



Illusory Localization of Stimuli Flashed in the Dark Before Saccades

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A photic stimulus flashed just before a saccade in the dark tends to be mislocalized in the direction of the saccade. This mislocalization is not only perceptual; it is also expressed by errors of ocular targeting. A particular situation arises if the point of light is flashed twice at the same place, the second time, just before a saccade. The point of light may appear at two different places even though neither the site of its retinal image nor the direction of gaze change between the flashes. Experiments were run on five human subjects, head fixed in the dark, with flashes repeated at the site of the saccade goal or at the initial point of fixation. In both cases, the test stimulus was mislocalized. However, its apparent displacement never produced the perception of a streak. Streaks were reported only when there was an actual stimulus movement on the retina (e.g. by flashing the stimulus during the saccade). Mislocalization did not occur if the two flashes were not separated by a dark interval. This implies that, as long as a steady stimulus remains continually visible, there is no updating of the internal representation of eye position assumed to be used for stimulus localization.

Eye position signal Illusion Localization Saccades

INTRODUCTION

In the absence of other cues, the localization of a brief photic stimulus in the dark must rely on some internal knowledge of the direction of gaze at the time of stimulus presentation (Hallett & Lightstone, 1976a, b; Gresty & Leech, 1976; Hansen & Skavenski, 1985). To account for this knowledge, assuming that the head is fixed, the existence of an internal representation of eye position has been postulated. We shall call it eye position signal (EPS). Ideally, the EPS should be a perfect copy of any change in eye position, and its timing should be adjusted to indicate the eye direction precisely *at stimulus presentation*. But, for at least 25 yr, the EPS itself—or its reading—has been suspected to be incorrect near the time of saccades since stimuli flashed at that time are perceptually mislocalized (Matin & Pearce, 1965; Bishof & Kramer, 1968; Kennard, Hartmann, Kraft & Glaser, 1971; Monahan, 1972; Mateeff, 1978; Honda, 1989). Only recently has it been realized that the error of localization is not only perceptual but that it can also affect motor performances such as looking at the site of the vanished target [ocular targeting: Honda 1990, 1991; Dassonville, Schlag & Schlag-Rey, 1990a, 1992, 1995] or pointing to it manually (Miller, 1980, 1989).

Practically all eye or finger targeting studies relevant to this problem are based on the two-step paradigm: a brief photic stimulus “steps” from a first position (toward which an initial saccade has to be made) to a second position which is the one that the subject must reach. There is nothing in the paradigm that constrains the choice of the second stimulus position. Theoretically, the stimulus can be placed anywhere at the second step. This implies, in particular, that it can be at the same position as it was at the first step. Mislocalization in this case has already been shown by Honda (1990). Thus, an interesting illusion may occur if the stimulus is relit a second time *at the same place*, due to the fact that mislocalization starts growing 50 msec or more *before* a saccade and reaches a maximum at saccade onset. That illusion is: *a stimulus repeated at the same place before a saccade is judged to be at a different place, even though neither the position of its image on the retina nor the eyes have moved.*

To understand this paradox, let us consider the chain of events occurring at the input of the visual system, as schematized in Fig. 1. There is shown the initial algebraic summing junction included in practically all models of visually-guided saccades (e.g. Robinson, 1975) where the retinal coordinates of the stimulus (retinal input) are combined with the EPS. Note that no restricting assumption is made regarding the anatomical site where this summing takes place. Nor is it specified, in Fig. 1, whether the EPS is a continuous signal or a signal reset

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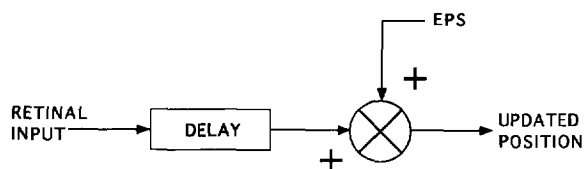


FIGURE 1. Input stage of classical visuo-oculomotor models, showing the summing junction where stimulus retinotopic coordinates (at RETINAL INPUT) are assumed to be updated when the eye position signal (EPS) changes. The outcome (UPDATED POSITION) is used for perceptual localization as well as for determination of the goal of saccades.

after each saccade [in the latter case, the sign is changed: the EPS should be subtracted instead of added (Goldberg and Bruce, 1990)]. The reason to postulate an initial summing junction is to explain how the brain can update the coordinates of an object as a function of the subject's own movements.

In Fig. 1, the delay on the visual input (mostly accounted for by retinal processing) is an important feature, to which a major role is attributed in producing localization errors near the time of saccades (for an early version of this hypothesis see Hazelhoff & Wiersma, 1924). Very likely, this delay has the same order of magnitude as saccade duration. If so, it is a potential source of considerable temporal mismatch between a visual signal and its contemporary EPS. To explain the mismatch, let us imagine a flash generating a visual signal, and let us follow it through its course. After due processing, the signal elicits a saccade. Just when this saccade is going to occur, let us repeat the flash exactly where it has been presented the first time. This means that a second visual input, identical to the first, travels again through the same channel. But now the other input of the summing junction—the EPS feedback—has acquired a new value: the model predicts a different output, i.e. an *erroneous* localization.

However, this is not at all what common experience tells us. Everybody knows that, if a stationary stimulus remains continuously visible until a saccade occurs, obviously it cannot be seen moving from one place to another. Why then should it be mislocalized?

Is there a contradiction between this common experience and the prediction made on the basis of the circuit drawn in Fig. 1? To answer this question, we have compared, in the same subjects, the ability to localize the second of two flashes (presented at the same place but separated by a temporal gap) with the ability to localize a single stimulus, lasting from the onset of the first flash to the offset of the second (i.e. no-gap). We have paid special attention to the trials in which the stimuli terminated just before a saccade because these are the cases that interest us. Indeed, once a saccade starts, other factors come into play, such as the displacement of the stimulus on the retina with the resulting smearing, which offers good but more trivial reasons for mislocalization.

The present study consists of three experiments. The first compares the Gap and No-gap conditions as just described. The results will show that a stimulus presented before a saccade can be mislocalized in the Gap but not in the No-gap condition, although in neither case is there stimulus displacement. Experiment 2 is designed to extend the observation of mislocalization to the other particular condition in which the stimulus is repeated at the same place: in this case at the site of the initial fixation point. In other words, can we err even in localizing the point that we are fixating? Experiment 3 concerns a problem arising from the observations made in the first two experiments. If two points of light are seen apart when they are not, could they appear moving from one place to the other? Practically, we verify that the perception of streaks of light, taken as an indication of stimulus movement, does not occur for stationary stimuli presented before a saccade, but selectively during the saccade, when there is a real displacement of the image on the retina. Some of these results were presented in a brief report (Schlag & Schlag-Rey, 1993).

