



Postsaccadic Target Blanking Prevents Saccadic Suppression of Image Displacement

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Displacement of a visual target during a saccadic eye movement is normally detected only at a high threshold, implying that high-quality information about target position is not stored in the nervous system across the saccade. We show that blanking the target for 50–300 msec after a saccade restores sensitivity to the displacement. With blanking, subjects reliably detect displacements as small as 0.33 deg across 6 deg eye movements, with correspondingly steep psychophysical functions. Performance with blanking in a fixation control is inferior, evidence for a saccadic enhancement of sensitivity to image displacement. If blanking is delayed so that the target is visible immediately after the saccade in its displaced position, performance declines to non-blanking levels. Blanking the target before the saccade, and restoring it during the saccade, yields a similar but weaker effect. We interpret these results with a model in which the visual system searches for the postsaccadic goal target within a restricted spatiotemporal window. If it is not found, the assumption of stationarity of the world is broken and the system makes use of other information such as extraretinal signals for calibrating location.

Displacement threshold	Eye movement	Saccade	<u>Extraretinal eye position information</u>
Saccadic suppression	Space perception	Spatial vision	

INTRODUCTION

Though saccadic eye movements occur several times per second throughout waking life, their perceptual consequences remain incompletely understood. It is clear that visual processing is interrupted during saccades. This was first described by Dodge (1900) as an increase in threshold of a flashed target, and others have since elaborated on this result (Latour, 1962; Volkmann, Riggs, Moore & White, 1978). This saccadic suppression effect is fairly small, about 0.5–0.7 log units, and even this is seen only if the flashed stimulus is near threshold. If the position of a visual target rather than its brightness is changed during a saccade, however, the strength of saccadic suppression can reach more than 4 log units above the normal displacement threshold (Bridgeman, Hendry & Stark, 1975). In these experiments a continuously present target is abruptly displaced during a saccade, and remains in the displaced position afterwards. The effect was discovered at least three times. First noted by Ditchburn (1955), it was rediscovered independently by Wallach and Lewis (1966) and

by Brune and Lücking (1969), and has been replicated many times (reviewed in Bridgeman *et al.*, 1975). The saccadic suppression of image displacement effect follows a time-course similar to that of flash suppression, beginning before the eye begins to move, reaching a maximum near the beginning of the saccade, and continuing to the end of the saccade.

The saccadic suppression of image displacement has a disturbing consequence, however: it implies that information about the location of the visual world is severely degraded across saccades, for large displacements of the visual world go unnoticed. We remain spatially oriented in the visual world, though, being able to perform accurate spatial motor actions, despite this disturbance. This seeming paradox was addressed by Bridgeman, Lewis, Heit and Nagle (1979) and by Prablanc and Martin (1992), who showed that motor orientation measured by pointing to a target can remain accurate even though the perceived displacement of the same target is masked by saccadic suppression. Subjects pointed equally accurately to a displaced and extinguished visual target whether they had cognitively detected its displacement or not. Similar sparing of motor ability despite a perceptual saccadic suppression of displacement has been observed by Hansen and Ska-venski (1977) with ballistic motor activity. Thus precise extraretinal information about the change in location of the target, defined egocentrically, must have been preserved at some level in the nervous system to correct

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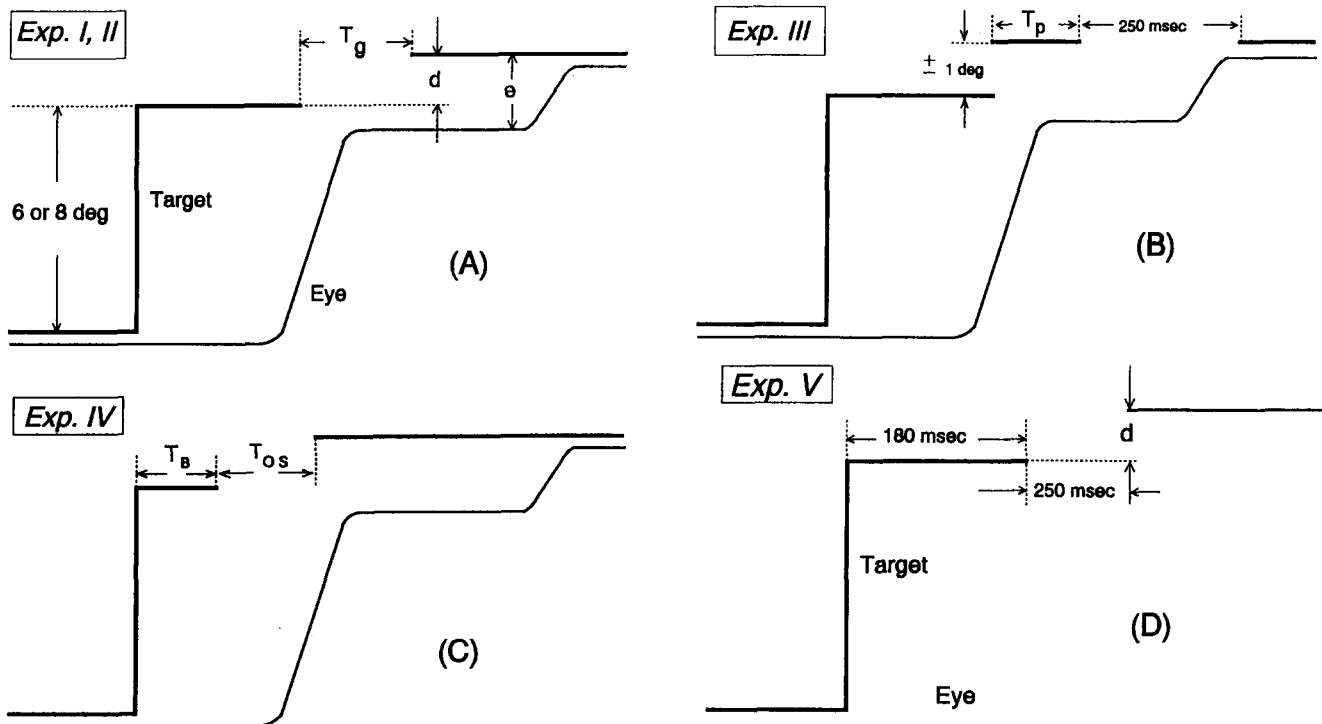


