm has seduced experimenters into attempting it with less-than-adequate eye movement recording.

7.3.1. *Visual masking*

Visual masking in a two-flash paradigm with an interleaved saccade was studied by Davidson et al. (1973) and Irwin et al. (1988), with roughly similar procedures and results. In Irwin et al.'s experiment, subjects were presented first with a 10 ms exposure of a row of five letters. This was followed by a 40–70 ms blank interval during which, on some trials, a saccade occurred. After the saccade, a masking pattern was superimposed on one of the letters. The masking pattern was found to exert its masking effect primarily when it occurred at the same retinal location, not the same spatial location, as the letters.

Does interposing a saccade between the first and second flash alter the masking effect of the masking pattern? With a δt between onsets of the first and second flashes of 40–70 ms, retinotopic masking results suggest that an eye movement would make no difference for this kind of masking. However, neither Davidson et al. (1973) nor Irwin et al. (1988) report a no-movement control condition, so we can only conjecture that masking is the same in real and simulated saccades.

7.3.2. *Spatial localization*

To compare masking and spatial localization during saccades, Irwin et al. (1988) used a two-flash background presentation like that described above. Again, the first flash was a 5-letter array; the second flash was a bar marker rather than a masking field. The bar marker was a short vertical line segment which instructed the subject to report the name of the letter below it (Averbach and Sperling, 1961). These experiments are essentially spatial localization experiments completely analogous in many details of procedure, theory and results to those described in the section on spatial localization during saccades (section 6.2). Irwin et al.'s results show that the bar marker changes its apparent location relative to the stable letter array with approximately the same time course during the saccade as did Sperling and Speelman's (1965) short-line segment relative to their dot array in the localization experiments described earlier. The comparison between experiments is only approximate because Irwin et al. did not make precise measurements of the time course.

Irwin et al. observed that, even though a masking flash that masks an earlier letter was at the same retinotopic location, the apparent spatial location of the masking pattern corresponds to its new spatiotopic retinal coordinates. That is, the apparent spatial location of a masking pattern is computed in the same way as the apparent location of other spatial patterns, such as bar markers.

7.3.3. *Motion detection and perception*

The two-flash paradigm naturally lends itself to the study of motion perception between the two flashes. Perceiving motion requires some form of correlation to be computed between the first and second stimulus, so motion perception implies at least an elementary form of pattern memory. The issues that arise in the two-flash paradigms are precisely the same as those which emerged in section 6.5. However, in experiments that measured the ability of subjects to detect object displacements during saccades, no attempt was made to ascertain whether detection was based on perceived motion or on perceived change in location.

Shioiri and Cavanagh (1989) attempted to determine whether motion could be perceived during a saccade by using random-dot patterns which offered good motion cues but only weak locational cues when they were displaced. When pattern displacements occurred between two fixations in an explicit two-flash paradigm, their subjects failed to discriminate displacement from no-displacement trials. The subjects were also unable to use apparent motion to correctly identify the direction of displacements that occurred around the time of saccades.

Unfortunately, Shioiri and Cavanagh's procedures illustrate the hazards of violating the three methodological precepts proposed above. They did not measure eye movements accurately enough to know the actual retinal placement of their stimuli. Perhaps for this reason, they did not use feedback to teach the observers to use all the available movement information. Therefore, the most we can know is that their observers habitually do not use retinal movement information to determine whether stimuli have moved during saccades – not that motion information is unavailable or suppressed. And the investigators did not run the simulated-movement control experiment within a fixation to permit comparisons of movement perception in retinally matched sequences of displays within and between saccade-separated fixations. Thus, while it is clear that people tend not to report perceiving motion between two saccade-separated flashes, the question "To what extent *can* motion be perceived between two saccade-separated fixations?" remains unanswered.

7.3.4. Recognition memory for images related by translations

While motion perception is an elementary computation that compares two (or more) views of the world, there may well be analogous higher-level computations. Consider that saccadic eye movements convert the visual input into essentially a series of still frames at a typical rate of about two or three frames per second. When the environment is stationary, all these successive images are related by simple translation. Might there be a specialized memory for recognizing and storing images which differ only by translation? How are the relationships between images coded to enable the observer to build up a coherent internal model of the world.

Recognition memory for translated images in the stationary eye. Let two successive images, such as might be produced by successive saccades, be produced on the stationary eye. Does the observer have any special ability to recognize relationships between such successive images? In one procedure, Roseanne Speelman and I presented subjects with two successive images, each consisting of ten shapes. One shape was changed; the remaining ones were the same in both presentations. The subject's memory was tested by asking which shape was different. Shapes were chosen that were not as easily named as alphanumeric characters, and brief exposure durations were used in order to selectively probe visual memory (and to reduce the role of verbal memory). The ten shapes were arranged in a horizontal row, and translated upward or downward. The direction of translation (up or down) and the distance between frames was varied randomly.