METHODS

Subjects sat in a chair, their head immobilized by a bite-plate. The horizontal movements of the dominant eye were recorded via infra-red detection goggles (Ober2 eye-orbit scanner): the other eye was patched. Subjects wore their corrective lenses. The experiments were run in complete darkness. Test stimuli were 0.23-deg diameter blue-green spots generated on a 608 Tektronix oscilloscope (P11 phosphor) and projected through a wide-angle lens on a translucent screen 132 cm in front of the subject. Dim stimuli were chosen because they produced no halo, did not illuminate the screen, and created no afterimages. Stimulus intensity was 10–25 mcd/m², i.e. dim enough for spots of equal duration to appear brighter when presented 10 deg eccentrically than when presented on the fovea, yet still visible without prior dark adaptation. However, actual experiments were not started until the subject had been in the dark for 10 min.

Each trial consisted of two or three successive stimuli, always horizontally aligned at eye level: starting with the point of fixation F, then S₁, the target of the initial saccade and, finally S₂ the stimulus to be localized. In Expts 1 and 3, there were two types of trials, illustrated in Fig. 2. In so-called Gap trials, S₁ was brief and temporally separated from S₂. In so-called No-gap trials, S₁ was prolonged until it fused with S₂ onset. Thus, in No-gap trials, S₂ was undistinguishable from S₁ unless it was presented at a different place (control trials, see later). Experiment 2 included only Gap trials [see Fig. 7(E)]. To vary durations, delays, or locations of stimuli in successive trials, the values of these parameters were read by the computer software (MacProbe) from a pseudo-random table. Since it was desirable to present S₂ frequently near the time of saccades and, especially, just before their onset, the initial saccade latencies of the

last four trials were measured on-line by the program and, in the subsequent trial, S_2 timing was automatically set to a prearranged variable delay with respect to the running average of the last four latencies. Timing precision was 1 msec for the display. Data were digitized at 1 kHz, and latency, duration and amplitude in each trial were measured off-line from visually detected inflection points on stored records of eye movements (records similar to the one shown in Fig. 3). The precision of these measurements was ± 1 msec for timing and ± 0.2 deg for position.

The eye signal recorded by the Ober2 system was displayed on a slave 608 Tektronix oscilloscope together with the stimuli presented to the subject. The calibration of the recording system was performed at the start of each session. For this purpose, the point of fixation F was presented for the same duration as in the experimental trials, followed by S_1 to which the subject made a saccade, but S_1 remained lit as long as necessary (usually several seconds) to adjust the gain and offset to match eye position with stimulus position, simultaneously viewed on the screen of the slave scope. At least eight calibration trials were run to complete the adjustment. Correct gain and bias were again checked at the end of recording. Calibrations were occasionally repeated in mid-session and, if found in error, the preceding trials were discarded. Our experience with the Ober2 system is that the gain is stable, particularly if the background illumination is kept low (it was kept to zero). Typically, for a 17-deg saccade, horizontal eye position measurement remained correct within 0.5 deg. Small adjustments of the offset were needed from time to time but this caused no problems because trials could not start if the subjects' gaze did not stay inside a 3-deg window around the point of fixation for a predetermined time randomly varied from 800 to 1800 msec. This window was used for safety, as only trials starting within 0.5 deg from the point of fixation were retained for analysis. Trials lasted about 2–3 sec. That included: a variable time to adjust gaze on the point of fixation, fixation for 800–1800 msec, a first saccade to S_1 , eventually a second saccade to S_2 and, if required, pressing a switch. Then the subjects waited in the dark for the next trial starting by the reappearance of the point of fixation. No feedback information was given to indicate to the subjects how accurate was their last response. For the naive subjects, trials were initiated by the experimenter at irregular intervals of 5–9 sec. In some sessions, the experienced subjects initiated the trials themselves (which usually resulted in a faster pace). A session comprised 250–300 trials. Unless otherwise indicated, the data shown were collected in a single session.

Data are reported for two experienced and three naive subjects. They were pretested for their ability to move their eyes to the site of a flash in a single saccade; five potential subjects who often did it in multiple saccades were rejected. Two other naive subjects rarely made more than one saccade even when they saw two stimuli apart. The data of one of them are included

for comparison in Fig. 6(D). Three further subjects were discarded because their data were incomplete. The experienced subjects knew the purpose of this experiment and the general hypotheses under test. Having served in a previous study (Dassonville *et al.*, 1992), they were familiar with the set-up and, therefore, could handle more complicated tasks. Therefore, they served in an experiment requiring simultaneous perceptual judgment and ocular targeting, which was designed to compare, trial by trial, the two ways of expressing localization errors. The naive subjects were paid undergraduate students. They were informed that the purpose of the investigation was "to find out how accurate can be a saccade that you make to a target briefly flashed near the time of another saccade". The display was described to them before starting the session, and they were instructed "to bring gaze as accurately as possible to the site where the last spot of light was seen . . .". Saccade latencies varied appreciably since subjects were not urged to respond fast. Mean values are given with individual results. The study was authorized by the UCLA Human Subject Protection Committee and each subject was asked to sign a statement of informed consent.

RESULTS

Experiment 1: Localization difference between Gap and No-gap conditions

The stimulus display and timing of this experiment are illustrated in Fig. 2. The amplitude of the initial saccade was 17 deg: from F at 15 deg left of center to S_1 at 2 deg right of center (see Fig. 2). S_2 was projected at the same

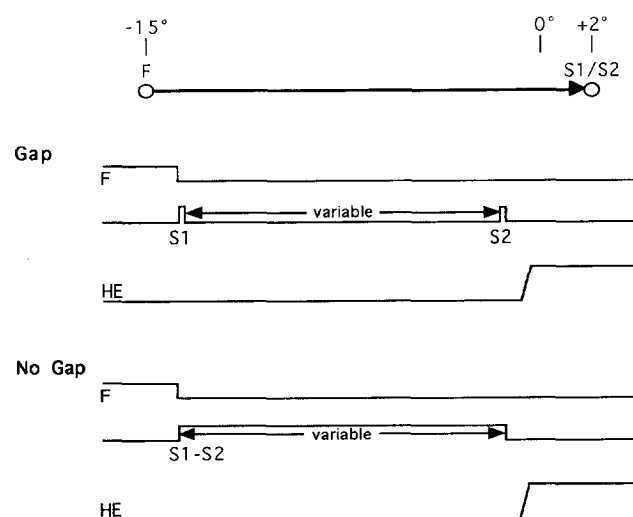


FIGURE 2. Schematic description of Expt 1. Initial saccade from point of fixation F (at -15 deg) to S_1 (at $+2$ deg). Amplitude of initial saccade was 17 deg. In Gap trials, S_1 lasted 10 msec and S_2 4 msec. In No-gap trials, S_1 remained lit, so that there was no blank interval between flashes as in Gap trials. The timing of the offsets of S_2 was varied. In test trials, S_2 was presented at the same place as S_1 . In control trials, S_2 was presented 2 or 4 deg farther to the right. Gap and No-gap trials (including control and test trials) were randomly interleaved. HE, horizontal eye position.

