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Smooth eye movements and spatial localisation

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Abstract

We asked subjects to align a target that flashed as their eyes rotated to the right in pursuit of a moving ring, with a target that flashed as their eyes rotated to the left in pursuit of the ring. Subjects systematically mislocalised the targets in the direction of pursuit. When the ring and flashes were the only structures that were visible, the alignment error was about 4 cm, corresponding to a timing error of about 100 ms. The timing error was independent of the position along the ring's path, but did depend to some extent on pursuit velocity. Adding a textured background reduced the mislocalisation considerably, presumably because it enabled subjects to localise the targets relative to the surrounding. There was almost no mislocalisation if the subject was not pursuing the ring. It is suggested that the mislocalisation arises because incoming retinal signals are combined directly with outgoing oculo-motor commands, with no attempt to account for any of the involved neuronal and muscular delays. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Targets that are flashed during smooth pursuit tend to be mislocalised in the direction of pursuit (Mita, Hironaka, & Koike, 1950). Similar mislocalisation occurs for the position at which a pursued target disappears or at which its brightness changes (Mitrani, Dimitrov, Yakimoff, & Mateeff, 1979; Mateeff, Yakimoff, & Dimitrov, 1981). In order to localise a target that is flashed during smooth pursuit, its retinal signal must be combined with information about the orientation of the eyes (for an extensive review see Matin, 1986). A likely explanation for the mislocalisation is therefore that brain activity related to retinal stimulation by the flash is combined with brain activity related to the eyes' orientation at a different moment (Matin, Matin, & Pola, 1970). That this could happen is not surprising considering all the different delays involved.

The time it takes for a visual stimulus to reach the brain depends on many factors, including the target's size, luminance, contrast, retinal eccentricity, colour, and so on. And indeed, the mislocalisation of flashed targets becomes larger as targets are changed in ways that can be expected to make them more difficult to detect (Mita et al., 1950). Putative proprioceptive and retinal eye orientation signals also take time to reach the brain. In contrast, efferent eye orientation signals are in the brain before the eye orientation changes. Synchronising all these delays may simply not be feasible, especially if some of them vary extensively with all kinds of circumstances.

Mita et al. (1950) found that if pursuit velocity is the only thing that is varied, the spatial error is proportional to the eye's velocity. This is what we expect if the retinal image is combined with the eyes' orientation a fixed amount of time later. They found that varying the intensity or eccentricity of the flash, or the state of adaptation of the eye, all influenced the error considerably. There is also evidence that non-retinal properties, such as predictability, can influence the extent of the mislocalisation (Mateeff et al., 1981; Mitrani et al., 1979; Rotman, Brenner, & Smeets, 2000). Moreover, there appear to be systematic differences between perceptual and oculo-motor responses (Mitrani et al., 1979) and between subjects (Brenner & Cornelissen, 2000; Mateeff & Hohnsbein, 1989).

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Despite the many differences, in all the above-mentioned studies flashed targets were mislocalised in the direction of pursuit. There is one study in which this was not so. Hansen (1979) also had subjects pursue a moving dot with their eyes. While doing so they were to hit a flashed target with a hammer. Hansen's subjects did not make systematic errors. Could this be because Hansen's was the only study in which there was no visible reference? It seems surprising that the errors should be smallest when the least information is available. Moreover, Mita et al. (1950) mention, when describing their methods, that the two weak lights they used as a reference in their dark condition had no influence on the mislocalisation. On the other hand, Mateeff and Hohnsbein (1989) found that the way the reference is presented can make a difference. In most studies the extent to which the visible structures could be used as references for localisation is not certain. The main purpose of the present study was therefore to examine the influence of the presence of a salient visible reference.

A second purpose was to determine whether the mislocalisation only occurs for unexpected events. We have recently shown that the mislocalisation of flashed targets relative to *unpursued* moving ones[1] (Nijhawan, 1994) is reduced considerably if subjects can anticipate the flash (Brenner & Smeets, 2000). All the above-mentioned studies used single unexpected presentations. We developed a method that reduces uncertainty about when and where the target will appear without giving the subject additional information about its position.