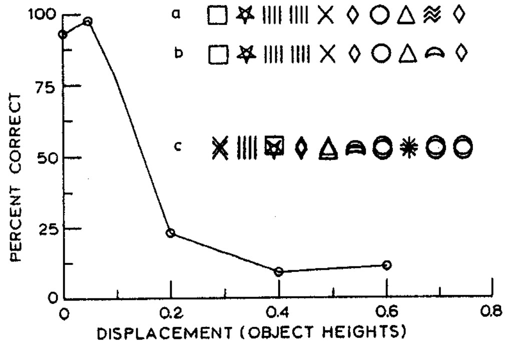


Fig. 14. Stimuli and results from a two-flash, simulated saccade memory experiment. The first stimulus is *a*; the second stimulus is *b*; the subject's task is to locate the changed position. Stimuli *a* and *b* occur in quick succession separated vertically, as shown. (*c*) Two stimuli that overlap by about 0.2 object heights. This small shift reduced performance from near perfect to less than 25% correct. The graph shows recognition accuracy (identification of changed locations) from an experiment in which displacement between memory and test stimuli was varied. The data points are the average of three subjects; the accuracies have been corrected for chance guessing. (Sperling and Speelman, unpublished data, AT&T Bell Labs, 1968.)

Fig. 14 shows typical results of the study in which the second flash immediately followed the first and the duration of each was 167 ms. When the shapes moved, strong motion cues were produced by the movement. In addition, the changed target item produced dramatically more local flicker and random apparent motions. The combined flicker/motion cue allowed the subjects easily to identify the location of the changed shape. However, the subjects had no special ability to identify the first of the two shapes in a location. Virtually identical results were obtained when shapes were moved horizontally or diagonally, when they were viewed from different distances, and when the subject knew in advance the probable direction of movement. There is a potential technical problem in studying large displacements which place the two rows one above the other, because visual persistence of the first array facilitates comparison with the second. However, under conditions that minimize visual persistence or when post-stimulus masks are used (Sperling, 1963), performance continues to decline monotonically with the magnitude of displacement regardless of its direction.

When the shapes moved for 1/5 of their extent or more, or there was a sufficiently long interstimulus interval so that motion cues did not selectively point to the altered shape, subjects did quite poorly. Subject's asymptotic performance can be characterized as indicating a memory of slightly more than one of the ten shapes. If the altered stimulus was the stimulus they had memorized, they detected the change; if not, they guessed randomly. There was no indication whatever of a special memory for translated images.

7.3.5. *Trans-saccadic perceptual fusion*

The perceptual fusion paradigm. Perceptual fusion refers to the phenomenon in which two consecutive displays are perceptually combined and perceived as a unitary display. For example, in the two-flash display of Eriksen and Collins (1967), some subareas of a stimulus letter are displayed in the first flash and the remaining ones in the second flash. When the first and second flashes occur in extremely close succession, the resulting stimulus is not discriminably different from a single exposure of the whole stimulus, and the letter is clearly identifiable. As the time between flashes is increased, perceptual fusion becomes increasingly difficult and, at around 100 ms of separation, depending somewhat on stimulus conditions, accuracy of letter identification drops to chance. In the two-flash stimulus developed by Hogben and DiLollo (1974), the first flash contains 12 dots randomly chosen from a 5×5 square array; the second flash contains 12 of the remaining 13 dots; and the subject's task is to locate the missing dot. Again, when the two flashes are presented in extremely close succession, the subject perceives 24 dots simultaneously, and the location of the missing dot is found effortlessly. As the interval between flashes is increased, performance eventually drops to chance levels. How does interposing a saccade between the two flashes affect perceptual fusion?

Fusion requires retinal, not spatial, superposition. An early study (Jonides et al., 1982) of perceptual fusion in the missing-dot paradigm erroneously reported that when flash 1 was presented in the periphery before a saccade, and flash 2 in the fovea after the saccade, there was good perceptual fusion. That is, the two flashes in the same physical location, but different retinal locations, could be combined to solve the missing-dot problem. Subsequently, this result was discovered to be an artifact of luminous persistence in the CRT display (Jonides et al., 1983).*

With correctly constructed displays, there is not more perceptual fusion in the between-fixation (interposed saccade) condition than in the within-fixation control. This was demonstrated in a letter-fusion paradigm by O'Regan and Levy-Schoen (1983) and in missing-dot paradigms by Bridgeman and Mayer (1983), Irwin et al. (1983) and Rayner and Pollatsek (1983). With an interposed saccade, two flashes that originate at the same physical location strike different retinal locations, but perceptually they seem to have originated from the same physical location. In the control condition in the stationary eye, flashes that fall on the same two retinal locations appear to have occurred at quite different physical locations. Each of these perceptions is correct. However, correctly perceiving retinally separated flashes to have occurred in the same spatial location does not imply useful trans-saccadic perceptual fusion.

