

Sensorimotor Integration Compensates for Visual Localization Errors During Smooth Pursuit Eye Movements

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Sensorimotor integration compensates for visual localization errors during smooth pursuit eye movements. *J Neurophysiol* 85: 1914–1922, 2001. To localize a seen object, the CNS has to integrate the object's retinal location with the direction of gaze. Here we investigate this process by examining the localization of static objects during smooth pursuit eye movements. The normally experienced stability of the visual world during smooth pursuit suggests that the CNS essentially compensates for the eye movement when judging target locations. However, certain systematic localization errors are made, and we use these to study the process of sensorimotor integration. During an eye movement, a static object's image moves across the retina. Objects that produce retinal slip are known to be mislocalized: objects moving toward the fovea are seen too far on in their trajectory, whereas errors are much smaller for objects moving away from the fovea. These effects are usually studied by localizing the moving object relative to a briefly flashed one during fixation: moving objects are then mislocalized, but flashes are not. In our first experiment, we found that a similar differential mislocalization occurs for static objects relative to flashes during pursuit. This effect is not specific for horizontal pursuit but was also found in other directions. In a second experiment, we examined how this effect generalizes to positions outside the line of eye movement. We found that large localization errors were found in the entire hemifield ahead of the pursuit target and were predominantly aligned with the direction of eye movement. In a third experiment, we determined whether it is the flash or the static object that is mislocalized ahead of the pursuit target. In contrast to fixation conditions, we found that during pursuit it is the flash, not the static object, which is mislocalized. In a fourth experiment, we used egocentric localization to confirm this result. Our results suggest that the CNS compensates for the retinal localization errors to maintain position constancy for static objects during pursuit. This compensation is achieved in the process of sensorimotor integration of retinal and gaze signals: different retinal areas are integrated with different gaze signals to guarantee the stability of the visual world.

INTRODUCTION

When the eyes move, the image of a static object moves across the retina, yet the visual world remains stable. It has been suggested that the CNS achieves this stability by integrating the current direction of gaze with the object's retinal location (Andersen et al. 1993; Bridgeman 1995; Mon-Wil-

liams and Tresilian 1998; Pouget et al. 1993; von Helmholtz 1925). In this paper, we investigate this process by examining the localization of static objects during smooth pursuit eye movements. We show that during smooth pursuit localization of static objects is indeed fairly accurate, but briefly flashed objects can be mislocalized considerably. These results are not consistent with a simple combination of a single gaze signal with all retinal locations.

Localization of static objects during pursuit consists of three components: determining the gaze direction with respect to the body, eye-centered localization on the basis of retinal information, and integration of the retinal and gaze signals. We will now discuss each of these components in turn.

First, the direction of gaze must be known to localize objects relative to the observer. For head-fixed conditions gaze direction is equivalent to eye position.

Second, the eye-centered localization of moving objects has been extensively studied. Many studies have reported substantial errors in localizing moving objects during fixation. This is illustrated by the flash-lag effect (Nijhawan 1994) in which a flash shown in alignment with a moving object is seen to lag the moving object. Several explanations have been suggested for this effect, such as extrapolation of the moving object's path (Khurana and Nijhawan 1997; Nijhawan 1994), different visual latencies for moving and flashed objects (Patel et al. 2000; Purushothaman et al. 1998; Whitney and Murakami 1998; Whitney et al. 2000a,b), spatiotemporal filtering mechanisms (Eagleman and Sejnowski 2000; Krekelberg and Lappe 1999, 2000; Lappe and Krekelberg 1998), an interaction of visual focal attention and metacontrast (Kirschfeld and Kammer 1999), and the need to sample the moving target's position in response to the flash (Brenner and Smeets 2000). Although the explanation of the flash-lag effect is still under debate (Krekelberg et al. 2000; Patel et al. 2000), it is clear that it reflects a mislocalization of the moving object, not of the flash. For instance, Eagleman and Sejnowski (2000) showed that the flash-lag effect can be reduced to a misperception of the initial position of a suddenly appearing, moving object relative to a flash. This parallels the Fröhlich effect (Fröhlich 1923) in which a suddenly appearing, moving object is misperceived relative to a static frame. In addition, the flash-lag effect is

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larger in size for objects moving toward the fovea (foveopetal) than for objects moving away from it (foveofugal) (Mateeff and Hohnsbein 1988; Mateeff et al. 1991b).

Third, the classical idea of the integration of retinal and gaze signals is that it amounts to a vector addition of the point at which the gaze is directed and the object's location on the retina (Andersen et al. 1993; von Helmholtz 1925). Integration is in fact more complicated than a simple vector addition because of the complex three-dimensional properties of the retina and their dependence on eye orientation (Crawford et al. 2000; Henriques and Crawford 2000). We will, however, only consider localization in a (vertical) plane under head-fixed conditions, and in those conditions, the vector addition model is valid. Most models further assume that the information from the entire retina is combined with a single gaze signal (Andersen et al. 1993; Bridgeman 1995; Mon-Williams and Tresilian 1998; Pouget et al. 1993; von Helmholtz 1925). This process requires that retinal signals be integrated with gaze signals relating to the same moment in time. Since retinal signals and oculomotor efferent signals have very different latencies, temporal matching of these signals creates a computational problem for the CNS. Any temporal mismatch between the signals would produce localization errors. Mislocalization due to incorrect synchronization of the two signals has been shown to occur around the time of a saccade (Cai et al. 1997; Matin and Pearce 1965; Morrone et al. 1997; Ross et al. 1997). During pursuit, flashed stimuli are generally mislocalized in the direction of pursuit; this has also been interpreted in terms of a temporal mismatch between the retinal and gaze signals (Hazelhoff and Wiersma 1924; Ward 1976).