FIGURE 1. Experimental paradigms for Expts I–V. In each graph the vertical axis represents horizontal position on the screen; the horizontal axis represents time. Bold line: target position. Thin line: eye position. In Expts I–IV, the first target step occurs to the left or to the right, with a magnitude of 6 or 8 deg, selected at random. (A) Experiments I and II. Triggered by the primary saccade, the target disappears for a variable gap duration T_g . After the gap, the target reappears at a position displaced by d and is stationary until the subject's decision; displacement occurs into the same or the opposite direction of the first step ("forward" vs "backward"). e is the retinal error, eventually eliminated by a corrective saccade. The subject indicates, in a two-alternative forced-choice procedure, the direction of displacement with respect to the initial target step ("forward" vs "backward"). After the decision, the next trial starts, with the actual target position being the new fixation position. (B) Experiment III. The target is displaced by 1 deg during the saccade, and switched off after a variable pulse duration T_p . The target reappears 250 msec later. The next trial starts after the subject's decision upon displacement direction. (C) Experiment IV (presaccadic gap). The target is blanked at variable delays T_B after the first target step. T_B is varied randomly between 50 and 150 msec, leading to variable time intervals T_{OS} between target offset and saccade onset. Triggered by the saccade, the target reappears at a position displaced by ± 1 deg. (D) Experiment V (fixation condition). The target is deleted 180 msec after the initial target step, and reappears after 250 msec at the displaced position. Displacement size d is varied between -2 and $+2$ deg (mixed design). The subject has to maintain fixation at the central position throughout the experiment.

the pointing response, but that information could not be used to detect the displacement of the same target.

In another experiment that showed behavioral ability to respond appropriately to a saccade target at a motor level despite perceptual illusions, Wong and Mack (1981) displaced a background so that a small target appeared to jump in the opposite direction [stroboscopic induced motion (Duncker, 1929)]. In some trials the target jumped in the same direction as the background, but not far enough to cancel the entire induced motion effect. Thus the target seemed to jump in one direction relative to the subject but actually jumped in the other. Saccadic eye movements, if they occurred close in time to the target jump, followed the egocentric direction even though it was opposite the perceived direction. So the subjects made a saccade in one direction even though they perceived a target displacement in another. Clearly, these experiments show that precise information about target position or displacement is held in the brain despite its inaccessibility to normal perception.

The current experiments explore an experimental paradigm in which this precise information, normally

available only to motor control, becomes also available to perception. The observation began with an analysis of corrective saccades (Deubel, Wolf & Hauske, 1982). When a subject has the task of following a target that jumps across the visual field, a tracking saccade is often followed by a smaller corrective saccade that brings the target into the fovea. The corrective saccade is often controlled by visual input, and can be modified in size by adding a second jump to the target during the primary saccade. This second jump is normally undetectable due to saccadic suppression of displacement. In order to study the corrective saccade more closely, it was delayed artificially by blanking the target during and after the primary saccade [Fig. 1(A)]. This forced the eye movement control system to wait until the target was again available before launching the corrective saccade. Surprisingly, this lack of a visible target after a saccade led to the perceptual reappearance of the target jump during the saccade. The aim of the current experiments was to quantify this effect, and then to study its implications for perceptual localization in connection with saccadic eye movements. Preliminary reports of the

experimental findings were presented elsewhere (Deubel & Schneider, 1994; Deubel, Schneider & Bridgeman, 1994).

METHODS

Subjects

Between four and seven paid subjects participated in each of the experiments. The subjects' ages ranged from 21 to 32 yr. They were naive with respect to the object of the study, but were experienced with the equipment from other eye-movement related tasks. All subjects had normal visual acuity. Depending on the experiment, each subject performed three to six separate sessions, producing 600–1200 single reactions for each paradigm.

Apparatus

The experiments were controlled by a 486 PC, which also served for the automatic off-line analysis of the eye movement data in which saccadic latencies and saccade start and end positions were determined. Two different methods for stimulus presentation and for measuring eye movements were applied. With the exception of Expt IIa, we used a CRT monitor for stimulus presentation, and a Dual-Purkinje-image eyetracker for eye position registration.

The stimuli were presented on a 21 in. color video monitor (CONRAC 7550 C21). In combination with a TIGA graphics board (KONTRAST 8000), the monitor provided a spatial resolution of 1024×768 pixels at a frame rate of 100 Hz. The visual target consisted of a small white cross subtending a visual angle of 0.2 deg. Screen background luminance was set to 2.2 cd/m^2 ; the luminance of the saccade target was 25 cd/m^2 . In order to assure that the results were not affected by phosphor persistence, we measured the temporal decay of the phosphor luminescence with a linear PIN diode (for the technique, see Wolf & Deubel, 1993). Due to the steady background luminance, the contrast of the saccade targets decayed to 0.4% within 10 msec, excluding any effect of phosphor persistence on the data.

The subject viewed the screen binocularly from a distance of 80 cm. Head movements were restricted by a biteboard and a forehead rest. Eye movements were measured with a SRI Generation 5.5 Purkinje-image eyetracker (Crane & Steele, 1985) and sampled at 400 Hz. The frequency response of this eyetracker is better than 250 Hz with a noise level equivalent to about 20 sec arc r.m.s. The eyetracker can follow saccadic movements of 15 deg or more without losing the eye.

For a control experiment (Expt IIa), we combined a luminous laser target dot with a high-resolution scleral search coil technique for measuring eye movement. The dot (diameter 0.15 deg, intensity approx. 80 cd/m^2) was backprojected on a large translucent screen and could be displaced by means of fast x - y galvanometer scanner motors. Viewing distance was 1.5 m. Under computer control, the laser could be switched off electronically within a few microseconds. With this apparatus we could

work in complete darkness, with only the target visible in the visual field, and without the delay caused by the frame raster. For the eye position recording, the subject was placed in the center of a $70 \times 70 \times 70$ cm horizontal and vertical magnetic field created by coils (SKALAR, Delft) driven by high-frequency alternating current (20 kHz). The subject's head was stabilized with a forehead and chin rest. A standard two-dimensional silicon contact coil (SKALAR, Delft) was placed on the sclera after anesthesia of the right eye. The electromagnetic field induced a voltage in the coil representing the eye position. The subject's eye movements were calibrated at the beginning of each session by sequential fixation of 10 positions arranged on a circular array of 12 deg radius around the central fixation spot. After calibration, the overall accuracy of the system was better than 5 min arc and the signal-to-noise ratio better than 1 min arc.

By digital differentiation of the sampled eye position signal, the computer derived a trigger signal indicating saccade onset. The saccade trigger was adjusted at high sensitivity: when instantaneous eye velocity exceeded 30 deg/sec, saccade-related sensory events were triggered. Early triggering is important because of a considerable delay in Purkinje-image eyetracker records due to slippage of the lens within the eye (Deubel & Bridgeman, 1995) and a display delay of up to 10 msec because of screen raster delays. The early triggering ensured that stimulus modifications occurred before the eye reached maximum velocity.

Calibration and data analysis

Each session started with a calibration procedure in which the subject had to sequentially fixate 10 positions arranged on a circular array of 8 deg radius. The tracker behaved linearly within 8 deg around the central fixation. Overall accuracy of the eyetracker for static fixation positions was better than 0.1 deg. Dynamically, however, the eyetracker records considerable artifactual overshoots at the end of each saccade which we ascribe to the movement of the eye lens relative to the optical axis of the eye (Deubel & Bridgeman, 1995). In order to determine direction of gaze, an off-line program for evaluation of saccade parameters searched the eye position record for the end of the overshoot and then calculated mean eye position over a 40 msec time window. The automatic eye movement analysis program calculated latencies and start and landing positions of all saccades occurring in each trial.