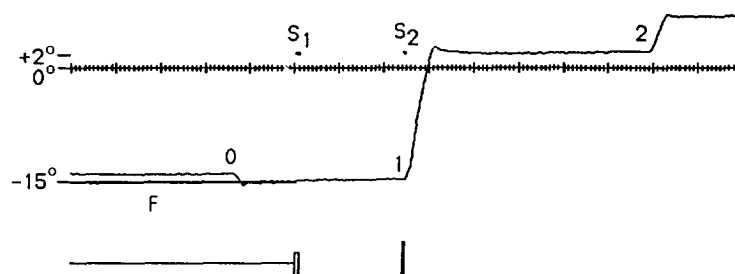


FIGURE 3. Record of horizontal eye movements during a Gap trial of Expt 1. Saccade 0 aligned the eye on point of fixation F at -15 deg (left). Saccade 1 was directed from F to S_1 at $+2$ deg (right). Saccade 2 was an attempt to reach S_2 that, in this particular case, the subject reported as "not at the same place" as S_1 . Time scale (drawn at the 0 deg level): 10 msec per small divisions. Bottom line shows timing of stimuli.

place as S_1 in 86% of the trials (test trials), and at 4 or 6 deg right (instead of 2 deg) in 14% of the trials (control trials, not shown in Fig. 2). These control trials served two purposes: first to test the subjects' ability to distinguish two stimuli in the easy condition where they were flashed long before or after a saccade and, second, to convince the subjects, in this easy condition, that the sequence of trials, indeed, included occurrences of stimuli at different places. We opted to have all the control stimuli displayed in the saccade direction (i.e. farther right) because, in preliminary experiments, it was found that stimuli presented before saccades tended to be mislocalized in that direction and, in trials with other stimulus timing, we wanted to compensate for this tendency. In the Gap trials, S_1 duration was fixed at 10 msec whereas, in the No-gap trials, S_1 was not turned off until S_2 onset. The influence of the gap (i.e. blank between flashes) on localization was the independent variable under investigation in Expt 1.

Two experienced subjects were instructed to make saccades to the site of S_1 and then to the site of S_2 if appearing different from S_1 . They were also asked to press a switch after each trial in which S_2 was perceived as "not at the same place" as S_1 .

First, we shall describe the results obtained in the control Gap trials (called controls because S_1 and S_2 were spatially distinguishable and, therefore, ought to be reported as "not at the same place"). Such a report of "not at the same place" was given in 93% of these trials. Since 100% of control Gap trials included a second saccade (as expected if subjects attempted to aim gaze at another stimulus presented elsewhere), there was a slight discrepancy between the subjects' perceptual judgments and their saccadic responses (in 7% of the cases, subjects reported seeing only one stimulus but made two saccades).

In test Gap trials, in which S_2 was simply S_1 relit at the same place, a second saccade was also frequently made. Such a saccade can be seen in a typical record (Fig. 3). It was an attempt to reach the site of S_2 from which the eye, in fact, moved away, clearly overshooting. This figure illustrates what we call a targeting error. Targeting errors were not random. They were definitely more frequent in specific circumstances: when stimuli were flashed near the time of saccades. This

finding can be illustrated in several ways. One is to plot the second saccade size as a function of stimulus timing; this is the mode of display we shall later consider in Fig. 6. Another way, used in Fig. 4, is to plot the final eye position attained after one or two saccades occurring within 600 msec after the test flash, against the time of S_2 presentation relative to the onset of the initial saccade (0 msec on the abscissa). Gap results pooled for the two experienced subjects are shown in Fig. 4(A), No-gap results in Fig. 4(B). Dots and triangles represent final eye position but, contrasted to dots, triangles identify the cases when the subjects pressed the switch to indicate that the stimulus was judged "not at the same place". Were the subjects aiming accurate, all the data points would be horizontally aligned around 17 deg. In fact, they were considerably scattered as commonly

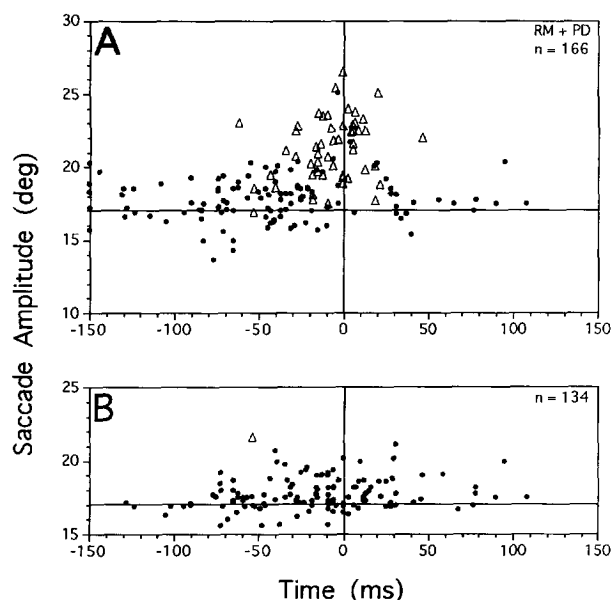


FIGURE 4. Dots and triangles indicate final eye position as a function of S_2 timing with respect to the onset of the initial saccade (at 0 msec on the abscissa). In all cases, correct saccade termination should have been 17 deg (i.e. F- S_2 distance, see Fig. 2). Triangles identify trials in which S_2 was reported "not at the same place" as S_1 . Data pooled from the two experienced subjects RM and PD. (A) Gap trials. (B) No-gap trials. Average latency of initial saccade was 273.1 msec (SD = 25.22) for RM, and 236.2 msec (SD = 36.31) for PD. Average saccade duration was 54 msec for RM and 51 msec for PD.