Errors in object localization have been used to investigate these processes. We compare mislocalization of flashed and constant stimuli during fixation and pursuit. We use the term *constant* to mean a stimulus that is not transient, and is thus present for long enough to induce retinal slip, if either the eyes or the stimulus moves. Therefore a constant stimulus may move during fixation, while during pursuit a constant stimulus may be static according to our definition.

We have used relative and egocentric localization methods to examine the sensorimotor integration process during pursuit. In the first experiment, we replicate earlier studies (Mateeff and Hohnsbein 1988; Mitrani and Dimitrov 1982) showing that flash-lag effects are similar in size in retinally equivalent conditions during fixation and pursuit, and we extend these results, showing similar effects for different directions of eye movement. In a second experiment, we examine how relative mislocalization of flashed and static stimuli during pursuit varies across the visual field. This experiment shows that localization errors occur primarily along the direction of the pursuit eye movement. In the third experiment, we examine whether the relative localization errors that we observed during pursuit are due to mislocalization of the flashed or of the static stimulus. This experiment shows that in pursuit it is the flash that is mislocalized, whereas in fixation the moving object is mislocalized. In a final experiment, we use egocentric localization methods to show that the earlier experiments measured genuine egocentric localization errors rather than errors in localizing visual stimuli relative to one another.

METHODS

Four experiments were performed. In all experiments, stimuli were presented on a Dell D1028LR monitor (P22 phosphor, 85 Hz refresh rate, $1,024 \times 768$ resolution) in a dark room. Subjects viewed the stimuli binocularly from 37 cm with their head supported by a chin rest. The computer screen subtended 46° horizontally and 36° vertically. The procedures were approved by the local ethical committee and informed consent was obtained from every subject. All subjects had normal or corrected-to-normal vision. Prior to their inclusion in an experiment, subjects were tested for their ability to track the pursuit target while performing the task. This was done by visual inspection by the experimenter who looked at the subjects' eye movements in a mirror mounted on the monitor's frame. The pursuit eye movements of the subjects who participated in the first experiment were recorded with an eye tracker (see following text). This confirmed the reliability of their pursuit as initially assessed by the experimenter's visual inspection. In the later experiments, we excluded subjects who showed any signs of difficulty in pursuing targets based on the experimenter's visual inspection. In total, six subjects were excluded based on poor pursuit movements.

Fixation and pursuit experiment

In this experiment, we compared the relative localization of flashed and constant stimuli during fixation and during pursuit. We replicated the experiments of Mitrani and Dimitrov (1982) and of Mateeff and Hohnsbein (1988) in a setup different from theirs that allowed direct comparison of the positions of the two stimuli. Five subjects (the 3 authors and 2 naive subjects) were tested in two conditions.

In the fixation condition, subjects fixated a black circle (<0.1 cd m^{-2} with a diameter of 0.31°) placed straight ahead of them while two similar circles (reference points, separated vertically by 4.72°) moved leftward at $19.1^\circ s^{-1}$ on a red background (12 cd m^{-2}). Each trial could consist of many sweeps. When the reference points disappeared at the left a new sweep started from the right 1 s later. During each sweep, a vertical line (0.093° wide and 1.63° high) was flashed for 12 ms (1 frame) at a fixed horizontal distance from the fixation point. The task was to adjust the time of this flash, and thus the position of the moving reference points at the time of the flash, so that the flash appeared aligned with the reference points (see Fig. 1A). Subjects used the computer arrow keys to adjust the time of the flash for subsequent sweeps. They could continue adjusting the time for as many sweeps as they wished. When satisfied that the flash appeared aligned between the reference points, they pressed the space bar to register their judgement and to initiate a new trial. The initial timing of the flash for each trial was randomized, and seven different positions of the flash relative to the pursuit target were tested (see Fig. 1D). Five repetitions were employed for each stimulus, and the different flash positions were tested in a random order.

In the pursuit condition, the retinal information was the same as in the fixation condition, but now subjects made smooth pursuit eye movements. They pursued a circle (pursuit target with a diameter of 0.31°) moving rightward at $19.1^\circ s^{-1}$. During each sweep, a vertical line was flashed on the pursuit target's path at a fixed horizontal distance from the pursuit target and thus at an approximately fixed retinal location. Again, subjects adjusted the time of the flash so as to align it with two reference points that were continuously visible straight ahead (see Fig. 1B). Eight different positions of the flash relative to the pursuit target were tested (see Fig. 1E). All other details were identical to those of the fixation condition. In a separate session, eye movements were recorded at 60 Hz with an ASL 504 eye tracker. For this purpose, viewing distance was increased to 61 cm with the stimuli rescaled to subtend the same retinal angle as in the experiment proper (this was necessary because the eye tracker could not cover the whole range of eye positions in the configuration used in the experiment proper).