Behavioral paradigm

Figure 1 shows the stimulus sequences used in the five experiments (Expts I–V). The subject's task in the first four experiments was first to maintain fixation on the target, and then to track it with a saccade if it jumped across the visual field. Thus saccades were elicited by a jump of the fixation target itself, not by some other stimulus. The fixation target was the only object present in the visual field. Experiment V was a control

experiment with similar stimulus parameters presented during ocular fixation.

In each trial the target jumped twice. The first step of 6 or 8 deg, selected at random, was the stimulus for a saccade, while the second displacement was smaller, e.g. 1 deg. We interspersed 6 and 8 deg saccades so that subjects would not be able to predict the saccade amplitude, and they would make true target-driven refixating saccades rather than preprogrammed saccades. On the other hand, the size difference is too small to yield significantly different results for the different amplitudes. Indeed we did not observe any significant differences in performance for the 6 deg vs the 8 deg target steps, and therefore the data from both conditions were pooled in the analysis of performance. Saccades beginning earlier than 140 msec or later than 400 msec after the initial target step were discarded from the analysis. The second jump was triggered by the computer when it detected the saccade elicited by the first target step. At the end of each trial, in a two-alternative forced-choice procedure, the subject's task was to report the direction of the second target shift with respect to the direction of the large initial target step ("forward vs backward"). The two-alternative forced-choice methodology, combined with a parametric range of stimuli, allows us to assess bias and sensitivity of discrimination separately. The subjects normally responded 500–1000 msec after the saccade; since the reactions were not performed under time pressure, we did not study manual reaction times in more detail. In most of the paradigms described below, the target spot was extinguished for various periods during the trial, then reappeared and was stationary until the subject's manual response; then the next trial started. A mixed design was used in which gap or stimulus durations, if varied, were selected at random from a set of predetermined values.

In Expt I we studied the effect of the duration of a post-saccadic stimulus gap of 0–270 msec on the discrimination of target displacement direction. Displacement size was kept constant at 1 deg. The displacement occurred either in the same direction as the saccade or in the opposite direction, selected at random.

In Expt II we analyzed the dependence of displacement discrimination on the size and direction of the target displacement. Here, gap duration was always either 0 or 250 msec (selected at random). The control Expt IIa used the same design except that the stimulus was a laser spot in total darkness, and eye position was monitored with a scleral search coil.

In Expt III, the target was displaced by 1 deg during the saccade, presented for various durations after the displacement, and then blanked for 250 msec.

In Expt IV, the effect of presaccadic target gaps was investigated by varying target offset in various time intervals before the saccade. The target reappeared, displaced by ± 1 deg, with the saccade trigger signal.

Experiment V consisted of a fixation condition. The stimulus sequence was like that used in Expt II, except that the subject maintained fixation at the central position throughout each trial.

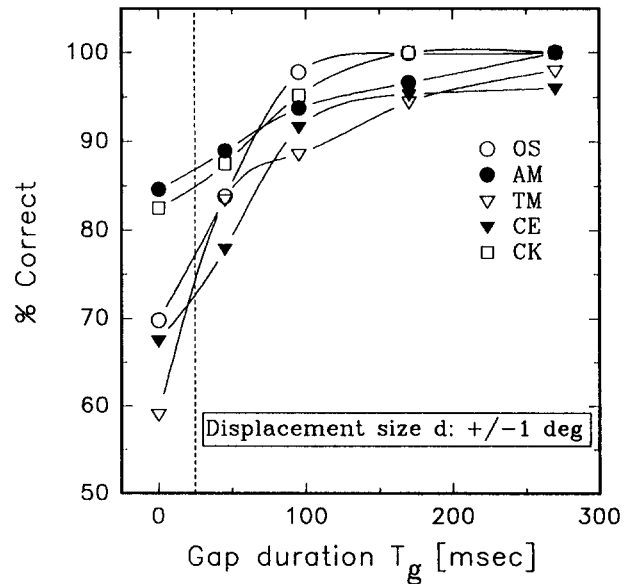


FIGURE 2. Discrimination performance as a function of gap duration in Expt I. The target is displaced with equal probability either to the left or to the right during the primary saccade, so that 50% correct represents no information about target displacement. Displacement size is 1 deg. In this and subsequent figures, each symbol represents one subject.

RESULTS

Experiment I

Experiment I studied the effect of target blanking on the discrimination between forward and backward secondary target displacements [see Fig. 1(A)]. Five subjects participated in this experiment. Gap duration was selected at random from 0, 50, 100, 180, and 270 msec (mixed design). Figure 2 displays discrimination performance (i.e., the percent of time the subject was correct in judging the direction of the target step) as a function of gap duration (T_g). The vertical dashed line indicates the approximate end of the fast, saccadic part of the eye movement.

The data reveal a strong dependency of discrimination performance on gap duration. Discrimination of forward vs backward steps is worst, in some subjects close to chance level (50%), for the non-gap situation, i.e. for $T_g = 0$. Under this condition, the subjects report that they have the firm impression of a stable target. Overall, they exhibit a bias towards perceiving forward displacements. This situation replicates the numerous saccadic suppression of displacement studies cited in the introduction.

Surprisingly, performance improves rapidly with the introduction of a target gap, leading to a steep increase in the percentage of correct responses when gap duration increases to 100 msec. For blanking periods of 170 msec or longer, subjects become almost perfect in their judgment of displacement direction. For these longer gap durations, the subjects report that they clearly perceive the shift of the target, without being able to report the target blanking itself. The question arises whether the striking improvement in performance between the no-gap and the gap situations is due to a