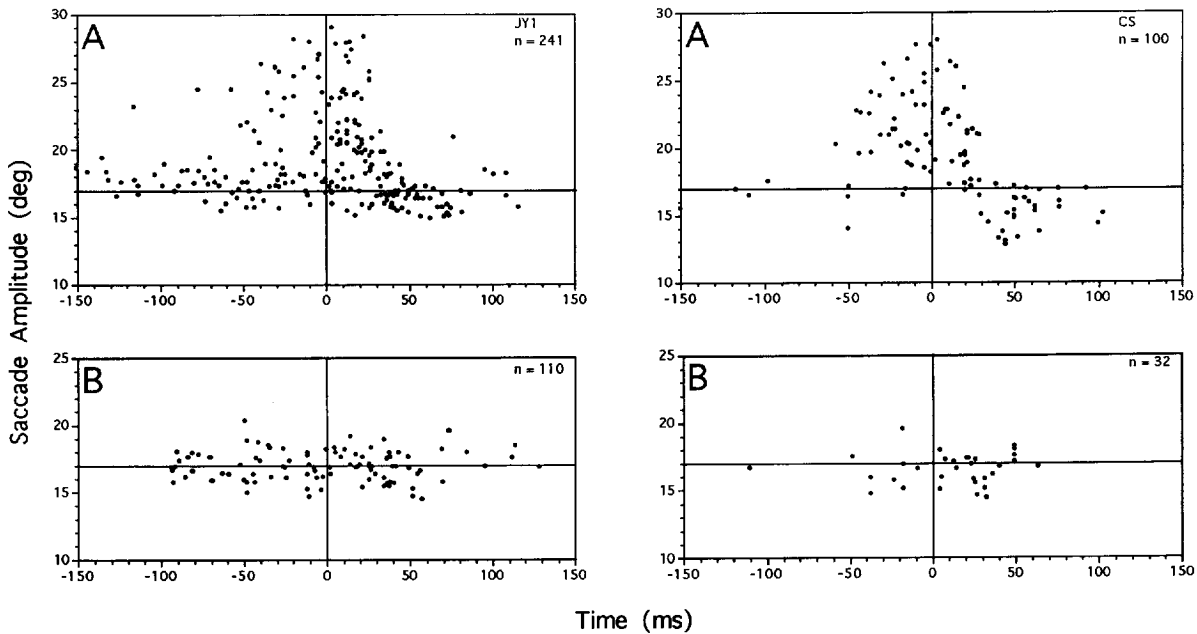


FIGURE 5. Data from two naive subjects (JY and CS) in Expt 1. Same presentation as in Fig. 4. Gap data in (A), No-gap data in (B). Data for JY were collected in three sessions. Average saccade latency was 258.1 msec (SD = 18.63) for JY, and 262.6 msec (SD = 44.53) for CS. Average saccade duration was 48 msec for JY and 51 msec for CS.

found with saccades to the remembered location of a target (e.g. Merton, 1961; Bishof & Kramer, 1968; Gresty & Leech, 1976). Figure 4(B), compared to Fig. 4(A), reveals many saccades terminating too far. They were made to stimuli flashed just before the initial saccade and their number reached a peak around its onset. One will notice that this is also the period when the triangles (switch presses meaning “not at the same place”) were concentrated. There was only one switch press in Fig. 4(B).

Control Gap trials (S_2 at 4 or 6 deg) are not included in Fig. 4(A) because their number was too small but, consistently, the amplitude of the second saccade in these trials was exaggerated for targets flashed before and just after saccade onset (see Honda, 1990).

Figure 5 summarizes the errors of targeting in similar experiments with two naive subjects. To avoid the possible risk that their oculomotor responses be influenced by having also to report their perception, these subjects were not required to signal when S_1 and S_2 were

“not at the same place”. They were asked to use the switch only to indicate when S_2 was not seen, in which case the trial was discarded. The presentation is the same as in Fig. 4, and again here it can be seen that the number and size of mislocalizations started to rise before the saccades (the time-course of mislocalization will be shown for all the experiments together in Fig. 9). The difference between the final eye positions in the Gap and No-gap conditions was statistically evaluated for successive 50-msec time bins. For all subjects, the difference was highly significant in the period of interest which is the 50-msec bin preceding saccade onset (see Table 1).

In Fig. 6, instead of the final eye position, the amplitude of the second saccade is plotted against time. All the trials in which only the initial saccade occurred are lined up along the 0 deg abscissa. This alternative way of displaying the data stems from the assumption that it is the inaccuracy of the first (large) saccade that contributes mostly to the variability of total amplitude, whereas the second (smaller) saccade is more correct, being adjusted to the perceived distance between S_1 and S_2 . Without trying to defend this assumption, we shall simply submit the results for comparison. They reveal that subjects differed appreciably from each other in their propensity to make two saccades. Some readily did, others were most often reluctant although, as pointed out by Honda (1991), they had little problem making perceptual judgments. However, one will notice that when they made a second saccade, our subjects, scarcely [as in Fig. 6(D)] or generously, tended to make it to reach stimuli presented near the time of saccade. This analysis suggests that the difficulty of making a second saccade may account for much of the scattering seen in Figs 4(A) and 5(A). Otherwise,

TABLE 1. Statistical comparison of Gap vs No-gap data (Expt 1) within 50-msec bin preceding saccade

	Subject		
	RM + PD	JY	CS
<i>Gap</i>			
Mean	19.09	20.68	21.05
SD	2.27	3.81	3.20
<i>No-gap</i>			
Mean	17.87	16.96	16.56
SD	1.14	1.33	1.52
t-test	3.95	6.66	6.48
P	<0.0005	<0.0005	<0.0005

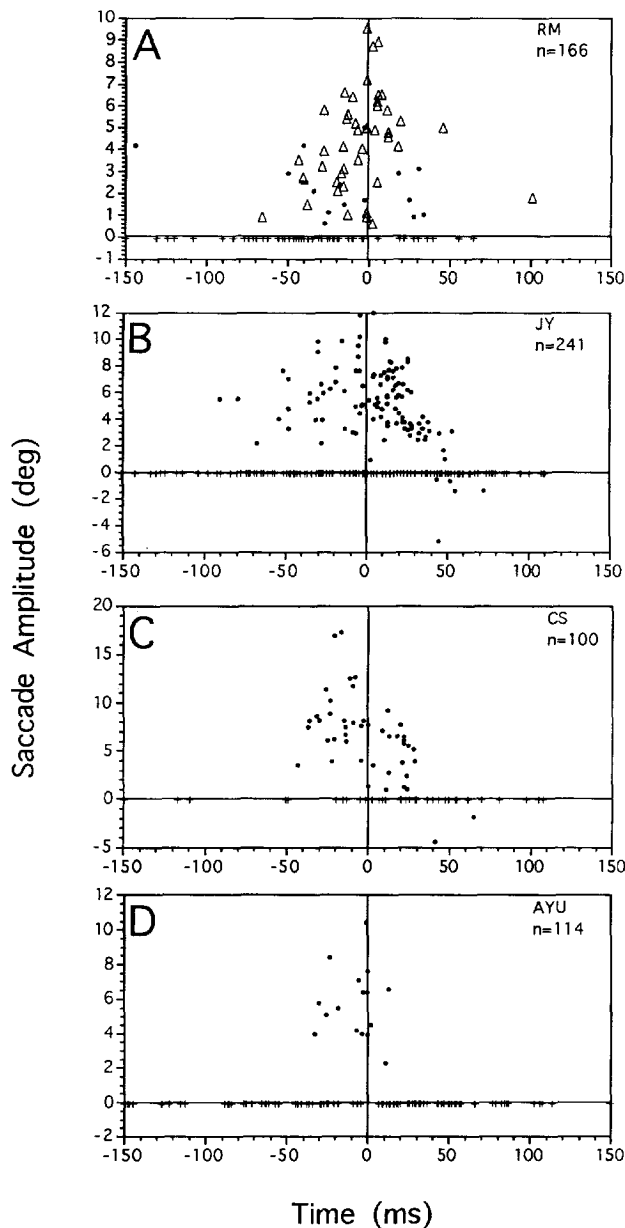


FIGURE 6. Amplitude of second saccade, in Expt 1, plotted against S_2 timing relative to the onset of the initial saccade (at 0 msec on the abscissa). (A), (B), and (C) present the same data as Figs 4(A) and 5(A). Triangles in (A) identify trials in which S_2 was reported "not at the same place as S_1 ". (D) Naive subject AYU who made very few second saccades. All trials that included only one saccade are plotted on the 0 deg line. Average saccade latency was 235.3 msec (SD = 27.00) for AYU.