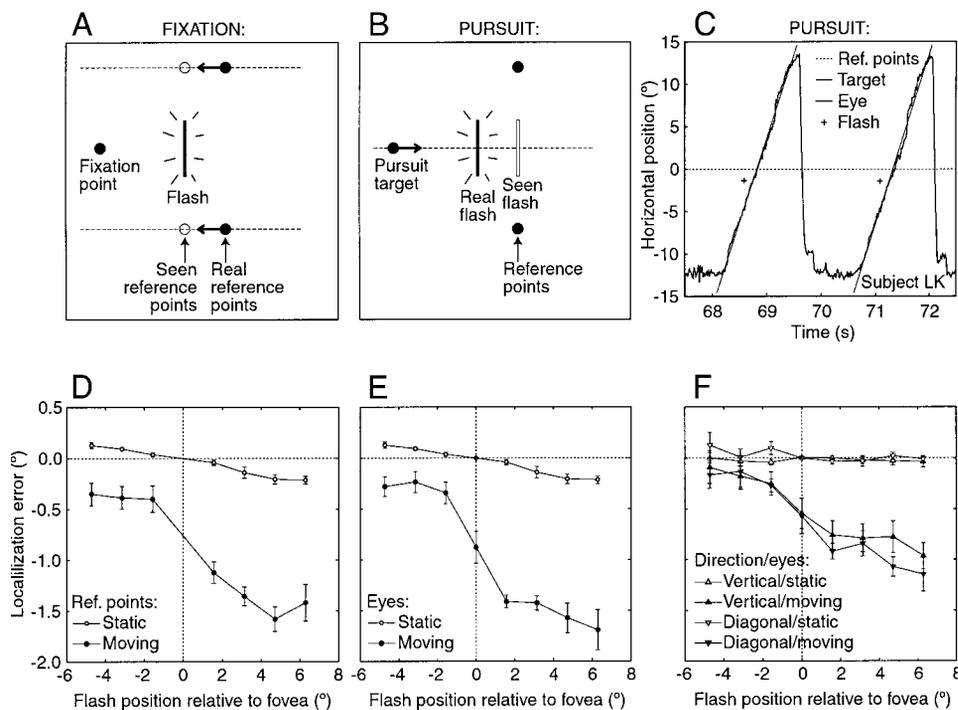


FIG. 1. Fixation and pursuit experiment. *A*: during fixation, subjects adjusted the time of a flash so as to align it with 2 moving reference points. *B*: while pursuing a target, subjects adjusted the time of a flash so as to align it with 2 static reference points. The position of the flash relative to the pursuit target was fixed in each trial. *C*: example of recorded eye movements in the pursuit condition. *D*: mean alignment error for 5 subjects in the fixation condition as a function of the flash's retinal location for moving and static reference points. Negative errors mean that subjects adjusted the flash to occur to the left (ahead) of the reference points. Error bars are standard errors reflecting variability across subjects. *E*: mean alignment error in the pursuit condition as a function of the position of the flash relative to the pursuit target. A negative error implies that the flash was adjusted to appear to the left of the reference points. *F*: mean results of 5 subjects in the pursuit condition in which the pursuit target moved in different directions. Note that in this condition a lower pursuit speed was used than in the horizontal pursuit condition in *E*.

In addition to the fixation and pursuit conditions, subjects also performed a control condition in which both the fixation point and the reference points were static. Subjects thus aligned static reference points to flashes during fixation. This quantified the mislocalization of peripheral flashes (van der Heijden et al. 1999), which had to be subtracted from the localization errors in the fixation and pursuit conditions to obtain the mislocalization due to the motion of the target or the eyes.

To examine whether the mislocalization depends on the motion direction, five subjects (the 1st author and 4 naive subjects) also performed the pursuit condition when the pursuit target moved downward or diagonally at 45° down and to the right. Flashed stimuli were similarly rotated. A lower pursuit target speed (11.5° s⁻¹) was used in this condition.

Two-dimensional pursuit experiment

We examined in this experiment how the size of the mislocalization during pursuit varies across the two dimensions of the retina. The first author and four naive subjects participated in this two-dimensional variant of the pursuit condition of the first experiment. Subjects pursued a pursuit target (similar to that in the 1st experiment) that

moved to the right at a constant speed of 19.1° s⁻¹ on a red background. During each sweep, a larger black circle (0.70° in diameter) was flashed for 12 ms at a fixed location on the screen when the eyes were looking straight ahead. Subjects adjusted the position of a continuously visible black cross-hair (4 diagonal lines, 0.093° thick and 1.08° long, leaving a central gap of 1.59°, see Fig. 2A) such that the flash appeared at its center. They used the computer arrow keys to adjust the position of the cross-hair in both the horizontal and the vertical direction. The initial position of the cross-hair for each trial was randomized. The flash position was varied across trials over an 8 × 5 grid (see Fig. 2B) with five repetitions of each stimulus. In control trials (50%), subjects fixated a static target straight ahead and aligned the cross-hair to the flash location as before. The order of trials (pursuit and fixation) and flash positions was randomized separately for each subject.

Sequential localization experiment

We tested in this experiment whether it is the flash or the static stimulus that is mislocalized during pursuit. Five subjects (the 3 authors and 2 naive subjects) participated. A black pursuit target

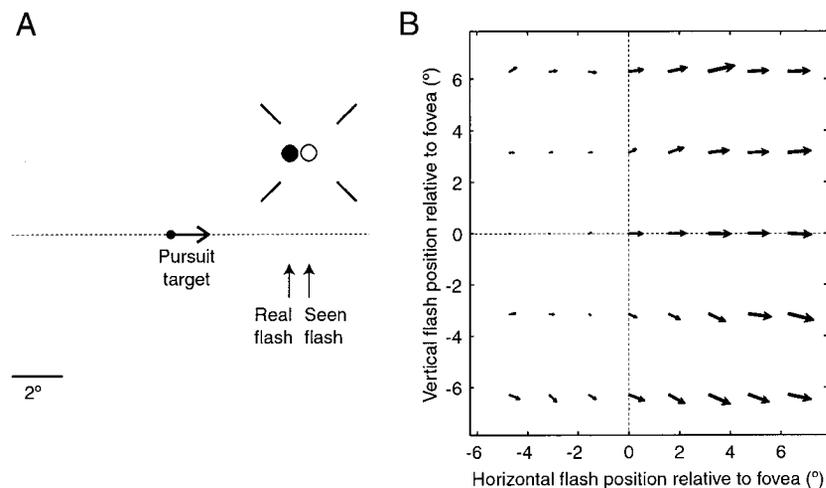


FIG. 2. Two-dimensional pursuit experiment. *A*: while pursuing a target, subjects adjusted the position of the cross-hair to align it with the flashed circle. *B*: mean results of the 5 subjects tested. The flashes were presented at the base of the arrows. The tip of the arrow shows the position of the cross-hair, as adjusted by the subjects. The arrows depict the difference of the errors during pursuit and those during fixation. Thus the arrows show the pure pursuit effect, removing the small errors observed during fixation due to mislocalization of peripheral flashes.