Can perceptual fusion occur when two flashes strike the same retinal location but a saccade has intervened so that they appear to have occurred at different spatial locations? This question is quite similar to the two-flash motion question posed in

---

* Jonides et al. (1982) are not the only investigators to have erroneously reported trans-retinal perceptual fusion. See Irwin et al. (1983) for a critique.

an earlier section. In both cases (achieving perceptual fusion, detecting small retinal displacements) to succeed in the trans-saccadic task, the subject must succeed in ignoring or cancelling the nonvisual signals arising from the saccade. And because in both cases there are formidable technical and procedural difficulties in conducting the experiments, we do not yet have adequate answers.

7.3.6. Other tests of trans-saccadic memory: conclusion

Among the contexts in which the notion of a special trans-saccadic memory has been proposed is reading (McConkie and Rayner, 1976). Here, too, experimental attempts to demonstrate such a specific memory have failed (McConkie and Zola, 1979; Rayner et al., 1980; McConkie et al., 1982). Psychophysical discriminations which require memory for line length and for the shape of rectangles demonstrate that there is trans-saccadic memory (Palmer and Ames, 1989). However, that subjects remember length or shape from one fixation to the next is hardly a novel discovery. The particular issue that concerns us here is whether a saccade, as compared to a simulated saccadic display in the fixated eye, facilitates or inhibits performance in the memory task. The reading and psychophysical experiments have not been designed to answer this question.

The two-flash experiments have not yielded any data to suggest that interposing a saccade facilitates performance relative to the simulated saccade in the stationary eye. Indeed, there remains the as yet unproved possibility that when a task requires the subject to ignore nonvisual signals generated by a saccade, performance may suffer relative to the simulated saccade.

7.4. Organizing information from sequences of saccades

7.4.1. Spatially coordinating successive retinal images

A failure to coordinate successive images. Subjects with extreme tunnel vision are unable to coordinate the information from successive eye movements. A similar failure to coordinate images in the stationary eye was found by Hochberg (1968). Subjects viewed a sequence of frames that represented successive views of a complex shape. The subjects were unable to deduce the overall shape from these views. Apparently, the information about relative locations of points in successive views is not easily derived from a sequence of images.

7.4.2. Both image content and spatial location are represented symbolically

Spatial location as a tag. In the retina and visual cortex, spatial location is coded retinotopically and anatomically. It is taken as axiomatic that at higher levels of processing, spatial location is ultimately coded as a tag, not as an anatomical brain location. That is, successive views are stored not in a topological arrangement corresponding to their two-dimensional relationships in the environment, but in more complex symbolic form in which information about relative positions in space is carried as a tag or feature in the representation. A visual object is described by a set of visual features and the relationships between them.* The representation of spatial location of the object relative to other objects, to the body, and to the environment is not logically different from the representation of other relationships. In this respect, the representation of visual space is not essentially different from the representation of tactual space defined, for example, by the hands moving over a surface and attempting to learn about it.

Must spatial tags be derived from eye and body movements? One interesting question is whether the information about spatial position that is derived from the position of the body, head and eyes can be replaced with position information derived from other modalities. For example, can a repre-

---

* See Ballard (1987) and Feldman (1985) for discussion of the frames of reference within which observer-object relationships are best represented.

sentation of the environment be built up when the information about location is provided by the position of the hand rather than the eye. To investigate this question, the eye is fixated on a display screen. The subject places a finger at various spots on a surface and an image is produced corresponding to the neighborhood of each spot pointed at. To the extent that the subject can learn to substitute finger movements for eye movements, the visual processing of successive saccadically produced visual images is not uniquely linked to the oculomotor system but can utilize other channels which provide reliable spatial information.