the timing, direction, and size of the errors were in good agreement with oculomotor and perceptual errors reported in the literature on the two-step experiment (Kennard *et al.*, 1971; Mateeff, 1978; Sperling, 1990; Honda, 1989, 1990, 1991; Dassonville *et al.* 1992).

Experiment 2: Mislocalization of foveal stimuli

In Expt 1, S_2 was presented at the position of S_1 or close to it. One may argue that localization of a brief dim peripheral stimulus cannot be very precise, and flashing it near the time of a saccade only heightens the uncer-

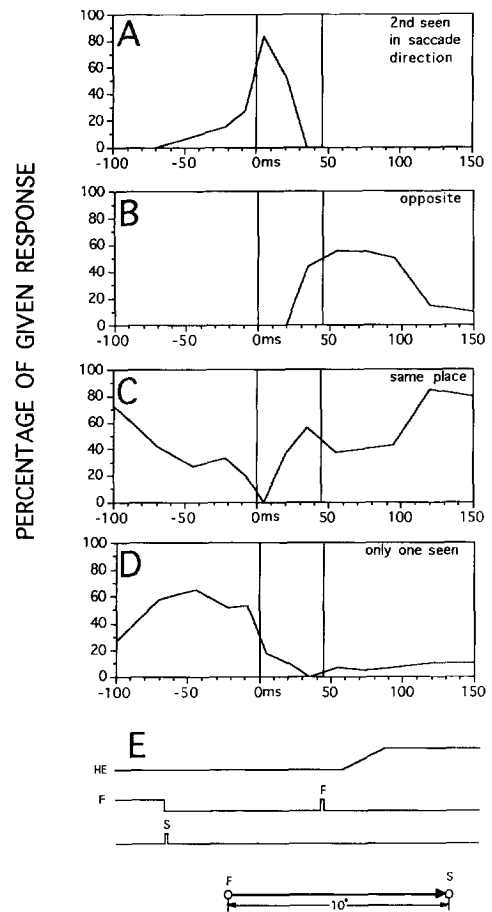


FIGURE 7. Perceptual judgments in Expt 2. Schematic description in (E). The main difference with Expt 1 is that S_2 was replaced by F relit; S was the target of the initial saccade at 10 deg from F. Percentages of the four allowed types of responses plotted against the timing of the initial saccade. Second F (test stimulus) perceived as displaced in the direction of the saccade in (A), opposite the direction of the saccade in (B), at the same place as first F in (C), and not detected in (D). The percentages add to 100% for each point, which represent from 12–26 trials. Average saccade duration (45 msec) indicated by vertical lines.

tainty. Perhaps, the subjects' flawed performance is due to the difficulty of the task, and there would be much improvement if the test stimulus were viewed foveally.

Experiment 2 was run under two conditions. In the first one, an experienced subject was instructed to make perceptual judgments on the location of the second flash, that we call F instead of S_2 , since this flash was at the site of the fixation point F. No targeting movement was required. In 37% of the trials (serving as controls), S_2 was 1 or 2 deg away from F. In 63% of the trials, it was located at the site of the point of fixation F. The results in Fig. 7 concern only these trials ($n = 168$) and are expressed as percentages of four mutually exclusive responses allowed by switch presses. These responses were: Fig. 7(A), the second stimulus F is perceived as displaced to the right (of the first F), i.e. "in the saccade direction". The data show that this happened for stimuli presented before or during the saccade but, most frequently, at saccade onset. This also happened in all control trials (but these are not

included in Fig. 7). Figure 7 (B), reciprocally, the second F could be perceived as displaced in the direction opposite to that of the saccade, and this happened for post-saccadic presentations. Figure 7(C), the second stimulus F is perceived at the "same place" (its veridical position). This was the only correct response, and it was given at various delays except at saccade onset. Figure 7(D), if the second F was not detected as a separate stimulus, the subject pressed the switch indicating "only one seen". Missing the detection of the second F occurred rarely except for stimuli flashed just before the saccade. Each point in Fig. 7 represents 12–26 trials and the four possible responses add up to 100%. One will notice that the time distribution of the first two judgments (case A, same direction; case B, opposite direction) corresponds well to the direction and timing of targeting errors obtained in similar oculomotor tasks (e.g. Honda, 1990; Dassonville *et al.*, 1992; and this study).

In the second condition, Experiment 2 was run as an oculomotor task with the following modifications. (1) The brightness of the initial fixation point F was decreased (about halved) to facilitate the discrimination of the second F as a separate event. Indeed, F first lit for

800–1800 msec could mask the second F lasting only 4 msec. (2) For the same purpose, a constant 50-msec delay was interposed between the offset of F and the onset of S, thus also lengthening the blank interval between the two F stimuli. (3) Most importantly, the whole display, composed of F, S, and F again, was randomly shifted 1, 2, or 3 deg right or left from trial to trial. As the task was now to make a saccade back as correctly as possible to F, there was a risk that the subject uses the site of the fixation point of the next trial as a feedback indicating where the last saccade should have terminated. This would have been a valid cue if F had been systematically presented at 0 deg on the screen, but shifting the display from trial to trial prevented the subject from relying on this cue.

One experienced and two naive subjects were tested under the second condition, and the results are presented in Fig. 8. There could not be any No-gap trial in this experiment, and there were no controls with test stimuli actually displaced by a few degrees. Subjects were requested to report failure to detect the second F stimulus by pressing a switch, and these trials were discarded since, in these cases, the second saccade was not an attempt to reach a particular goal, but simply a return to the eye primary position.

These results suggest that a foveal stimulus, presented to a steady eye just before a saccade, is mislocalized to the same extent as a peripheral stimulus. Two comparisons were made between the results of Expts 1 and 2. First, sliding averages of data points in Figs 4, 5, and 8 were plotted in Fig. 9. The bin width is 25 msec and means are presented for successive times 5 msec apart. The error in representing the real time course of mislocalization is, therefore, <12.5 msec. The results suggest that mislocalization started at least 50 msec before saccades in practically all cases. To verify this conclusion, we inquired whether the data points in the last 50 msec preceding saccades statistically differed from the baseline. However, in Expt 2, there were no No-gap data available as in Expt 1, for comparison. Therefore, data within the -150 to -100 msec range pooled with data in the 100 to 150 msec range relative to saccade onsets, were used as baseline reference. Table 2 shows that, in all six cases illustrated in Fig. 9, tested in the same manner, the difference was statistically significant.