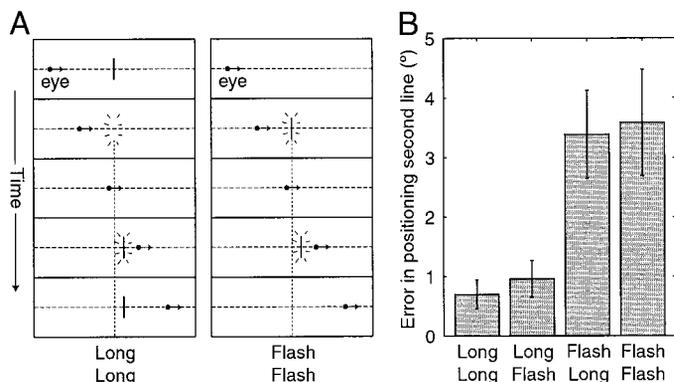


FIG. 3. Sequential localization experiment. *A*: subjects tracked a rightward moving target and saw 2 vertical lines during every sweep. They adjusted the location of the 2nd line to align it with the perceived position of the 1st. Each line was either flashed or of long duration. *Left*: a schematic of a long/long sweep. Splash marks indicate the appearance/disappearance of the stimuli. The 1st line was present from the beginning of the sweep and was extinguished shortly before the subject would foveate it (2nd snapshot from top). The 2nd line appeared shortly after the pursuit target had passed its position (4th snapshot) and remained visible till the end of the sweep. In a flash/flash sweep (*right*), lines were flashed briefly, as indicated by the splash marks in the 2nd and 4th snapshots. Long/flash and flash/long conditions were also tested (not shown). *B*: mean alignment errors for the 5 subjects with standard error bars showing the variability across subjects. Positive errors mean that the 2nd line was placed to the right of the 1st line.

moved to the right on a red background (similar to that in *experiment 1*). During each sweep, two vertical lines (0.093° wide and 1.63° high) were presented sequentially. The first one was shown to the right of the fovea (ahead of the fovea) when the pursuit target was straight in front of the subject. The second line was later shown behind the fovea (Fig. 3A). The subjects adjusted the horizontal position of the second line to align it with the first one. Adjustments were made by pressing the left and right arrow keys, which controlled the position of the second line for subsequent sweeps. Subjects pressed the space bar when they perceived both lines in the same position, to register their judgement and to start a new trial. Each line could be either flashed (12 ms) or of long duration ($>1,000$ ms). A long duration line presented ahead of the pursuit target was visible from the beginning of the sweep and was extinguished when the target was 3.14° to the left of it, i.e., 164 ms before the eyes would foveate it (see Fig. 3A, *left*). A long duration line behind the target appeared when the target was 3.14° to the right of it, i.e., 164 ms after the eyes had passed its position, and remained visible till the end of the sweep. Flashed stimuli were presented at the same positions and times as the appearance or disappearance of the long duration lines (see Fig. 3A, *right*). All four possible combinations of flashed and long duration lines were tested in randomized order within a single session. Each stimulus was presented five times.

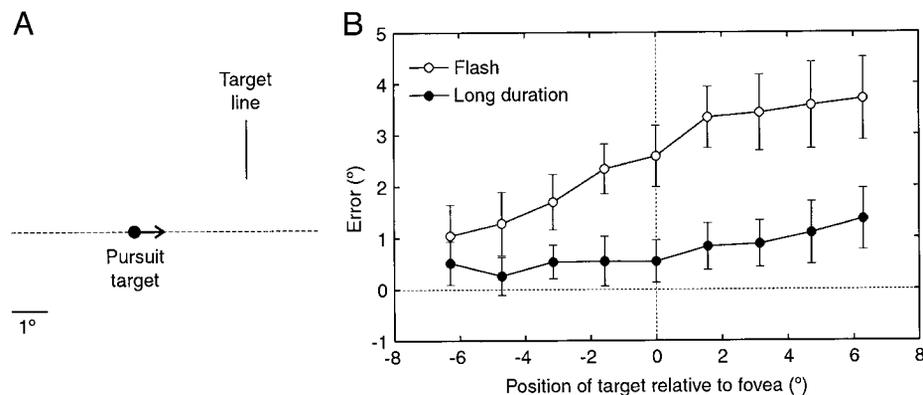


FIG. 4. Egocentric localization experiment. *A*: while subjects in complete darkness tracked a rightward moving circle, a vertical target line was shown. This vertical target line was either flashed (for 12 ms) or shown longer (for 1 s). The line was shown at 1 of 9 positions with respect to the pursuit target. After the target line had disappeared and the pursuit sweep had finished, subjects used the mouse to position a test line at the location where they had perceived the vertical target line. *B*: mean errors for the 7 subjects with standard error bars representing the variability across subjects. Positive errors denote responses too far to the right. The figure shows long-duration stimuli at the retinal position they occupied at the moment of disappearance.