8. Summary and conclusions

Smooth and saccadic eye movements are uniquely adapted to acquire information via an eye that is organized into a specialized fovea and a wide periphery. The most useful working hypothesis is that, while both visual sensory processes and motor control have evolved to a high degree of specialization to deal with the eye movements, modality-specific processes yield to content-specific processes as early as practicable in the processing hierarchy. Thus, in processing information acquired by pursuit and saccadic eye movements, the earliest link between the retinal and extra-retinal components of the eye movement appears to occur at high levels of processing. As a consequence, when differences on psychophysical tests of perception in responses to self-produced image motion and to imposed image motion were observed they were attributed, for the most part, to failures to provide truly equivalent retinal stimuli in the moving and the stationary eyes. For example, acuity seems to be determined by retinal slip, and it makes no difference whether the object or the eye is moving. Similarly, the visual system is designed so that the kind of motion smear produced during saccades is not perceived even when it is produced on a stationary retina by a simulated saccade. The many reports of changes of visual sensitivity during saccades are adequately explained by the masking effect of the actual sequence of stimuli on the retina and by the uncertainty in where a test stimulus that is flashed during a saccade will appear to be located.

Spatial localization of flash seen during a 4-degree saccadic eye movement did not differ from localization of a flash during the equivalent imposed image movement. Errors of localization could be explained by assuming that there was a temporal uncertainty of about 6 ms in when a visual test flash occurs relative to saccadically produced image movement. Additionally, for some subjects, the subjective duration of their saccadic image movement was somewhat longer than its objective duration, and the subjective movement began too soon (relative to a test flash). This slightly inaccurate internal representation of the imposed image movement produced characteristic localization errors. For larger saccades, there were significant differences between localization judgements in eye movements and imposed movements because extra-retinal information contributed significantly to saccadic localization.

Extra-retinal information about the time of saccadic occurrence is used to suppress sensations of visual apparent motion, which would otherwise occur with saccadic image motion on the retina. This saccadic motion suppression is similar to re-interpretation of sensory inputs following voluntary movement in other modalities. The extent to which subjects can learn to ignore extra-retinal information in making visual judgements during saccades is not yet known.

Other than the ability to compute apparent motion between related images (based on correlations between elementary local features), subjects have no special memory for images that are related by simple translation. To coordinate images produced by successive fixations, the visual/cognitive system needs spatial information about the direction of gaze. This directional information cannot easily be extracted from the image sequence but is normally provided by the oculomotor system in conjunction with the head and body. Possibly even this oculomotor directional information could be replaced by equivalent directional information acquired from other modalities.

While saccades are usually remarkably efficient, it was possible to create a search task in which performance was substantially improved by eliminating saccades and presenting stimuli at a rate five times faster than saccades (25 new search arrays per second). Sudden onsets of stimulation such as might be caused by saccades were shown not to be necessary to initiate information-processing episodes; gradual ramp onsets served equally well.

Most of these results should not have been surprising – hindsight is easier than insight – from the point of view of processing efficiency. Both the visual sensory system and the oculomotor system have evolved extremely specialized and extraordinarily sensitive processing capacities near their respective receptors and effectors. In the brain, however, motor signals concerned with eye movements and visual signals, the result of post-retinal image processing, apparently interact only at high levels where the visual signal, at least, is far removed from its sensory origin. Because visuo-motor interactions occur at a high level, it suggests that they may be modifiable and substitutable. For example, when the extent of saccadic eye movements is optically modified, visuo-motor recalibration quickly occurs.

The hypothesis that emerged was that direct sensory control of vision by the oculomotor system is unnecessary. For example, in order to avoid confounding motion signals produced by eye movements with real object motion, it is not necessary to desensitize the retina during saccades. It is sufficient to process all such motion signals equally, and then to disregard saccadic motion outputs at what might be regarded as an 'interpretive' level. On the other hand, to avoid noticing saccadic motion smear, the visual system has evolved to ignore smear-followed-by-clear signals independently of how they are generated. Again, there is no visuomotor interaction here, merely an effective adaptation of the visual system to a mode of seeing.

Acknowledgements

The preparation of this chapter was supported by The Air Force Office of Scientific Research, Life Sciences Directorate, Visual Information Processing Program Grant 88-0364 and by the Office of Naval Research, Cognitive and Neural Sciences Division, Grant N00014-88-K-0569. The author wishes to express his appreciation for the assistance provided by the late Roseanne G. Speelman in the experiments reported herein.

References

Adelson, E.H. and Bergen, J. (1985) Spatiotemporal energy models for the perception of motion. J. Opt. Soc. Am. A, 2, 284–299.

Averbach, E. and Sperling, G. (1961) Short term storage of information in vision. In: C. Cherry (Ed.), Information Theory. Butterworths, Washington DC, pp. 196–211.

Ballard, D.H. (1987) Eye movements and spatial cognition. Technical Report 218, University of Rochester Computer Science, 50 pp.

Bischof, N. and Kramer, E. (1968) Untersuchungen und Ueberlegungen zur Richtungswahrnehmung bei Willkuerichen sakadischen Augenbewegung. Physiol. Forsch. 32, 185–218.