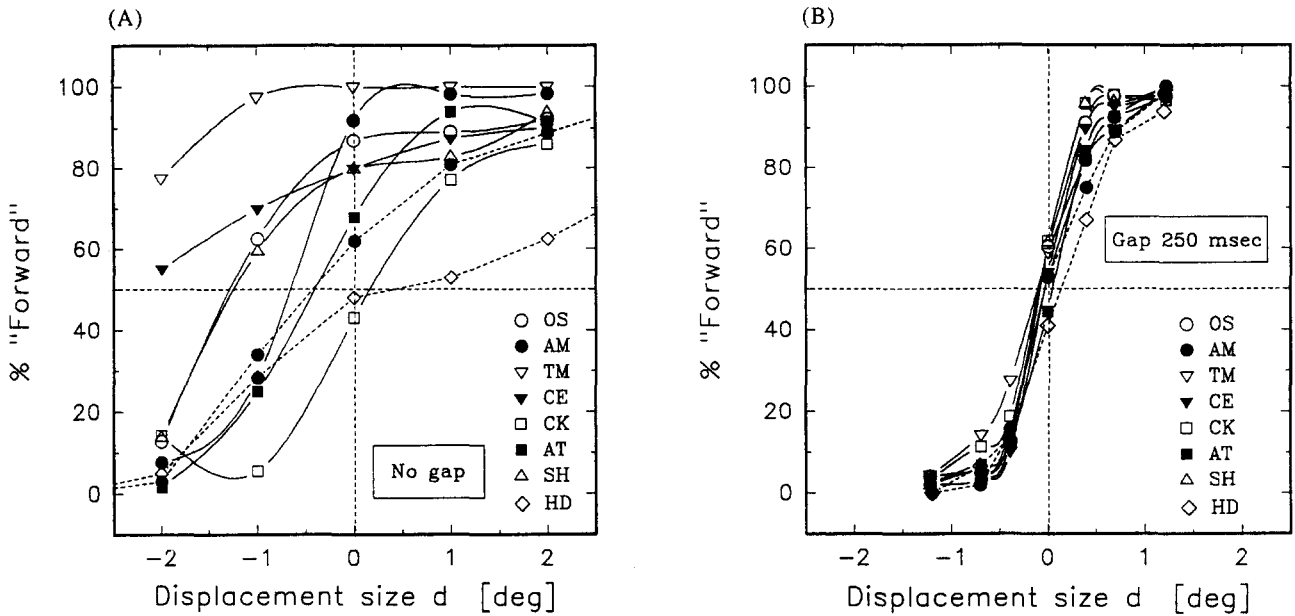


FIGURE 3. Percentage of displacements judged to be in the forward direction (the same direction as the primary saccade) vs displacement size in Expt II. Negative displacement sizes represent target jumps in the direction opposite the primary saccade. Each data point represents 100 trials. Stimulus conditions in the gap condition (B) are identical to those in the no-gap condition (A) except for a blanking of the target for 250 msec, beginning during the saccade. Dashed lines indicate the performance of two subjects in Expt IIa.

modification of some internal criterion or to an increase in sensitivity. The next experiment demonstrates that target blanking indeed results in higher sensitivity to target displacement.

Experiment II

Experiment II constitutes the central experiment of this study. Here we analyzed the dependence of perceived displacement direction on size and direction of the target shift. Gap duration was either 0 msec ("no-gap") or 250 msec, selected at random during a block of trials. Seven subjects participated in the experiment.

Figure 3(A) shows the percentage of "forward" decisions in the no-gap condition as a function of displacement size and direction, plotted separately for each subject. The psychometric functions confirm that in this situation the subjects are rather unsure concerning their judgment of the direction of the target displacement: the transitions between "forward" and "backward" responses are broad, showing a high intersubject variability. Moreover, there is a considerable bias towards reporting forward target shifts which is especially obvious for the case without target displacement. Even with backward target shifts as large as 2 deg, two of the subjects still report predominantly forward target displacements.

This picture changes drastically when the target is blanked for a sufficient amount of time after the saccade. Figure 3(B) presents the data for the gap duration of 250 msec. The psychometric functions become considerably steeper, indicating that the subjects are now able to correctly indicate the direction of target displacements with jump sizes as small as 0.3 deg. Both intersubject variability and response bias have largely disappeared.

These data demonstrate that subjects can correctly report target displacements when the target is absent for a short period immediately after the saccade. As a simple explanation for this superior performance in the gap situation, the subjects in this condition may be able to monitor the effective post-saccadic retinal error, or the size and direction of their corrective saccade, and take this signal as an indicator of target displacement. This hypothesis predicts a close relationship of post-saccadic refixation error and indicated displacement direction. For this reason we analyzed discrimination performance as a function of the refixation error remaining after the end of

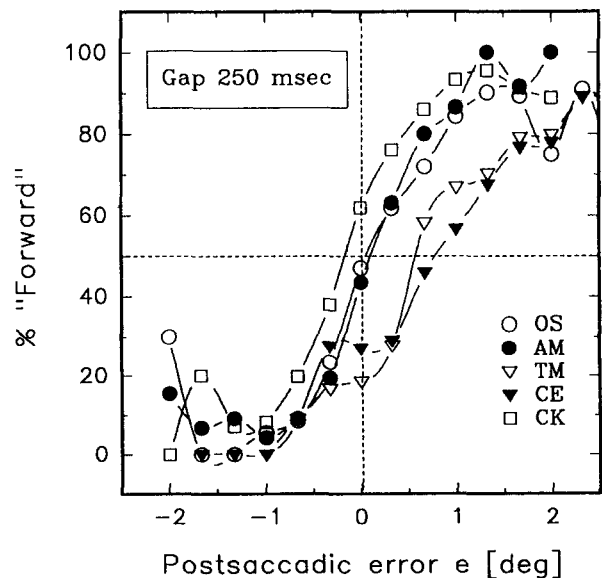


FIGURE 4. The data of Fig. 3(B) replotted as a function of postsaccadic eye fixation error [e in Fig. 1(A)].

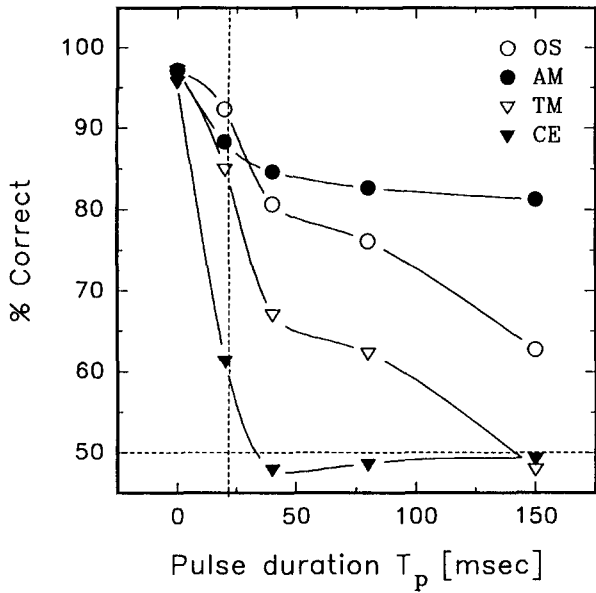


FIGURE 5. Displacement discrimination in Expt III as a function of duration of a target pulse that begins during the saccade and ends at the time indicated on the horizontal axis. Gap duration after the end of the pulse is constant at 250 msec. The vertical dashed line indicates the approximate end of the primary saccade.

the primary saccade. Figure 4 shows the same data as Fig. 3(B), but now plotted as a function of postsaccadic error size. A positive error indicates a corrective saccade in the same direction as the primary saccade. The variable bias shown in Fig. 4 reflects the various saccadic undershoots produced by the subjects. Both increased intrasubject variance and intersubject variability of bias demonstrate that performance correlates much less with postsaccadic error than with the real exocentric target displacement

[cf. Fig. 3(B)]. This indicates that improved displacement discrimination in the gap situation is not based on the evaluation of the refixation error but corresponds to the veridical target displacement, independent of the actual landing position of the saccade.