Egocentric localization experiment

In this experiment, we tested egocentric localization of flashed and long duration stimuli during pursuit. Seven subjects (the 1st author and 6 naive subjects) participated in this experiment. They visually tracked a red circle (4 cd m^{-2} with a diameter of 0.31°) moving on a black background at a constant speed of $19.1^\circ \text{ s}^{-1}$. Before the circle started to move, it was shown statically at the left edge of the screen for 1 s. Subjects fixated the circle during this period and began to pursue it once it started to move. During each sweep, a red vertical target line (0.093° wide and 1.63° high) was shown 2.25° above the pursuit target's path at one of nine possible horizontal positions relative to the pursuit target (see Fig. 4A). The vertical line was either flashed (shown for 12 ms) or shown longer (for 1,000 ms). The position of the pursuit target at the time the vertical line was shown was randomized. This line appeared after the pursuit target started to move, so subjects never saw it during fixation. Subjects kept tracking the circle until it was extinguished 353 ms after the target line had disappeared. Four hundred ninety-four milliseconds later, a test line, identical to the vertical target line, appeared $\sim 14^\circ$ above the pursuit target's path. This line could be moved by moving the computer mouse. The task was to position the test line at the location at which the vertical target line was seen. The subjects clicked the mouse to register their judgement and to end the trial. If subjects did not track well in a particular trial or thought they could not make a proper response for another reason, they pressed the spacebar to restart the trial. The starting position of the mouse cursor was randomized in both the horizontal (in a 5.4° window) and the vertical direction (in a 1.4° window) to prevent subjects reproducing previous response movements. Ten repetitions of each stimulus were employed, comprising a total of 180 trials. These were conducted in four blocks of 45 trials each. Different stimulus types and stimulus positions were presented in a novel random order within each block. Blocks were separated by breaks of 1 min. Only the errors in the horizontal direction were analyzed.

We stress that this experiment was performed in a completely dark room; the pursuit target and the vertical lines were the only things subjects could see. The computer screen did not produce any visible glow apart from the stimuli. This was achieved by waiting several minutes after the screen was made dark until the afterglow from pixels that had previously been turned on was no longer visible. The experiment was started after the subject reported that the edges of the screen were no longer visible. We validated this procedure in a control experiment. Subjects viewed flashed lines on the computer screen and reported whether the flash was in the left or the right half of the computer screen. When the computer screen was moved to the left or right, the subjects' reports were head-centered rather than screen-centered. For instance, they reported "left" when the computer screen had been moved to the left, and the flash was presented in the right half of the screen. This confirmed that subjects could not see the screen edges.

Analysis

We used two-tailed paired *t*-tests to test for differences between subjects' mean errors in the two hemifields (foveopetal vs. foveofugal). In the sequential localization experiment, we used a two-factor ANOVA to evaluate the effect of long and short-duration stimuli. The two factors were the nature of the first stimulus (flash or long duration) and the nature of the second stimulus (flash or long duration), and the dependent variables were each subject's mean errors. In the egocentric localization experiment, a two-factor ANOVA with factors nature of stimulus (flash or long duration) and hemifield (ahead and behind pursuit target) was used. The dependent variables were each subject's mean errors in each hemifield and for each stimulus duration.

RESULTS

Fixation and pursuit experiment

Figure 1D shows the results of the fixation condition of *experiment 1* in which subjects adjusted the position of two moving reference points to align it with a flash (see Fig. 1A). For all flash positions, subjects adjusted the reference points such that at the time of the flash the reference points were still moving toward the flash's position, in accordance with the flash-lag effect. Moreover, the size of this effect was significantly larger ($P < 0.001$) when the reference points moved toward the fovea than when they moved away from it. This replicates the earlier findings (Mateeff and Hohnsbein 1988; Mateeff et al. 1991a,b) that the flash-lag effect is larger for foveopetal than for foveofugal motion. Figure 1D also shows that errors in localization of peripheral flashes relative to *static* reference points are much smaller than those relative to moving reference points. This suggests that the errors in the condition with moving reference points reflect mislocalization of the moving objects, not of the flash. However, the motion of the reference points per se could also influence the perceived position of a flashed object (Whitney and Cavanagh 2000). The reported size of those effects, however, is much smaller and in the opposite direction than the effects we found, so that we can safely conclude that our effects mainly reflect mislocalization of moving objects.

The results of the pursuit condition are shown in Fig. 1E. While pursuing a moving dot, subjects adjusted the time of a flash to align it between two static reference points (see Fig. 1B). Again, a flash-lag effect is observed for all flash positions, and, in accordance with earlier findings of Mateeff and Hohnsbein (1988) and Mateeff et al. (1991b), the effect is significantly larger ($P < 0.001$) for foveopetal motion than for foveofugal motion. The eye movement recordings (Fig. 1C) showed that subjects had the normal features of pursuit with a gain slightly less than unity and occasional small catch-up saccades (Collewyn and Tamminga 1984). In particular, the flashed line and reference points rarely evoked anticipatory or reactive saccades so that the vast majority of the spatial judgements were made during smooth pursuit.

To find out whether the effects are specific for horizontal motion, we repeated the pursuit condition for vertical (downward) and diagonal (down and to the right) motion. Figure 1F shows that also for these directions, the flash-lag effect is larger for foveopetal than for foveofugal motion. This suggests that the shape of the differential flash-lag effect during pursuit is

determined by the direction of retinal slip induced by the eye movement.