Bridgeman, B. and Mayer, M. (1983) Failure to integrate visual information from successive fixations. Bull. Psychonomic. Soc. 21, 285–286.

Bridgeman, B., Hendry, D. and Stark, L. (1975) Failure to detect displacement of the visual world during saccadic eye movements. Vision Res. 15, 719–722.

Brooks, B.A. and Fuchs, A.F. (1975) Influence of stimulus parameters on visual sensitivity during saccadic eye movement. Vision Res. 15, 1389–1398.

Brooks, B.A. and Impelman, D.M. (1981) Suppressive effects of a peripheral grating displacement during saccadic eye movement and during fixation. Exp. Brain Res. 42, 489–492.

Brooks, B.A., Impelman, D.M. and Lum, J.T. (1980a) Influence of background luminance on visual sensitivity during saccadic eye movements. Exptl. Brain Res. 40, 322–329.

Brooks, B.A., Yates, J.T. and Coleman, R.D. (1980b) Perception of images moving at saccadic velocities during saccades and during fixation. Exp. Brain Res. 40, 71–78.

Bruno, N. and Cutting, J.E. (1988) Minimodularity and the perception of layout. J. Exp. Psychol. Hum. Percept. Performance, 117, 161–170.

Burr, D. (1980) Motion smear. Nature 284, 164–165.

Campbell, F.W. and Wurtz, R.H. (1978) Saccadic omission: why we do not see a grey-out during a saccadic eye movement. Vision Res. 18, 1297–1303.

Clocksin, W.F. (1980) Perception of surface slant and edge labels from optical flow: a computational approach. Perception 9, 253–269.

Collewijn, H., Steinman, R.M. and van der Steen, H. (1985) The performance of the smooth pursuit eye movement system during passive and self-generated stimulus motion. J. Physiol. 366, 19P.

Corfield, R., Frosdick, J.P. and Campbell, F.W. (1978) Greyout elimination: the roles of spatial waveform, frequency and phase. Vision Res. 18, 1305–1311.

Davidson, M.L., Fox, M.J. and Dick, A.O. (1973) Effect of eye movements on backward masking and perceived location. Percept. Psychophys. 14, 110–116.

Ditchburn, R.N. and Ginsborg, B.L. (1952) Vision with a stabilized retinal image. Nature 170, 36–37.

Dodge, R. and Fox, J.C. (1928) Optic nystagmus. I. Technical introduction with observations in a case with central scotoma in the right eye and external rectus palsy in the left eye. Arch. Neurol. Psychiatry 20, 812–823.

Dosher, B.A., Sperling, G. and Wurst, S.A. (1986) Tradeoffs between stereopsis and proximity luminance covariance. Vision Res. 26, 973–990.

Dubois, M.F.W. and Collewijn, H. (1979) Optokinetic reactions in man elicited by localized retinal motion stimuli. Vision Res. 19, 1105–1115.

Efron, R. (1970a) The relationship between the duration of a stimulus and the duration of a perception. Neurophysiologica 8, 37–55.

Efron, R. (1970b) The minimum duration of perception. Neurophysiologica 8, 56–63.

Eriksen, C.W. and Collins, J.F. (1967) Some temporal characteristics of visual pattern perception. J. Exp. Psychol. 74, 476–484.

Feldman, J.A. (1985) Four frames suffice: a provisional model of vision and space. Behav. Brain Sci. 8, 265–289.

Fisher, D.L. (1982) Limited-channel models of automatic detection: capacity and scanning in visual search. Psychol. Rev. 89, 662–692.

Gerrits, H.J.M. and Vendrik, A.J.H. (1974) The influence of stimulus movements on perception in parafoveal stabilized vision. Vision Res. 14, 175–180.

Haegerstrom-Portnoy, G. and Brown, B. (1979) Contrast effects on smooth-pursuit eye movement velocity. Vision Res. 19, 169–174.

Hansen, P.M. (1979) Spatial localization during pursuit eye movements. Vision Res. 19, 1213–1221.

Hansen, R.M. and Skavenski, A.A. (1977) Accuracy of eye position information for motor control. Vision Res. 17, 919–926.

Hansen, R.M. and Skavenski, A.A. (1985) Accuracy of spatial localizations near the time of saccadic eye movements. Vision Res. 25, 1077–1082.

Heeger, D.J. (1987) A model for the extraction of image flow. J. Opt. Soc. Am. A, 4, 1455–1471.

Hochberg, J. (1968). In the mind's eye. In: R.N. Haber (Ed.), Contemporary Theory and Research in Visual Perception. Appleton-Century-Crofts, New York.