Since superior gap performance is not based on the evaluation of the retinal error, the high sensitivity to target displacements in the gap situation suggests that a very precise extraretinal signal indicating eye position after the saccade is available and compared to the retinal reafference. Alternatively, the visual surround might provide a stationary frame of reference that makes the observed performance possible. In order to evaluate the latter possibility we performed the control Expt IIa, in which the target was a bright laser spot in darkness (see Methods). The results for two subjects are shown in the dashed curves in Fig. 3. It is obvious that performance is essentially identical to the findings described previously, indicating that information from the visual environment is not necessary for the observed effects.

Experiment III

The above findings suggest that saccadic suppression of target displacement tends to disappear when the target is absent for a short period immediately after the saccade. Next, we wanted to test whether a later target offset (especially, after saccade end) leads to similar enhancement, and for how long post-saccadic information must be available for this gap effect to disappear. For this purpose, in Expt III, the target was displaced by 1 deg during the saccade, and blanked for 250 msec after various post-displacement durations. Four subjects participated in this experiment. Figure 5 presents discrimination performance as a function of pulse duration, for

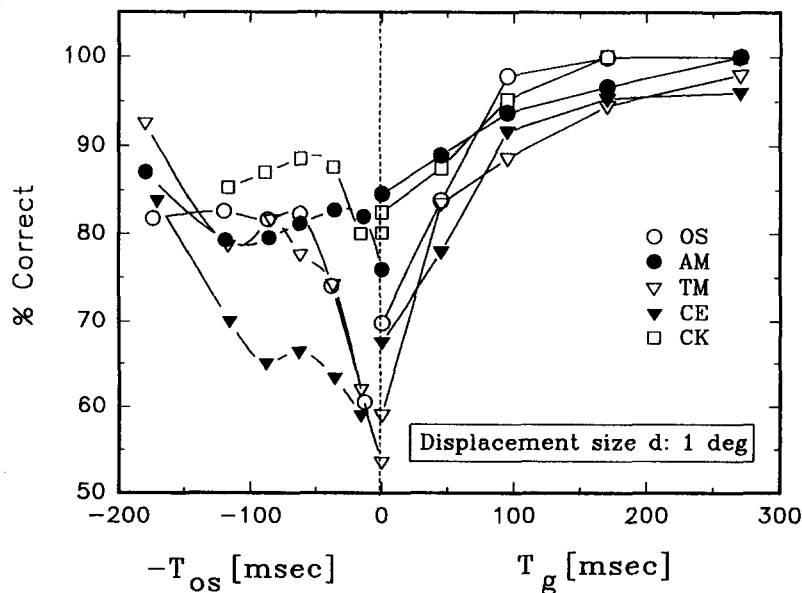


FIGURE 6. Effect of a pre-saccadic target gap on detection performance (left of dashed vertical line) in Expt IV, compared with detection after a post-saccadic gap (right of dashed vertical line) replotted from Fig. 2. The presaccadic gap durations [T_{0s} in Fig. 1(C)] were calculated from the target pulse duration T_B and the saccadic latency; and the performance data were binned in intervals of 50 msec for $-200 \text{ msec} < T_{0s} < -100 \text{ msec}$, and in intervals of 20 msec for $-100 \text{ msec} < T_{0s} < 0 \text{ msec}$. Displacement magnitude was always $\pm 1 \text{ deg}$.

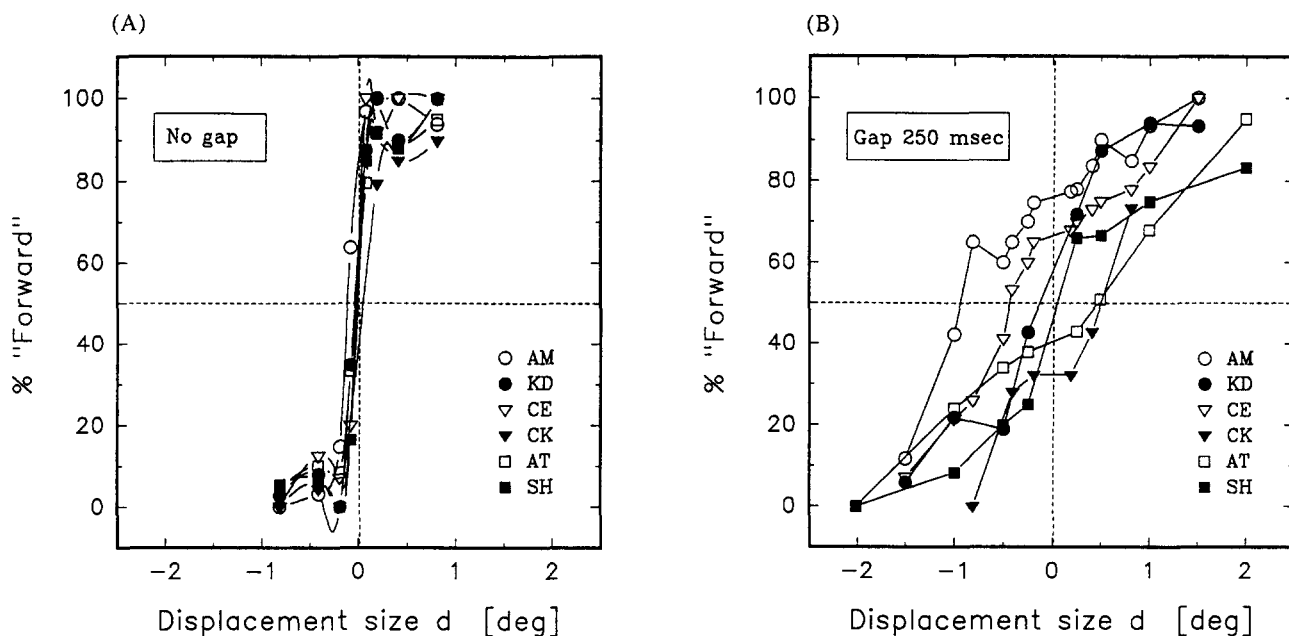


FIGURE 7. Displacement detection during fixation in Expt V without a gap (A) and with a constant gap of 250 msec (B), plotted in the format of Fig. 3.

four subjects. The case $T_p = 0$ is identical to the gap condition (cf. Fig. 3), and again yields very good performance. Performance deteriorates rapidly with increasing T_p , however. The data pattern suggests that, as soon as target presence extends beyond the end of the saccade, performance degrades to that of the no-gap situation. Thus we conclude that the *absence* of a visual target immediately after the saccade rather than (later) *target blanking per se* produces the observed enhancement.