Two-dimensional pursuit experiment

To further map out the differential flash-lag effect during pursuit, we measured its size over the two dimensions of the retina. Subjects tracked a pursuit target and adjusted the two-dimensional position of a continuously visible cross-hair such that a flashed circle was perceived in its center (see Fig. 2A). In Fig. 2B, the base of each arrow shows the actual flash location, and the corresponding arrow head shows the pursuit-induced localization error. The (small) mean errors in adjusting the cross-hair during fixation were subtracted from those during pursuit to eliminate the effect of mislocalization of peripheral flashes (van der Heijden et al. 1999). Most of the resulting error lies in the direction of eye movement, although there is also a small outward bias orthogonal to the eye movement direction (especially in the lower field). Figure 2B shows that errors are much larger ahead of the pursuit target than behind it not only on the line of eye movement but also above and below this line. Thus the differential localization errors are present throughout the entire retinal field studied, and they depend predominantly on the direction of eye movement but vary less in the direction orthogonal to eye movement.

Sequential localization experiment

Our first experiments showed a relative localization error between flashes and static stimuli during pursuit but could not establish which of the two is mislocalized. In the sequential localization experiment, subjects matched the perceived positions of two stimuli (either flashed or of long duration) presented at different times during pursuit (Fig. 3A). The first stimulus was always presented ahead of the fovea and the second one behind it. When first and second stimuli were both of long duration, localization errors were small (on average $< 1^\circ$; see Fig. 3B). However, when both stimuli were flashed, subjects made large localization errors (on average $> 3^\circ$). This difference suggests that flashes are mislocalized during pursuit, whereas static objects are less. Sequences of mixed stimuli showed that these effects depend only on the nature of the first stimulus [2-way ANOVA: $F_{(1,4)} = 16.91$, $P = 0.015$] and not on the nature of the second stimulus [$F_{(1,4)} = 2.07$, $P > 0.2$]. Specifically, large errors were made only when the first stimulus was a flash. Therefore it is the flash, not the static object, ahead of the eye that is mislocalized. Note that the results of this experiment are consistent with those of the previous experiments: flashes are largely mislocalized relative to static objects ahead of the fovea (condition flash/long vs. long/long and flash/flash vs. long/flash) but not behind it (condition flash/long vs. flash/flash and long/long vs. long/flash).

Egocentric localization experiment

In the egocentric localization experiment, subjects used the mouse cursor to indicate where they had seen flashed and long duration stimuli without being able to localize these stimuli relative to other seen objects (such as reference points or the screen edge). This experiment was performed in complete darkness, forcing subjects to use gaze direction information for localization. Figure 4B shows the mean location at which

subjects placed the cursor to indicate the perceived location of flashed and long duration stimuli both ahead of and behind the fovea. Subjects pointed too far to the right (ahead of pursuit target) when flashes were presented ahead of the pursuit target. Errors were significantly smaller ($P = 0.002$) when the flash was presented behind the pursuit target. In contrast, errors in localizing long duration stimuli did not differ between presentations ahead of the pursuit target and those behind it ($P > 0.1$). Most importantly, the difference in localization errors between flashed and long duration stimuli was significantly larger ahead of the pursuit target than behind it [2-way ANOVA interaction: $F_{(1,6)} = 36.44, P = 0.001$]. The egocentric localization experiment thus replicates the results of the sequential localization experiment, which implies that the localization errors found during pursuit in this paper reflect egocentric rather than relative mislocalization. It should be noted that in the design of this experiment, it was impossible to keep all factors other than the stimulus' retinal position constant. In particular, there was a correlation between the stimulus' retinal location and the gaze direction at the time of stimulus presentation. Although it is not clear how gaze direction per se could explain our results, we verified this was not the case. A simple analysis showed that the slope of a linear regression of error versus gaze direction was significantly ($P < 0.025, t$ -test) smaller than that of error versus retinal location. Therefore egocentric localization performance is explained better by retinal location than by gaze direction effects.

DISCUSSION

We have presented several localization experiments using three different paradigms to examine the sensorimotor integration process of retinal and gaze signals during pursuit. The first experiment showed that relative mislocalization of flashes and constant stimuli is present both in fixation and pursuit. The relative errors were greater for stimuli that approached the fovea (foveopetal) than for stimuli moving away from the fovea (foveofugal). The second experiment showed that during pursuit these relative errors are confined to the direction of eye movement. Further, the errors are present in the entire hemifield ahead of the fovea. The third experiment used sequences of two stimuli to show that it is mislocalization of the flash, not the constant stimulus, that underlies relative mislocalization during pursuit. This is in contrast to fixation in which the moving stimulus is mislocalized. The final experiment showed that the mislocalization of the flash during pursuit reflects egocentric mislocalization rather than mislocalization relative to other seen objects.

We found a clear difference between localization during fixation and during pursuit. Many previous studies have shown that constant (moving) objects are mislocalized during fixation, while flashes are not mislocalized (e.g., Eagleman and Sejnowski 2000; Nijhawan 1994). The key result of this study is that during smooth pursuit this pattern is reversed. During pursuit, flashed objects are mislocalized while constant objects are not. This reversal is particularly striking since the retinal information is identical in the fixation and pursuit conditions. Since the eyes move during pursuit but not during fixation, we suggest that this reversal of mislocalization errors must arise from the way gaze signals are used in sensorimotor integration.

We suggest that mislocalization of flashes, but not constant

objects, during pursuit reflects a compensation mechanism within the CNS. We now discuss this hypothesized compensation mechanism in more detail. During fixation, objects moving toward the fovea are seen too far ahead in their movement. This effect is absent or reduced for objects moving away from the fovea (Fig. 5, *A* and *B*). We therefore assume that the retinal location signal of stimuli that produce retinal slip is erroneous for foveopetal stimuli but not for foveofugal stimuli (Fig. 5*E*). Since the gaze direction is constant during fixation, the localization errors of moving objects are uniquely determined by the retinal signals (Fig. 5*C*). Flashes do not produce retinal slip and therefore are localized correctly (Fig. 5*D*).