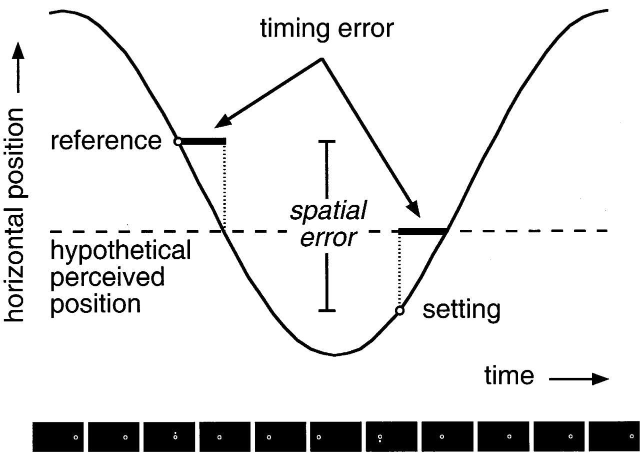

Fig. 1. Schematic representation of the relationship between spatial and timing errors. Curve: horizontal position of the ring as it moves sinusoidally back and forth (up = right). Dashed line: perceived position of the reference if retinal stimulation by the flash is combined with an eye orientation 'timing error' later (assuming perfect pursuit). In order for the adjustable target to be perceived at the same position it too must be presented 'timing error' before the gaze is directed at that position. The small images at the bottom of the figure indicate what the subject sees at each moment.

Subjects followed a ring with their eyes. The ring moved sinusoidally back and forth across a computer screen. The subjects' task was to align a target that flashed when their eyes rotated to the right, with one that flashed when their eyes rotated to the left. The cyclic nature of the stimulus meant that subjects could see the targets as often as they liked. Subjects did not indicate where they saw the targets directly, but the match reflects the sum of the errors with the eyes moving in the two directions (see Fig. 1). A pilot study in which ten subjects made such matches in complete darkness for a single pursuit velocity revealed that the proposed method is feasible (Brenner & Smeets, 1998). We examined whether subjects mislocalised flashed targets under such conditions, and how the mislocalisation depends on pursuit velocity.

2. Methods

Images were presented at 120 Hz on a 39.2 × 29.3 cm computer screen. The spatial resolution of 815 × 611 pixels was improved with anti-aliasing techniques. Subjects sat 60 cm from the screen with their chin and forehead supported (at this distance 1 cm corresponds with approximately 1°). The room in which the experiments were conducted was completely dark. All stimuli were red. A red filter was placed in front of the screen, and black cloth covered the table beneath the screen in order to make sure that no structures other than those presented on the screen were ever visible. The luminance values reported below are as seen through the red filter. We did not measure phosphor persistence for the screen, but we know that the phosphors are fast enough for presenting stereoscopic images at 120 Hz with shutter spectacles.

Subjects were presented with a ring (12 mm outer diameter; 1 mm wide; 5 cd/m^2) moving sinusoidally back and forth across the centre of the screen. The ring's motion was horizontal with a peak to peak amplitude of 20 cm (about 19°). On some trials subjects were instructed to follow this ring with their eyes. On others they were instructed not to do so. On some trials a background was visible on the screen. This background consisted of 1000 static, 3 mm diameter (5 cd/m^2), randomly placed dots. The dots remained at the same positions for all cycles of the ring's movement within each trial, but had new positions on every trial.

During each cycle of the ring's movement, two 8 mm diameter (10 cd/m^2) dots were flashed (i.e. were presented during a single frame of the computer screen).

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[1] Note that flashed targets are not mislocalised relative to constantly visible moving ones if the moving target is pursued (Nijhawan, 1997). However, this involves *relative* localisation of simultaneously visible structures. There is evidence that eye orientation is ignored when making such judgements, presumably because it is only essential for egocentric localisation (Brenner & Cornelissen, 2000).