Experiment IV

Experiment IV investigated whether *presaccadic* blanking of the saccade target leads to an improvement of discrimination performance comparable to the effect of a postsaccadic gap. For this purpose, the saccade target appeared in the periphery for short time periods [T_B in Fig. 1(C)], which were varied between 50 and 150 msec. Then the target was switched off until the trigger signal indicated the onset of the saccade. The target reappeared, displaced by ± 1 deg, immediately upon detection of the saccade. Five subjects participated in this experiment. Figure 6 presents the experimental results as a function of the time between target offset and saccade onset (T_{OS} , negative values). In the graph, the data signify average discrimination performance for presaccadic gap values binned in intervals of 50 or 20 msec. For comparison the figure replots, for positive gap durations, the data from Expt I already presented in Fig. 2. The results demonstrate that target blanking is also effective when it occurs before the saccade. Somewhat surprisingly, performance is best when the target is switched off long before the saccade, and worst when no or only a short blanking period is present. It should be emphasized that the data on the vertical dashed line indicate the no-gap condition.

Experiment V

The above findings suggest that the displacement of a visual target in the vicinity of a saccade can be re-discovered when a sufficient blanking period is introduced. The question arises how much of the "saccadic suppression of image displacement" effect actually remains with the introduction of a gap. Answering this question requires a comparison with a condition where the subject receives essentially the same stimulus while not making a saccade. For this reason, Expt V presented a target running through the same sequence of displacement and blanking as in Expt II. Now, however, the subject kept strict fixation at the center of the screen. Fixation was controlled on-line by computer, and trials were discarded if any saccadic eye movements were detected.

Figure 7 exhibits the results of varying the displacement size with no gap (A) or with a constant gap duration of 250 msec (B). For the cases without a target gap, performance is nearly perfect. The steepness of the psychometric functions indicates that the subjects can readily even detect displacements as small as 0.1 deg. Here, the subjects report seeing a short movement of the peripheral stimulus. For the cases with a 250 msec target blanking, however, discrimination performance deteriorates drastically as can be seen by the larger intersubject variability and by the considerably flatter psychometric functions. Obviously, subjects are amazingly unsure in indicating whether a peripheral stimulus reappears at the same position or at a displaced position after a sufficient stimulus blanking.

These findings indicate that displacement discrimination during fixation might be based on two different mechanisms: in the no-gap condition, a motion signal allows for sensitive discrimination. For longer gap durations, this motion signal becomes unavailable,

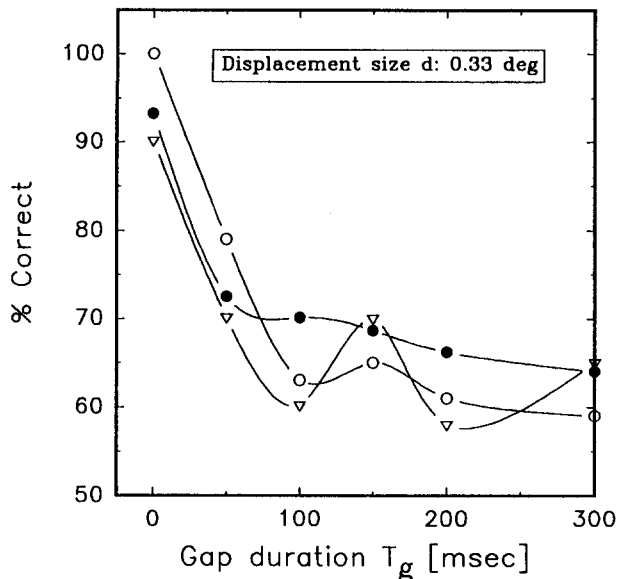


FIGURE 8. Displacement detection during ocular fixation in Expt V, plotted in the format of Fig. 2. Displacement size is 0.33 deg. At the time of the subject's decision, the target lies about 6.33 deg in the periphery.

leading to a deterioration in performance. In order to quantify the transition between the two situations, we varied the gap duration in the fixation condition. Figure 8 demonstrates that, with a small target displacement of 0.33 deg, good performance is limited to gap durations below 100 msec. Lengthening the gap from 100 to 300 msec has little additional effect.

Comparing the results of Expts II and V reveals that the accuracy of displacement detection with a postsaccadic gap is actually *better* than during fixation. For the purpose of comparison, we fitted the psychometric functions of both experiments with cumulative gaussian distributions and determined means (bias) and SDs,

separately for the gap and the no-gap conditions. Figure 9 shows both measures for the different conditions. Obviously, when no gap is present, performance in saccade trials is degraded compared to performance in fixation trials which is reflected in larger SDs and more variability in the biases. When a gap is present, however, the situation reverses: both SD and bias variability are lower in the saccade trials than in the corresponding fixation trials.

DISCUSSION

Saccadic suppression of displacement is of interest because of its implications for the processing of information about egocentric spatial location. The large thresholds found in the literature seemed to imply that information about perceived target position is not preserved from one fixation to the next, though perceptual space constancy and visual-motor integration in normal subjects remain intact across saccades. The present investigation shows that target position information is indeed preserved, but can be used for perceptual localization only under certain conditions.

We have found that introducing a stimulus blanking after a target has jumped during a saccade discloses information that is seemingly unused otherwise, facilitating detection of the target jump. The target must be extinguished during the saccade; if it is present for only a short time afterward, the enhancement effect disappears. Displacement detection improves with longer gap durations (up to about 300 msec). Most of the enhancement, however, occurs within 0–80 msec after saccade end. It should be noted that this is also the period of visual information intake for corrective saccade programming (Deubel *et al.*, 1982). Extinguishing the target before the saccade and reintroducing it in a new location during the saccade has a similar but weaker effect.