Now we consider localization during pursuit (Fig. 5*F*). Suppose that the retinal and gaze signals have the same errors and are integrated in the same way as during fixation. One would then expect mislocalization of constant objects during pursuit exactly as occurs for retinally equivalent moving objects during fixation (Fig. 5*C*). In this case, however, the constant objects are objects that are static in the outside world so that differential mislocalization in the foveopetal and foveofugal zones here would lead to a change in the perceived position of static objects during the eye movement. Specifically, static objects would be seen to change their position when they pass from the foveopetal to the foveofugal zone, that is, at the time they are passed by the eyes. This would produce an unstable visual world and large localization errors in a critical region of visual space. We suggest that the CNS compensates for these expected errors and thereby maintains the stability of the visual world during smooth pursuit eye movements by integrating the retinal signals not with a single but with a set of different gaze signals. Each retinal location then has to be integrated with a gaze signal that will compensate for the error in the retinal location signals due to the pursuit-induced retinal slip of static objects (Fig. 5*J*). This means that the foveopetal zone, i.e., the hemifield ahead of the fovea, is integrated with different gaze signals from those used in the foveofugal zone. As a result, no errors will be made in localizing static objects at any retinal location (Fig. 5*H*). This use of different gaze signals is normally functional but is revealed by flash localization during pursuit. Flashes do not produce retinal slip and therefore do not have differential errors in their retinal signals. As a result, their retinal locations will be integrated wrongly with different gaze signals, leading to mislocalization of flashes ahead of the eyes (Fig. 5*I*). This is exactly what we observed in the sequential and egocentric localization experiments. This mechanism also predicts the same pattern of mislocalization of constant stimuli relative to flashes during fixation and pursuit (Fig. 5, *B* and *G*) that we found in our first experiment.

Previous studies have investigated egocentric localization of flashes by examining the ability of humans to strike targets flashed during pursuit with a hammer (Hansen 1979) and the ability of humans (Ohtsuka 1994) and monkeys (Schlag et al. 1990) to saccade toward them. None of these studies, however, explicitly compared localization errors for stimuli ahead of and behind the pursuit target. Our results clearly show that flashes ahead of the eye *are* mislocalized during pursuit. We conclude that sensorimotor integration seems adapted to localize constant stimuli at the expense of the ability to localize flashes. Alternatively, our results could also reflect that the CNS uses different strategies during pursuit and fixation based on what it considers to be the safest reference signal. During fixation,

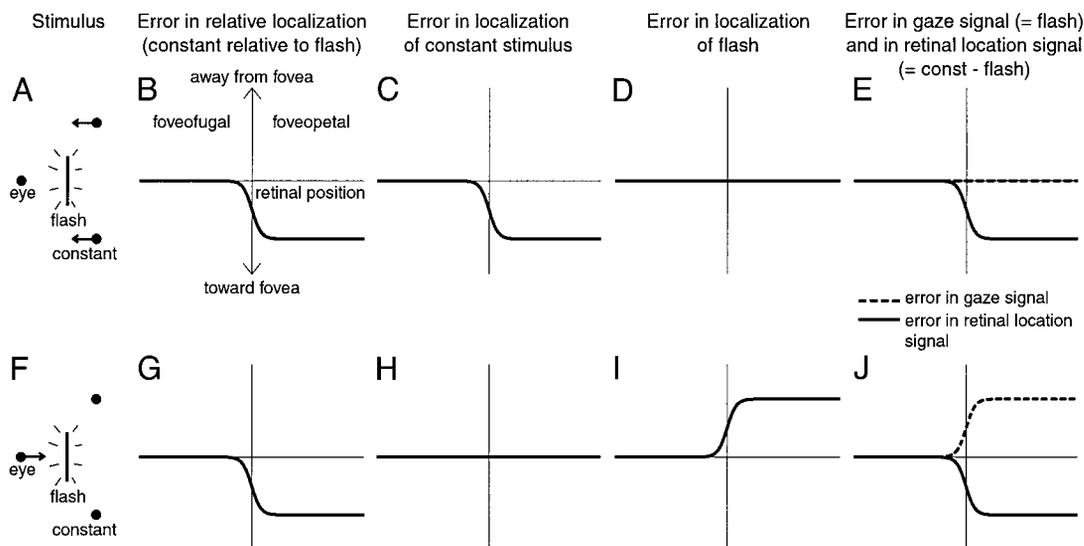


FIG. 5. Overview of localization errors in our experiments. All graphs show errors as a function of retinal position. For both fixation and pursuit, constant and flashed stimuli are considered. *A*: for fixation, the constant stimuli are moving objects. \leftarrow , direction of motion. *B*: in our 1st experiment, we found large errors in relative localization between the constant and flashed stimuli when the constant stimuli moved toward the fovea (foveopetal hemifield) and much smaller errors when they moved away from it (foveofugal hemifield). For the sake of clarity, we have omitted these small foveofugal errors in this figure to focus on the main effect of the difference between the 2 hemifields. *C*: the errors in relative localization are due to mislocalization of the moving stimuli. *D*: flashes are localized correctly during fixation. *E*: the explanation for the results during fixation is that in the foveopetal zone the gaze signals are veridical while the retinal location signals of moving objects are erroneous. In the foveofugal zone, both signals are veridical. Flashes at any location are localized correctly (*D*) because the gaze signals are veridical. Foveopetal stimuli are mislocalized (*C*) because the retinal location signals are erroneous. *F*: for pursuit the constant stimuli are static objects. *G*: relative mislocalization during pursuit is identical to mislocalization during fixation (*B*). *H*: the sequential localization and egocentric localization experiments showed that during pursuit static objects are localized (almost) correctly. *I*: these experiments also showed that flashes ahead of the pursuit target are seen too far ahead, whereas flashes behind are localized (almost) correctly. *J*: the explanation for the results during pursuit is that the retinal location signals have the same errors as during fixation (*E*) because the retinal information is the same, but now the gaze signals are biased in the opposite direction. These erroneous gaze signals are revealed by the errors in flash localization (*I*). Localization of static objects during pursuit is veridical (*H*) because the errors in the gaze signals compensate for those in the retinal signals.