Hoffman, D.D. (1982) Inferring local surface orientation from motion fields. J. Opt. Soc. Am. 72, 888–892.

Hogben, J.H. and Di Lollo, V. (1974) Perceptual integration of brief visual stimuli. Vision Res. 14, 1059–1069.

Irwin, D.E., Yantis, S. and Jonides, J. (1983) Evidence against visual integration across saccadic eye movements. Percept. Psychophys. 34, 49–57.

Irwin, D.E., Brown, J.S. and Jun-Shi Sun. (1988) Visual masking and visual integration across saccadic eye movements. J. Exp. Psychol. Gen. 117, 276–287.

Javel, L.E. (1878) Essai sur la physiologie de la lecture. Ann. d'Oculistique 82, 242–253.

Jonides, J., Irwin, D.E. and Yantis, S. (1982) Integrating visual information for successive fixations. Science 215, 192–194.

Jonides, J., Irwin, D.E. and Yantis, S. (1983) Failure to integrate visual information for successive fixations. Science 222, 188.

Keller, E.L. and Zee, D.S. (Eds.) (1986) Adaptive Process in Visual and Oculomotor Systems. Pergamon Press, Oxford.

Kelly, D.H. (1979) Motion and vision. II. Stabilized spatiotemporal threshold surface. J. Opt. Soc. Am. 69, 1340–1349.

Khurana, B. and Kowler, E. (1987) Shared attentional control of smooth eye movement and perception. Vision Res. 27, 1603–1618.

Koenderink, J.J. and van Doorn, A.J. (1986) Depth and shape from differential perspective in the presence of bending deformations. J. Opt. Soc. Am. A, 3, 242–249.

Kowler, E. and Sperling, G. (1980) Transient stimulation does not aid visual search: implications for the role of saccades. Percept. Psychophys. 27, 1–10.

Kowler, E. and Sperling, G. (1983) Abrupt onsets do not aid visual search. Percept. Psychophys. 34, 307–313.

Kowler, E. and Steinman, R.M. (1980) Small saccades serve no useful purpose: reply to a letter by R.W. Ditchburn. Vision Res. 20, 273–276.

Kowler, E., van der Steen, J., Tamminga, E.P. and Collewijn, H. (1984) Voluntary selection of the target for smooth eye movement in the presence of superimposed, full-field stationary and moving stimuli. Vision Res. 24, 1789–1798.

Krauskopf, J. (1957) Effet of retinal image motion on contrast threshold for maintained vision. J. Opt. Soc. Am. 47, 740–744.

Krauskopf, J. (1960) Effect of target oscillation on contrast resolution. J. Opt. Soc. Am. 50, 1306.

Krauskopf, J. (1962) Light distribution in human retinal images. J. Opt. Soc. Am. 52, 1046–1050.

Lennie, P. and Sidwell, A. (1978) Saccadic eye movements and visual stability. Nature 275, 766–768.

Loftus, G.R. (1972) Eye fixations and recognition memory. Cognitive Psychol. 3, 525–551.

Loftus, G.R. (1981) Tachistoscopic simulations of eye fixations on pictures. J. Exp. Psychol. Hum. Learn. Mem. 7, 369–376.

Longuet-Higgins, H.C. and Prazdny, K. (1980) The interpretation of a moving retinal image. Proc. R. Soc. Lond. Ser. B, 208, 385–397.

Mack, A. (1970) An investigation of the relationship between eye and retinal image movement in the perception of motion. Percept. Psychophys. 8, 291–298.

Mack, A. (1986) Perceptual aspects of motion in the frontal plane. In: K. Boff, L. Kaufman and J. Thomas (Eds.), Handbook of Perception and Performance, Vol. 1, Wiley, New York, Ch. 17, pp. 1–38.

MacKay, D.M. (1970a) Elevation of visual threshold by displacement of retinal image. Nature 225, 90–92.

MacKay, D.M. (1970b) Mislocation of test flashes during saccadic image displacements. Nature 227, 731–733.

MacKay, D.M. (1973) Visual stability and voluntary eye movements. In: R. Jung (Ed.), Handbook of Sensory Physiology, Vol. 7. Springer Verlag, Berlin, pp. 307–331.

Maloney, L.T. (1988) Spatially irregular sampling in combination with rigid movements of the sampling array. Invest. Ophthalmol. Vis. Sci. 1988, 29, 58.

Maloney, L.T. (1990) The consequences of discrete retinal sampling for vision. In: M.S. Landy and A.J. Movshon (Eds.), Computational Models of Visual Processing. Cambridge, MIT Press, Cambridge, MA.