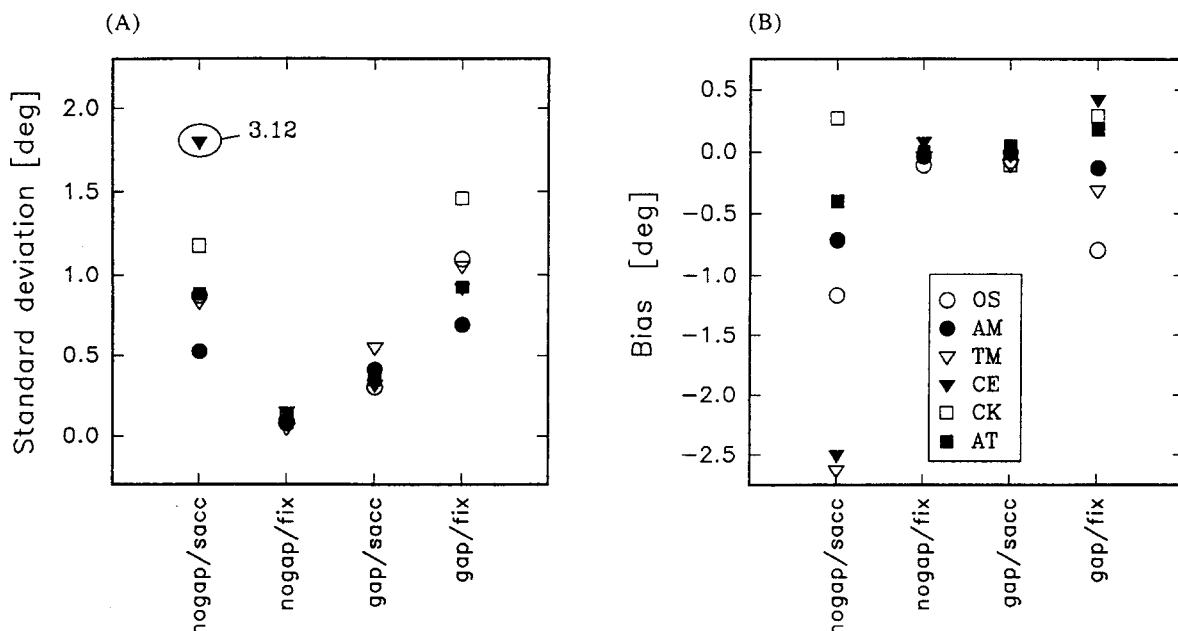


FIGURE 9. Standard deviation and bias of perceptual judgments in Expt II (saccade) and Expt V (fixation) compared.

Apparently something about the absence of the target after the saccade triggers a different mode of spatial information processing than normally occurs. This mode enables perception of a target jump that otherwise would be undetectable. The data show two distinct but correlated changes: first the psychophysical functions become much steeper, indicating greater sensitivity to changes in target location. Second, the zero-crossing point where a target is equally likely to be judged as moving backward or forward now occurs at the point where there is no change in target location on the screen, indicating reduced bias. In addition, individual differences are reduced. All of these changes demonstrate the improved ability to judge the target's post-saccadic position relative to its pre-saccadic position.

Why has this surprising effect of target blanking not been observed before? Indeed, only few studies exist on the effect of blanking on spatial localization. Li and Matin (1990) studied the effect of the duration of a postsaccadic target on the threshold of displacement and found that sensitivity increased by a factor of 2 with longer stimulus presence. One of their conditions also included a short-term postsaccadic target absence (of approx. 30 msec), similar to the conditions of our Expt I. Unfortunately, Li and Matin (1990) did not use any longer gap durations. For their short gap duration, their results show similar sensitivities as for a no-gap condition. Several methodological differences may account for this discrepancy, however. So, the stimuli in the Li and Matin (1990) study appeared on a dark background, leaving the subject in darkness after stimulation. This should allow the subject to evaluate the retinal stimulus streak and is in contrast to our experimental condition with relatively high background luminance; subjects here never perceived retinal streaks due to intrasaccadic stimulation. Also, while we extinguished the fixation point before illuminating our goal, those authors left the original fixation point on, and moved both the original fixation point and the saccade goal together. This leaves the question undecided whether the subjects detected displacement of the original target or of the goal point or both. Lack of relative motion of two points as in Li and Matin's paradigm might specify lack of displacement to the visual system, yielding relatively high thresholds even with a gap.

Matin, Matin and Pola (1970) showed that the relative localizations of two brief test flashes separated by a temporal gap could be affected by a subsequent saccade, and that the differences in localization grew as the second flash approached the time of saccade onset. Since they compared two presaccadic target positions, while we compare a presaccadic and a postsaccadic position, the experiments are not strictly comparable, but both their study and ours show changes in localization due to events before the saccade.

Our results address a number of questions about spatial localization. First, we will discuss whether the blanking effect reduces, eliminates, or reverses saccadic suppres-

sion of image displacement. Then we ask what aspects of the stimulus are relevant for inducing the blanking effect. Next we address the nature and accuracy of the information that is used in the gap condition to detect target displacement, and finally we analyze the implications of the results for normal perception and spatial localization.

‘‘Saccadic suppression’’ reverses to ‘‘saccadic enhancement’’

We have noted that interruption of the target induces an amazing precision of displacement detection: subjects routinely identify a 0.3 deg displacement that takes place within a 6–8 deg saccade. This threshold appears to exceed the precision of perceptual extraretinal signals as measured by others (reviewed below). Under these conditions, a question arises: can the effect still be described as ‘‘saccadic suppression’’, or has this effect disappeared or reversed? In the normal continuous-target paradigm, ‘‘suppression’’ is an appropriate term because performance is poor compared to thresholds achieved during fixation.

In the gap/saccade condition the target is in the retinal periphery just before the saccade, but is near the fovea after the saccade. Thus to identify the change in target position a subject must compare a peripherally presented target with a more centrally presented target. In the gap/fixation condition, however, the target lies about 6 deg in the retinal periphery both before and after its displacement. In this situation two sources of spatial error must be compared: in the fixation condition, there is a degradation of spatial information due to peripheral presentation of the target both before and after the displacement. In the saccade condition, there are possible errors in extraretinal signals, but a saccade brings the target near the fovea after its jump. Our results show that the localization error during fixation (perhaps due to peripheral presentation both before and after the target jump) is greater than the error during saccades (perhaps due to extraretinal signal errors and peripheral presentation before the saccade). Because the added positional uncertainty of two vs one retinally peripheral presentations in the fixation condition is minor, we conclude that localization performance is better in the gap/saccade condition than in the fixation control. Thus we can speak of a ‘‘saccadic enhancement’’ of localization ability.

Another way of interpreting saccadic suppression of image displacement is in terms of apparent motion vs displacement detection. The subject can detect target displacement by perceiving a motion from one location to another, or alternatively by detecting a difference in target positions. In the fixation condition, subjects perform better without a gap. This implies that they rely on accurate movement information in the non-gap case, but that a gap forces them to use another source of information about change in target position. The same applies for intrasaccadic target displacements without a gap. Here the motion transients are unavailable because they are masked during the saccade, leading to poor

performance. A fair evaluation of displacement detection—as opposed to motion detection—should compare conditions in which movement is not a possible source of information. Indeed, Shioiri and Cavanagh (1989) complained “The influence of a saccade on the mechanisms that detect change of position has not yet been explored independently from motion detection”. Dissociation from motion detection is indeed the case in our gap experiments; under these conditions comparison of the fixation and saccade conditions reveals better performance when the subject saccades to the target.

Why is the target blanking effective?

Which characteristics of target blanking are essential for enhanced displacement detection? Blanking introduces two changes in the stimulus configuration, either of which might be responsible for the changes we observe in saccadic suppression of displacement. One change is the absence of a target immediately after the saccade; the other is the introduction of an on-transient when the displaced target reappears. In interpreting these two changes, we begin with the assumption that the visual system evaluates contiguity with the equivalent of a null hypothesis: that the world is stable. Only a massive indication for change can force the system to revise this assumption, making perception of a jump of the world possible (MacKay, 1962; Bridgeman, Van der Heijden & Velichkovsky, 1994). Complementary reasoning applies to the presaccadic gap paradigm.