Experiment 3: What causes the perception of movement?

In the Gap condition of Expt 1, the two flashes S_1 and S_2 were often interpreted as being at different places. Does this mean that, if the stimulus had been continuously lit until the onset of the initial saccade, the stimulus would have appeared as starting at one point and finishing at another? In other words, in the No-gap condition, should not the stimulus appear to be moving? Actually, after completing Expt 1, subjects reported having sometimes the impression that the stimulus was moving. They described it as a streak of light.

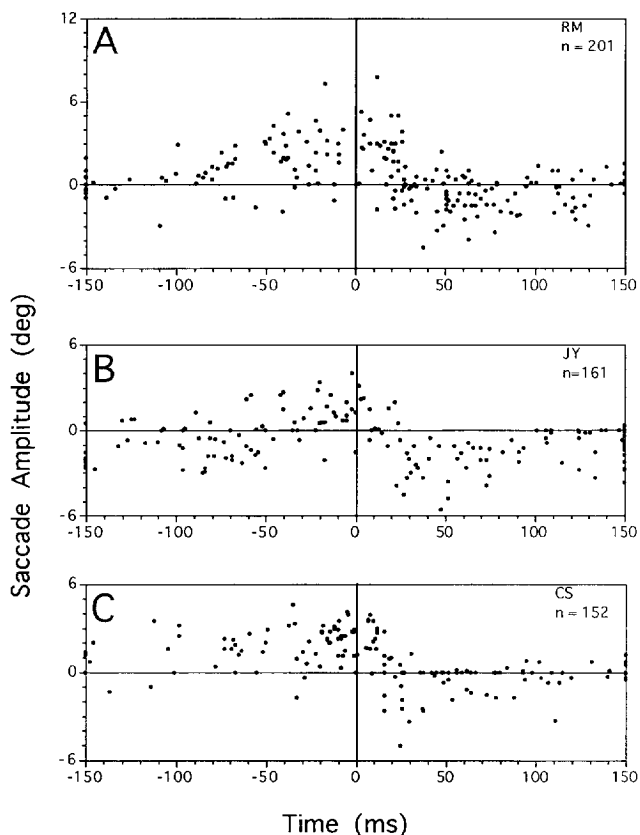


FIGURE 8. Oculomotor targeting in Expt 2: Gap paradigm. Experienced subject in (A), naive subjects in (B) and (C). Same presentation as in Fig. 4. Ordinate represents final eye position; correct aiming would have been to 0 deg (i.e. back to the initial site of fixation, origin of the first saccade). Average saccade latency was 224.9 msec (SD = 52.55) for RM, 218.7 msec (SD = 49.10) for JY, and 250.6 msec (SD = 46.80) for CS. Average saccade duration was 47 msec for RM, 39 msec for JY, and 44 msec for CS. RM data were pooled from two sessions.

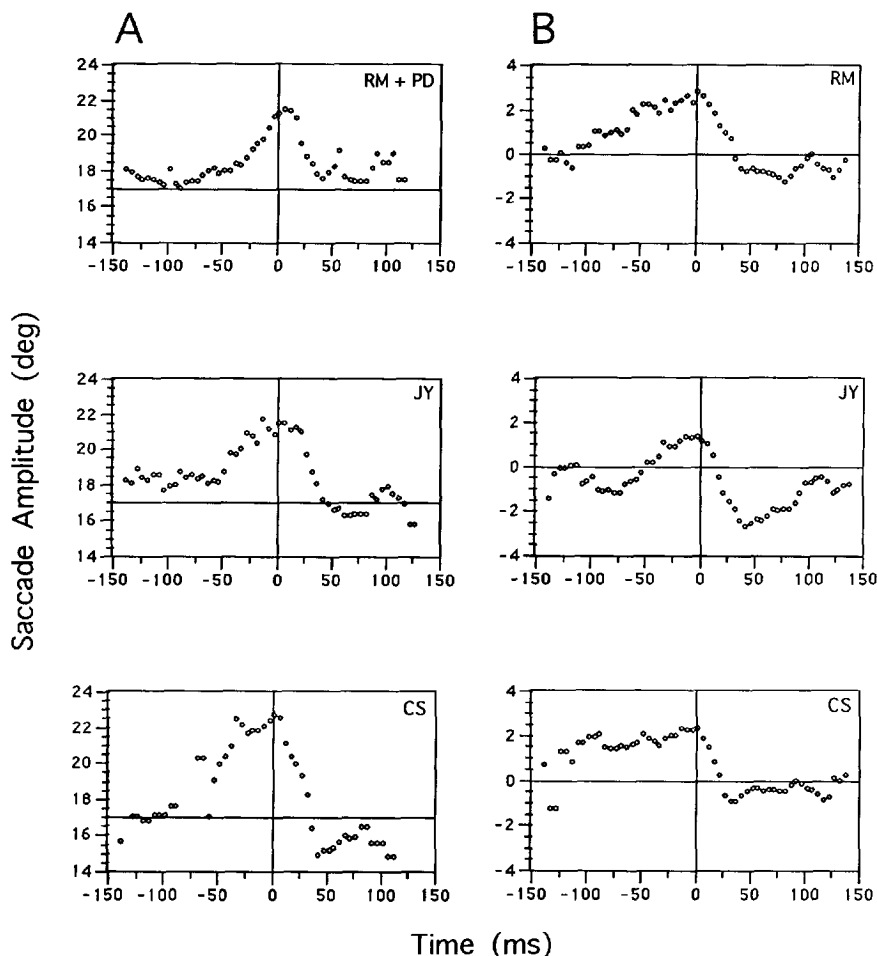


FIGURE 9. Sliding averages of final eye positions. (A) Shows data of Expt 1 plotted in Figs 4 and 5. (B) Data of Expt 2 plotted in Fig. 8. Every 5 msec, each point represents the average within a 25-msec bin centered on this point.

The objective of Expt 3 was to verify the validity of our asking whether the stimulus is seen at a different place when, actually, the relevant question would have been: is it moving from one place to another? We wanted to determine whether any streak could be produced by a stimulus occurring before the eyes moved. Although the answer to this question can be guessed from the literature (e.g. Holly, 1975;

Campbell & Wurtz, 1978; Mateeff, 1978), it was essential to obtain the answer in the situation under study.