Mateeff, S. (1978) Saccadic eye movements and localization of visual stimuli. Percept. Psychophys. 24, 215–224.

Matin, L. (1986) Visual localization and eye movements. In: K. Boff, L. Kaufman and J. Thomas (Eds.), Handbook of Perception and Performance, Vol. 1, Wiley, New York, Ch. 20, pp. 1–45.

McConkie, G.W. and Rayner, K. (1976) Identifying the span of the effective stimulus in reading: literature review and theories of reading. In: H. Singer and R.B. Ruddell (Eds.), Theoretical Models and Processes of Reading. International Reading Association, Newark, DE.

McConkie, G.W. and Zola, D. (1979) Is visual information integrated across successive fixations in reading? Percept. Psychophys. 25, 221–224.

McConkie, G.W., Zola, D., Blanchard, H.E. and Wolverton, G.S. (1982) Perceiving words during reading: lack of facilitation from prior peripheral exposure. Percept. Psychophys. 32, 271–281.

Meyer, C.H., Lasker, A.G. and Robinson, D.A. (1985) The upper limit of human smooth pursuit velocity. Vision Res. 25, 561–563.

Murphy, B. (1978) Pattern threshold for moving and stationary gratings during smooth eye movements. Vision Res. 18, 521–530.

Nachmias, J. (1961) Determiners of the drift of the eye during monocular fixation. J. Opt. Soc. Am. 51, 761–766.

Neisser, U. (1963) Decision time without reaction time: experiments in visual scanning. Am. J. Psychol. 76, 376–385.

Neisser, U. (1964) Visual search. Sci. Am. 210.

Neisser, U., Novick, R. and Lazar, R. (1963) Searching for ten targets simultaneously. Percept. Motor Skills 17, 955–961.

O'Regan, J.K. (1984) Retinal versus extraretinal influences in flash localization during saccadic eye movements in the presence of a visible backround. Percept. Psychophys. 36, 1–14.

O'Regan, J.K. and Levy-Schoen, A. (1983) Integrating information from successive fixations: does trans-saccadic fusion exist? Vision Res. 23, 765–768.

Palmer, J. and Ames, C.T. (1989) Measuring the effect of multiple eye fixations on size and shape discrimination. Invest. Ophthalmol. Vis. Sc. ARVO Suppl. 30, 159.

Pola, J. (1972) The relation of visual direction to eye position during and following a voluntary saccade. Unpublished doctoral dissertation. Columbia University.

Ratliff, F. and Riggs, L.A. (1950) Involuntary motions of the eye during monocular fixation. J. Exp. Psychol. 40, 687–701.

Rayner, K. and Pollatsek, K. (1983). Is visual information integrated across saccades? Percept. Psychophys. 34, 39–48.

Rayner, K., McConkie, G.W. and Zola, D. (1980) Integrating information across eye movements. Cognitive Psychol. 12, 206–226.

Reeves, A. (1977) The identification and recall of rapidly displayed letters and digits. Unpublished doctoral dissertation, City University of New York.

Reeves, A. and Sperling, G. (1986) Attention gating in short-term visual memory. Psychol. Rev. 93, 180–206.

Riggs, L.A., Ratliff, F., Cornsweet, J.C. and Cornsweet, T.N. (1953) The disappearance of steadily fixated visual test objects. J. Opt. Soc. Am. 43, 495–501.

Shiori, S. and Cavanagh, P. (1989) Saccadic suppression of low-level motion. Vision Res. 29, 915–928.

Skavenski, A.A., Hansen, R., Steinman, R.M. and Winterson, B.J. (1979) Quality of human retinal stabilization during small natural and artificial body rotations in man. Vision Res. 19, 675–683.

Sperling, G. (1960) The information available in brief visual presentations. Psychol. Monogr. 74, No. 11 (Whole No. 498).

Sperling, G. (1963) A model for visual memory tasks. Hum. Factors 5, 19–31.

Sperling, G. (1966) Comparisons of real and apparent motion. J. Opt. Soc. Am. 56, 1442.

Sperling, G. (1967) Successive approximations to a model for short-term memory. Acta Psychol. 27, 285–292.

Sperling, G. (1979) Critical duration, supersummation, and the narrow domain of strength-duration experiments. Behav. Brain Sc. 2, 279–282.

Sperling, G. and Dosher, B.A. (1986) Strategy and optimization in human information processing. In: K. Boff, L. Kaufman and J. Thomas (Eds.), Handbook of Perception and Performance, Vol. 1, Wiley, New York, Ch. 2, pp. 1–65.