gaze signals may be trusted more than retinal signals. During pursuit, however, it may trust the gaze signals less and rely more on retinal signals of objects that it assumes are stable in the world.

Could artifacts such as visual structure from the background (O'Regan 1984) or visual memory (Henriques et al. 1998) explain our results? In general, to measure localization performance not only the target but also a reference object has to be presented for subjects to respond. This can be achieved in two ways: the stimuli can be presented either simultaneously or sequentially. With simultaneous presentation, memory effects are eliminated, but a reference object producing background visual information needs to be present at the time of target presentation.¹ With sequential presentation, background visual information is eliminated, but visual memory must be used. There is no way to measure localization performance which removes both memory effects and background visual information. We used both simultaneous presentation without visual memory (relative localization experiments) and sequential presentation without background visual information (egocentric localization experiment) and found comparable results in both experiments. We therefore conclude that effects due to visual

memory or visual background information are unlikely to have caused our results.

Did the egocentric localization experiment measure localization based on the stimulus' retinal location combined with gaze information? An alternative could be that subjects judged the stimulus position relative to the pursuit target and made errors in judging the timing or the location of the flash relative to the pursuit target. The egocentric mislocalization would then reflect relative rather than true egocentric mislocalization. However, there is no evidence for misjudging either the timing or the position of the flash in a way that could explain our results. Reaction times to suddenly appearing stimuli ahead of the pursuit target are shorter rather than longer than those to stimuli behind it (van Donkelaar 1999), whereas the opposite would be required to explain the flash mislocalization we found. Misjudging the position of the flash during pursuit (and not during fixation) would lead to different error patterns for localizing the flash relative to a constant stimulus during pursuit and fixation, but similar relative mislocalization errors were found (our 1st experiment) (also in Mateeff and Hohnsbein 1988). Therefore we conclude that the egocentric localization experiment measured true egocentric localization.

We will now discuss the differential foveopetal/foveofugal mislocalization. This difference was present in all our experiments. In the results of the fixation and pursuit experiment and the relative localization experiment, there seems to be a rather sharp transition between these zones: the transition seems to

¹ Other modalities, "internal norms" or "absolute identification" could also be used (Matin 1986), but these are known to have a much poorer spatial acuity than vision and can also induce cross-modal interactions (Welch and Warren 1986).

take place in less than 3°. In the egocentric localization experiment, we found a more gradual transition. Here effects of pointing and of memorizing a position in complete darkness may have smeared out a sharper transition. We suggest the actual transition is at least as sharp as 3° and possibly sharper.

It is also interesting to ask why there is such a difference between foveopetal and foveofugal motion. Mateeff and Hohnsbein (1988) and Mateeff et al. (1991a) attributed this to the latency for foveopetal motion being shorter (about 80 ms) than that for foveofugal motion. However, the finding of Eagleman and Sejnowski (2000) that the initial position of a suddenly appearing moving object is misperceived makes this interpretation unlikely. They argue that the misperception is a result of retrospective interpolation of the moving object's past positions. Such a mechanism, however, does not make clear why there should be a foveopetal/fugal difference. The explanation, or even the nature (temporal, spatial, . . .), of the differential mislocalization is therefore not clear. However, a detailed explanation of the differential mislocalization is not required to understand the essential point of this paper: namely that the CNS compensates for any such effects during pursuit to guarantee the stability of the perceptual world. Our aim here is to show that the CNS actively performs this compensation, rather than to address the nature of the errors requiring compensation.

We suggest that the CNS uses the sensorimotor integration of retinal and gaze signals to compensate for the differential mislocalization for foveopetal and foveofugal motion. How does the CNS accomplish this? A possible way to do this is by integrating different retinal areas with gaze signals from different moments in time. Specifically, the retinal hemifield ahead of the fovea could be combined with a gaze position that is temporally advanced with respect to the one used for the hemifield behind the fovea. A temporally advanced signal could be generated by a forward internal model, possibly located in the cerebellum (Wolpert et al. 1998). Alternatively, temporal misalignments could be achieved by delaying certain signals relative to other ones, in accordance with the postdiction idea (Eagleman and Sejnowski 2000). Purely spatial mechanisms, such as a spatial expansion of a part of the retinal field, or even more complicated integration mechanisms can also lead to the same result.

In conclusion, our results are not consistent with the general assumption that the CNS localizes visual stimuli by integrating all retinal signals simply with a single gaze signal (Andersen et al. 1993; Bridgeman 1995; Mon-Williams and Tresilian 1998; Pouget et al. 1993; von Helmholtz 1925). Instead the integration of retinal and gaze signals takes a more complicated form that ensures the stability of the visual world during smooth pursuit. Such a mechanism is fundamental in maintaining veridical percepts of the outside world and for the visual guidance of action.

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