In similar conditions as in Expt 1, one experienced and one naive subjects were instructed to press a switch every time they saw a streak of light. To avoid any ambiguity, before the experiment, the subjects were shown real streaks of light generated under computer control, by moving the stimulus for 10 msec at the speed of a

TABLE 2. Statistical comparison between data within 50-msec bin preceding saccade and two other bins serving as baseline, in Expts 1 and 2

	Experiment 1			Experiment 2		
	RM + PD	JY	CS	RM	JY	CS
<i>- 50 msec*</i>						
Mean	19.09	20.68	21.05	2.25	0.97	2.18
SD	2.27	3.81	3.20	1.89	1.47	1.27
<i>Baseline†</i>						
Mean	17.83	18.09	16.30	-0.21	-0.81	0.13
SD	1.28	1.67	1.23	1.19	1.14	1.39
<i>t</i> -test	3.02	3.94	7.05	6.47	5.36	5.47
<i>P</i>	<0.005	<0.001	<0.0005	<0.0005	<0.0005	<0.0005

* - 50 msec = data within last 50 msec bin preceding saccade.

† Baseline = data within -150 to -100 msec bin (i.e. before saccade) and 100-150 msec (i.e. after saccade), pooled under the assumption that the effect of the saccade on mislocalization is minimal in those bins.

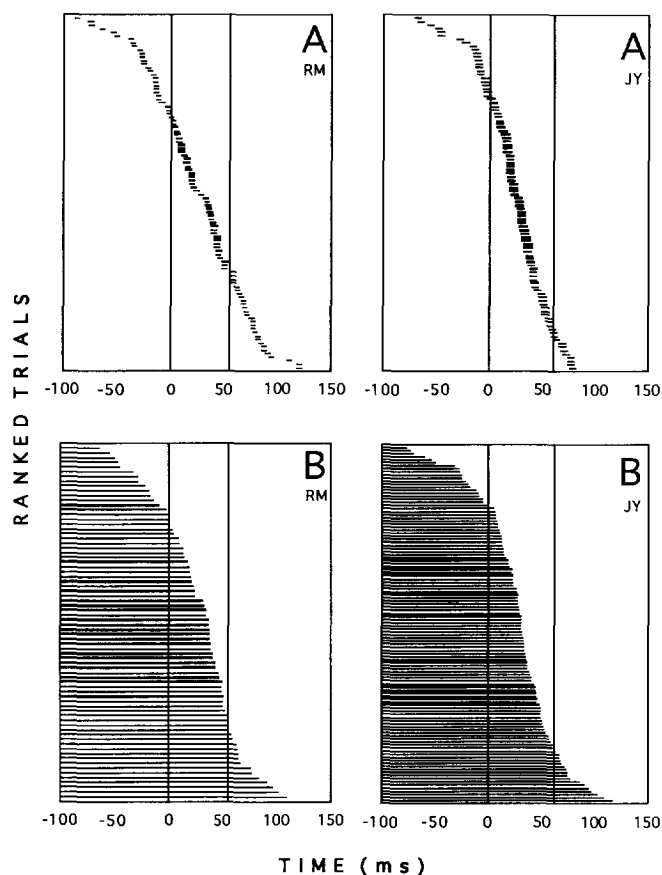


FIGURE 10. Timing of stimuli perceived as "streaks" in Expt 3. Horizontal bars represent S_2 stimuli (Gap trials) in (A), and the late portion of the S_1 - S_2 stimuli (No-gap trials) in (B), with respect to saccade onset. Thick bars identify trials in which streaks were reported. For clarity, trials have been ranked in order of increasing delay with respect to saccade onset. Initial saccades occurred between the two vertical bars. Duration of average initial saccades was 55 msec (17 deg saccades) for subject RM, and 46 msec (14 deg saccades) for subject JY. S_2 lasted 4 msec in the experiment with RM and 6 msec in the experiment with JY. For stimuli that fell close to the end of the saccade, the timing has been measured from saccade offset to report exactly if the stimulus was present during the saccade and for how long.

saccade. This was done practically by extracting a segment of saccade from one of their previous record, generating a 6–7 deg ramp of equal velocity and duration, and playing it back to the subject. Furthermore, 12% of the stimuli in the Gap trials were actually moving stimuli interleaved with stationary ones. The moving stimuli were all recognized when displayed before or after saccades. Figure 10 shows the timing of stationary stimuli for which a report of "streak" was given in the Gap situation in Fig. 10(A) and No-gap in Fig. 10(B). A thick line means that a streak was reported for that trial (without specifying, of course, when exactly the impression occurred during the trial itself). The results were clear-cut for both subjects: streaks were exclusively reported for stimuli present during saccades, that is when the image was actually displaced on the retina. In the No-gap condition, the naive subject was more hesitant to report seeing a streak. Neverthe-

less, in both cases, streaks were not reported if the stimulus outlasted the duration of the saccade, despite the preceding displacement of the stimulus on the retina.

The hypothetical eye position signal of our subjects

Finally, for comparison, theoretical EPS measurements were derived from data of different experiments. This was done, trial by trial, by subtracting the retinal error from the final eye position, representing the subject's estimate of S_2 location. The result of this subtraction is the hypothetical eye position at the time of S_2 presentation, as evaluated by the brain. Referring to Fig. 1, the operation we are describing corresponds to subtracting, point by point, the retinal input from the output, to find out the value of EPS. A set of two EPS curves is shown in Fig. 11 for comparison with similar curves obtained in other studies. For simplicity, these curves have been calculated on the assumption of a three-segment model (Dassonville *et al.* 1992) and should not be construed as providing the best fit.

DISCUSSION

If each of the reported experiments is considered separately, it may not be difficult to find studies in

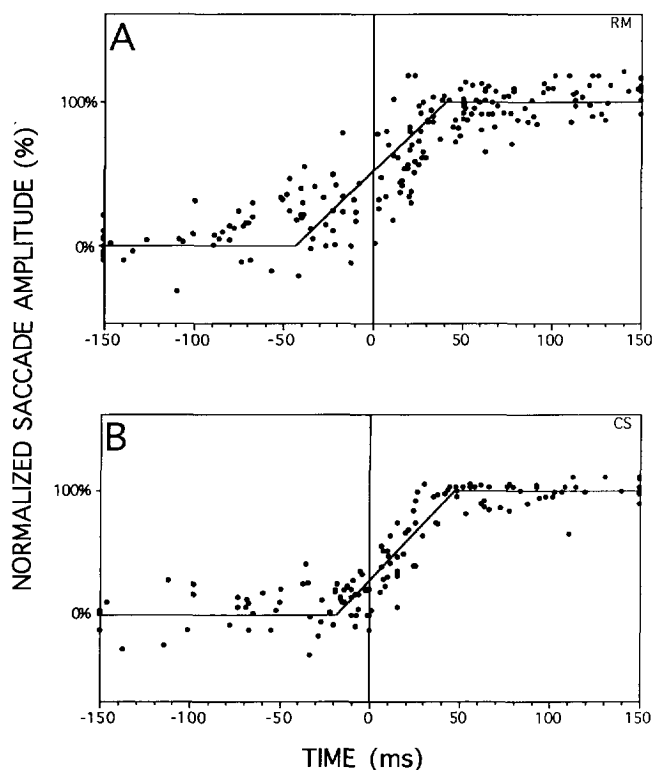


FIGURE 11. Two typical EPS curves derived from aiming errors recorded in this study: (A) from subject RM [data from Fig. 8(A), average saccade duration: 47 msec] and (B) from subject CS [data from Fig. 8(B), average saccade duration: 44 msec]. Saccade onset at 0 msec, and amplitude normalized at 100% for comparison. Lines represent the best linear approximation of the time-course of EPS.

the literature that would predict its outcome. But collectively, these results illustrate a paradox that we shall now try to explain.