Sperling, G. and Melchner, M.J. (1978) The attention operating characteristic: some examples from visual search. Science 202, 315–318.

Sperling, G. and Reeves, A. (1980) Measuring the reaction time of a shift of visual attention. In: R. Nickerson (Ed.), Attention and Performance, Vol. VIII. Erlbaum, Hillsdale, NJ, pp. 347–360.

Sperling, G. and Speelman, R.G. (1964) Spatial localization during eye movements. Am. Psychol. 19, 526–527.

Sperling, G. and Speelman, R.G. (1965) Visual spatial localization during object motion, apparent object motion, and image motion produced by eye movements. J. Opt. Soc. Am. 55, 1576.

Sperling, G. and Weichselgartner, E. (1989) Movement dynamics of spatial attention. Mathematical Studies in Perception and Cognition, 89–14. Department of Psychology, New York University.

Sperling, G., Budiansky, J., Spivak, J.G. and Johnson, M.C. (1971) Extremely rapid visual search: the maximum rate of scanning letters for the presence of a numeral. Science 174, 307–311.

Sperling, G., Landy, M.S., Dosher, B.A. and Perkins, M. (1989) Kinetic depth effect and identification of shape. J. Exp. Psychol. Hum. Percept. Performance 15, 826–840.

Sperling, G., Dosher, B.A. and Landy, M.S. (1990) How to study the kinetic depth effect experimentally. J. Exp. Psychol. Hum. Percept. Performance 16, 445–450.

Stark, L., Kong, R., Schwartz, S., Hndry, D. and Bridgeman, B. (1976) Saccadic suppression of image displacement. Vision Res. 16, 1185–1187.

Steinman, R.M. and Collewijn, H. (1973) Binocular retinal image motion during active head rotation. Vision Res. 20, 415–429.

Steinman, R.M., Haddad, G.M., Skavenski, A.A. and Wyman, D. (1973) Miniature eye movement. Science 181, 810–819.

Steinman, R.M., Levinson, J.Z., Collewijn, H. and Steen, J. van der (1985) Vision in the presence of known natural retinal image motion. J. Opt. Soc. Am. A, 2, 226–233.

Thurstone, L.L. (1927) A law of comparative judgment. Psychol. Rev. 34, 273–386.

van Santen, J.P.H. and Sperling, G. (1984) A temporal covariance model of motion perception. J. Opt. Soc. Am. A, 1, 451–473.

van Santen, J.P.H. and Sperling, G. (1985) Elaborated Reichardt detectors. J. Opt. Soc. Am. A, 2, 300–321.

Volkmann, F.C. (1986) Human visual suppression. Vision Res. 26, 1401–1416.

Watson, A.B., Ahumada, A.J. and Farrell, J.E. (1986) The window of visibility: a psychophysical theory of fidelity in time-sampled motion displays. J. Opt. Soc. Am. A, 3, 300–307.

Watson, A.B. and Ahumada, A.J. (1983) A look at motion in the frequency domain. NASA Tech. Memo. 84352.

Watson, A.B. and Nachmias, J. (1977) Patterns of temporal interaction in the detection of gratings. Vision Res. 17, 1143–1149.

Weichselgartner, E. (1984) Two processes in visual attention. Unpublished doctoral thesis. Department of Psychology, New York University, pp. 141.

Weichselgartner, E. and Sperling, G. (1985) Continuous measurement of visible persistence. J.Exp. Psychol. Hum. Percept. Performance 11, 711–725.

Weichselgartner, E. and Sperling, G. (1987) Dynamics of automatic and controlled visual attention. Science 238, 778–780.

Westheimer, G., and Campbell, F.W. (1962) Light distribution in the image formed by the living human eye. J. Opt. Soc. Am. 52, 1040–1045.

Whipple, W.R. and Wallach, H. (1978) Direction-specific motion thresholds for abnormal image shifts during saccadic eye movement. Percept. Psychophys. 24, 349–355.

Winterson, B.J. and Steinman, R.M. (1978) The effect of luminance on human smooth pursuit of parafoveal and foveal targets. Vision Res. 18, 1165–1172.

Woodworth, R.S. (1906) Vision and localization during eye movements. Psychol. Bull. 3, 68–70.

Woodworth, R.S. (1938) Experimental Psychology. Henry Holt and Co., New York.

Yarbus, A.L. (1957) The perception of an image fixed with respect to the retina. Biofiz. (USSR) 2, 703–712. (Translated by J.E.S. Bradley.)

Yellott, J.I. Jr. (1987) Consequences of spatially irregular sampling for reconstruction of photon noisy images. Invest. Ophthalmol. Vis. Sci. ARVO Suppl. 28, 137.