The first way of interpreting our data is in terms of target localization after a saccade. There is evidence that final target position is used preferentially to calibrate visual position at the end of a saccade, because motions of a target object during a saccade are frequently misattributed to motions of the original fixation point (Heywood & Churcher, 1981). This seems to imply that target location can serve as a reference for spatial localization. Consequently, we must postulate that the lack of a visual stimulus after a saccade prevents post-saccadic information from working effectively in visual stabilization, and forces the system to use other sources of information such as efference copy and stored target location. In the course of normal perception, theorists have indeed assumed that these sources are neglected in favor of more reliable information available from the image itself, and there is some evidence for this idea (Matin, Picoult, Stevens, Edwards, Young & MacArthur, 1982; Stark & Bridgeman, 1983) in that visual context can reduce the apparent contribution of extraretinal signals to visual localization.

The question of transients can best be approached with a combination of our results and those of others. Experiment III showed that the gap had to begin (or end) during the period of saccadic suppression for the enhancement to appear. But a gap that occurs only during a saccade has little effect on saccadic suppression of displacement (Li & Matin, 1990). Thus the essential characteristic of the gap is that one of its transients must occur during the period of saccadic suppression, while

the other must occur outside this period. This on-transient, unmatched by a corresponding off-transient, may signal the system that something has changed in the visual world, so that a re-evaluation of the egocentric positions of objects is necessary. Information not normally used postsaccadically may come into play to accomplish this re-evaluation.

Implications for extraretinal signals

A cognitive decision about whether a target has been displaced is normally made relative to any available visual background. This has the result of reducing the apparent effect of extraretinal signals when a background is present, consistent with the results of Bridgeman and Graziano (1989). Our data demonstrate that veridical extraretinal information about spatial location of a visual target and its displacement is potentially available, but it is used for localization only when consistent visual information is missing immediately after (or before) a saccade.

When no background is present, only extraretinal signals remain to influence the decision about target displacement, and they assume a relatively greater role. To evaluate the intrasaccadic target displacement accurately, the visual system must possess three pieces of information. First, it must have precise information about the presaccadic target position; second, it must have an accurate extraretinal signal describing the saccade; and third, there must be a precise retinal error signal after the saccade. The high accuracy of discrimination performance in the gap condition demonstrates that such signals indeed exist.

This conclusion, however, seems to contradict abundant evidence that the extraretinal signals used for perceptual judgments are of relatively poor quality. This is true even when the extraretinal signals for motor control are accurate, as reviewed in the Introduction. Further, the gain of efference copy (defined as the ratio of efference copy to saccade magnitude) is normally less than 1 (Grüsser, Krizič & Weiss, 1987; Pola & Wyatt, 1989); thus the magnitude of the efference copy is less than the size of the saccade. Proprioception has a very low gain (Gauthier, Nommay & Vercher, 1990), and even a combination of efference copy and proprioception measured separately in the same experiment reveals a gain of less than 1 (Bridgeman & Stark, 1991). Further, the apparent gain of the extraretinal signals is lower for abrupt transients of the eye than for slower or for less frequent movements (Bridgeman, 1994). There is also evidence that the extraretinal signals result in a rather slow influence on visual position perception, compared to the fast dynamics of saccades themselves (Matin, 1972). In our experiments, however, introduction of a gap may give the extraretinal signals time to catch up to veridical or near-veridical levels before a judgment is made about whether the target has been displaced or not, making an accurate assessment possible.

Implications for visual stability and normal perception

Our results imply a seemingly paradoxical dissociation of perceptually available information from internally stored information about visual space: in the no-gap condition a target displacement cannot be detected perceptually, even though the gap condition reveals that information about the same-sized displacement is stored in the nervous system and can be accessed under other conditions.

If spatial information used in the gap condition is not available during perception of continuous targets, of what use is it to the observer? The hidden spatial information revealed in the gap condition might be used to resolve a conflict that the system faces in the normal saccadic suppression of displacement paradigm, and by implication in some normal perceptual situations. First, temporal contiguity of the target provides information that the same object is present both before and after the saccade, and no motion transient is attributable to the target, because the transient is masked by saccadic suppression. But second, there is a mismatch between the extraretinal information after the saccade and the retinal position of the target. Following the general rule that perceptual systems tend to reject coincidences, the system apparently resolves this situation with a decision that the target has not been displaced during the saccade. In the gap condition, though, the first piece of information (temporal contiguity) is degraded, and an on-transient is available. This forces the system to put more weight on the second (mismatch) source of information, biasing the decision toward perceiving a reappearance in a new location, or even to perceiving the appearance of a new object.

Is visual stability across saccades based on a ‘store-and-compare’ mechanism? A contiguity model of visual stability

Our data suggest that visual information available immediately after a target-directed saccade is of particular importance: if a consistent pattern is present, the visual system assumes that the world has been stable, identifying the present object as the old target.

In terms of this reasoning, we hypothesize that a number of processing steps are required with each refixation:

- When an object is selected as a future target for a saccade, that object is specifically analyzed (Schneider, 1995). Indeed, there is recent independent evidence that the future target object receives preferential perceptual processing allowing for selective object recognition (Schneider & Deubel, 1995; Deubel & Schneider, in press).
- The selected information is then stored in memory. This does not imply storage in an icon-like, retinotopic memory: rather, only certain higher-level discriminating visual features (Schneider, 1995) are stored in a non-retinotopic memory (perhaps in inferotemporal cortex). Recent neurophysiological findings (Chelazzi, Miller, Duncan & Desimone, 1993) are consistent with this proposal.

- When the saccade ends, the system tries to find the target again, comparing the stored expectations to the visual reafference within a restricted spatiotemporal window. Even a very brief target is adequate to establish the match. The found target serves for recalibration of spatial localization. This process was proposed by Wolf, Hauske and Lupp (1978), and by Deubel, Wolf and Hauske (1984): “the visual structure which was selected as target has to be relocalized after the primary saccade”. Irwin, McConkie, Carlson-Radvansky and Currie (1994) have recently made a similar proposal.

- If there is no match (such as with a post-saccadic target blanking), the assumption of contiguity of the visual world is broken. The system makes use of other sources of information for localization.

A similar multistep model has been put forward by one of the authors for mechanisms other than visual stability. Post-saccadic comparison of stored and reafferent information is also a prerequisite for motor control processes such as saccadic adaptive control (Deubel, 1991) and for the programming of corrective saccades (Deubel *et al.*, 1984). Both of these mechanisms are based on the evaluation of postsaccadic refixation error and require that the intended target be found and located within a complex visual environment. We are forced to the conclusion that temporal target contiguity makes an important contribution to the mechanisms of visual space constancy.

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