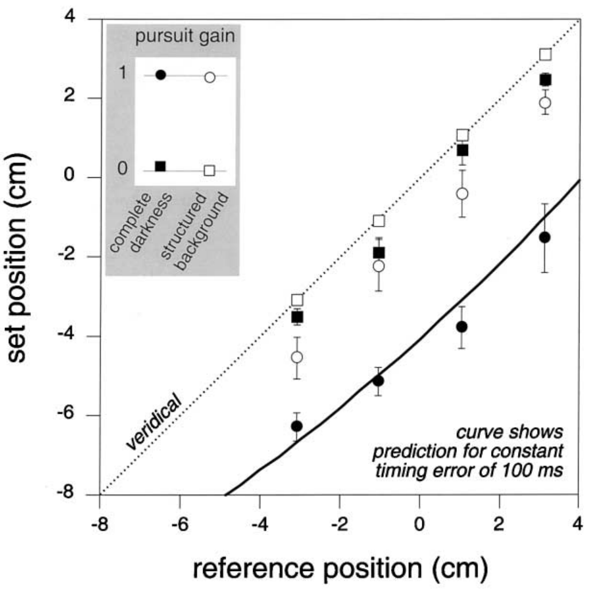

Fig. 2. Results of experiment 1. Averages with variability between subjects (SE). Subjects made errors of about 4 cm when pursuing the ring in the dark (●). When there was a structured background (○) the errors were considerably smaller. When subjects were not pursuing the ring the errors were even smaller if there was no background (■) and absent altogether if there was one (□). The inset shows the average gain of pursuit just before the flash was presented for each condition.

One dot, the reference, flashed 15 mm above the ring as it moved to the left. It did so at a predetermined position. On each trial this position was set to one of four values: 10 or 31 mm to the left or right of the centre of the screen. The dot flashed at the moment that the ring passed exactly below it (moving to the left). The second, adjustable dot flashed 15 mm below the ring as it moved to the right. The subjects manipulated this dot's horizontal position by moving the computer mouse. This also determined when it flashed, because it flashed at the moment that the ring passed exactly above it (moving to the right). The dot's initial position was chosen at random from within the full 20 cm range. Moving the mouse to the left made the dot flash further to the left (and earlier) during the ring's next cycle, and vice versa (within this range). The subject's task was to align the two flashed targets vertically; i.e. to make the targets flash as the ring passed the same position. Subjects indicated that they were content with the match by pressing a button. This terminated the trial. We refer to the adjustable target's position at that time as the setting for that trial.

Throughout the experiments the horizontal movements of the subject's left eye were recorded at 1100 Hz with an Ober2 eye tracker (Permobil, Meditech). We only recorded the left eye, while subjects looked with both eyes, because otherwise we would have had to reduce the sampling frequency to 550 Hz. When the instruction was to pursue the ring, the dots were only flashed if subjects pursued the ring with a gain of between 0.9 and 1.1. Obviously this was the gain *before* the flash. In fact, we determined the average gain of ocular pursuit between 110 and 10 ms before the ring passed the critical position. We could not get closer to the moment of the flash, because it took 10 ms to get the last eye movement sample, calculate the gain, and change the image. This delay was measured with the help of an artefact that arises if the 'inside' of the eye tracker's spectacles are directed toward the screen as the image changes. When the instruction was not to pursue the ring, the dots were only flashed if the pursuit gain was lower than 0.1 during this interval (which is not trivially simple in the absence of a fixation point). We only checked the velocity of the eye relative to the head, because the equipment we used is not suited for determining precise orientations of gaze.