Two stimuli flashed at the same place in the dark can appear located far away from each other. When this illusion occurs, it concerns stimuli flashed near the time of a saccade and the error reaches its maximum at saccade onset. This maximum can be as much as 70% of the amplitude of the initial saccade. The present study established five points. Experiment 1 showed that: (1) if the target light was turned on long before a saccade (No-gap), it was not mislocalized as was a brief flash (Gap); (2) in more than 90% of the cases, perceptual judgments were in line with the errors of ocular targeting; (3) the latter errors were the same whether or not the subject was required to express a perceptual judgment. In particular, oculomotor mislocalization was not obviously dependent on having to make an overt judgment. In Expt 2, we saw that (4), a stimulus S_2 could be mislocalized to the same extent if presented foveally instead of peripherally. Finally, in Expt 3, we saw that (5), the illusory displacement of the target before saccades never elicited any perception of streaks.

There is a natural explanation for the mislocalization observed. Actually, given the constraints under which the oculomotor system works, it is difficult to imagine how mislocalization could be avoided in the very destabilizing period when the eyes move at high speed. At that time, the brain has to shift rapidly the egocentric reference (EPS) for a visual image recorded in the dark. The critical point is that the visual input is slow (taking more than 40 msec in retinal processing) and variable [e.g. varying with stimulus brightness and eccentricity (O'Regan, 1984)]. This makes it practically impossible for the two inputs illustrated in Fig. 1 to be precisely synchronized. But, if they are not, a mismatch of a few milliseconds, at the speed of a saccade, is enough to create a localization error of several degrees. There is electrophysiological evidence that the EPS is not adequately delayed but that it is damped (Dassonville *et al.*, 1990b). This would account for the present psychophysical data as well.

The reason why the EPS is damped is not obvious. There are no known high-frequency limitations on neural circuits that would explain why a signal with a time-course as fast as a saccade should be distorted. Two interesting hypotheses have been offered. First, Pouget, Albright and Sejnowski (1992) have assumed that the neural summation effected at the junction shown in Fig. 1 operates on a visual signal that has a finite minimum duration possibly longer than the photic stimulus itself (see also O'Regan, 1984). Whether this duration is retinal persistence or any equivalent process occurring centrally does not affect the argument. The point is that the eye position sampled at the start and at the end of a stationary retinal error signal lasting for several tens of milliseconds may not be the same. If the value, entered into the summing junction is some intermediate between the initial and final samples, the EPS will appear to last longer than the saccade itself by as

much as the duration of the retinal signal. In other words, the EPS will be damped.

The second hypothesis derives from an observation by Sperling (1990). He noted that the mislocalization curve of a spot of light, flashed when a saccade was made between two stable markers, was the same as when the eyes remained fixed but the markers were displaced at the speed of a saccade. Sperling stressed the inherent uncertainty in recognizing the timing of an event like a flash with respect to rapidly displaced references. He argued that the only unambiguous references are the positions of the markers before and after their displacement whereas the characteristics (e.g. speed) of that displacement really do not matter. Subjects have to make a timing judgment that can be expressed as: did the event occur closer to "before" or "after"? and their decision is probabilistic. The resulting shift is likely to have its own time-course, independent of the temporal characteristics of the saccade. This interpretation cannot apply as such to our experiments since the tasks were performed in total darkness and no photic landmarks were present for localization. But a similar reasoning can be proposed regarding the EPS serving as a reference. Let us assume the EPS to be available or readable only when the eyes are stationary. During transitions, the brain would have to make a probabilistic estimate with respect to the positions before and after the saccade. That estimate would have to be done by neurons; it may happen to be slow, progressive, and perhaps its timing varies from trial to trial. Whatever the case, the outcome of this hypothetical "probabilistic estimation" mechanism is what we would call EPS, and it happens that this EPS appears damped.

In Expt 1, the size of targeting errors to No-gap stimuli was not dependent on the proximity of a saccade as it was for Gap stimuli. Is it because, lasting longer, No-gap stimuli were better detected and their position more reliably registered by the brain? If so, one would expect an overall increase in aiming accuracy, but such an improvement is not clear since the scatter of errors in all the (B) plots (No-gap condition) of Figs 4 and 5 was not uniformly narrower than in the (A) plots (Gap condition). The improvement specifically affected the localization of long-lasting stimuli terminating just before a saccade. Why? Comparing the Gap and No-gap situations, it is relevant to ask whether the brain determines the location of a long-lasting stationary stimulus when it is first seen or last seen. If the timing of these determinations leads to different estimates, either the stimulus will be perceived successively at different places (i.e. moving, but this was disproved by Expt 3) or one of the position estimates will take precedence of the other. One could expect the estimate made at stimulus offset, being most recent, to be selected. But, this was not what happened: in the No-gap situation, gaze landed close to the veridical location of the stimulus, as computed at its onset, when the eyes were stable long before the saccade, and this estimate was not up-dated. Thus, the observations made in both Expt 1 and 3 tell us something more about the summing junction in Fig. 1.

We already established that a change of the EPS input could be interpreted (wrongly) by the brain as a change in the visual input. Indeed, even though the latter remains constant, a changing EPS could produce a different output (i.e. a different estimate of target position). Now we can specify that this does not apply if the stimulus remains continuously on. Then, an EPS change seems irrelevant: the brain behaves as if this cue were superfluous and dispensable. In a very simplistic way, this option can be implemented in the model by placing a gate on the EPS input (in Fig. 1) that will allow EPS sampling when an event occurs on the visual input. But what is an event? A stimulus onset appears to qualify. Does a stimulus offset (occurring, e.g. just after a saccade) qualify too? Or a change of color?

If a changing EPS by itself cannot make a stimulus appear moving, then what can? Why did subjects sometimes see streaks of light in our experiments? In the conditions of our study, Expt 3 gave a definite answer. Stimuli were perceived as moving when their image traveled some distance across the retina. This happened almost as soon as the saccade started in front of a stationary light. But if the light was still present and steady after the saccade, no streaks were reported. This confirms previous observations. The censoring of movement perception in this case has been attributed to backward masking (Matin & Matin; 1972; Holly, 1975). Further psychophysical explorations probably will reveal other properties of the eye position signal and its effects on the visual input.

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