The same four subjects (including two of the authors) took part in two experiments. They each made five matches for each position of the reference dot. In the first experiment we varied the instructions concerning eye movements and whether there was a visible background. The ring moved back and forth with a frequency of about 0.33 Hz, corresponding to a duration per half cycle of 1.5 s. In the second experiment the instruction was always to pursue the ring and there was no visible background. We varied the speed at which the ring moved (by varying its frequency). The frequencies we used were 0.25, 0.3, 0.375 and 0.5 Hz, corresponding to durations per half cycle of about 2.0, 1.7, 1.3 and 1.0 s.

For experiment 1, the five settings for each reference position and viewing condition were averaged, and the mean and variability of these averages was determined across subjects. To obtain a measure of the reproducibility of the settings within each condition, we calculated the variability in the five replications, and averaged this variability across reference positions and subjects. For both experiments we also calculated average timing errors. The relationship between spatial error and timing error is shown schematically in Fig. 1. This relationship was used to convert each setting into a timing error. The 20 values (five timing errors for each of four reference positions) were then averaged for each subject and condition. The mean of (and variability between) the four subjects' averages was calculated for each condition (experiment 1) and duration of a cycle of the ring's movement (experiment 2).

3. Results

Fig. 2 shows the average set position (with the standard error across subjects) for each reference in each condition. The dotted diagonal line shows where settings would lie if subjects made no errors. The curve shows where they would lie if subjects judged the position on the basis of the eye's orientation 100 ms later (as explained in Fig. 1). Since the ring's velocity is not constant, the predicted error depends on the reference position. The different symbols represent the four conditions: with or without a visible background (open and solid symbols) and with or without ocular pursuit (circles and squares).

When pursuing the ring in complete darkness (solid circles), subjects mislocalised the targets systematically by about 4 cm. This corresponds with a timing error of about 100 ms (Fig. 3). Adding a structured background reduced the errors (open circles). The errors were even smaller if subjects were instructed not to pursue the target as it moved in complete darkness (solid squares). The errors disappeared completely if a structured background was visible and subjects did not pursue the target (open squares).

The inset in Fig. 2 shows the mean gain of ocular pursuit just before the flash in the four conditions. Only instances in which the target was shown are included. Since the targets only flashed if pursuit gain was within specified limits, it is not surprising that the values are nearly perfect. However, the average gain of pursuit was 0.054 (with a standard error of 0.004) when subjects were instructed not to pursue the target while in complete darkness. Almost half of the error in the set position in this condition (solid squares in Fig. 2) could be accounted for by the failure to refrain from pursuing the ring at the moment of the flash (and a timing error of 100 ms). When instructed to pursue the target the gain was slightly lower in the presence of a visible background.

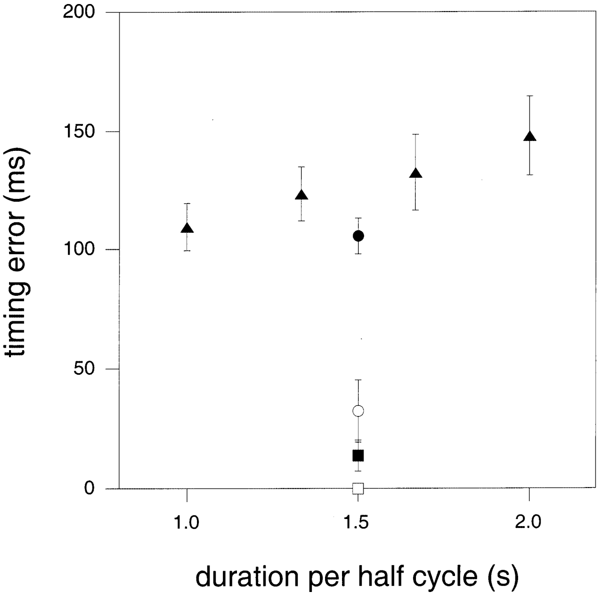

Fig. 3. Results of both experiments expressed as timing errors. Averages with variability between subjects (SE). The timing error increased with a decreasing velocity of pursuit (increasing duration). ▲: Data from experiment 2. Other symbols: data from experiment 1 (symbols as in Fig. 2).

The figure shows the variability between subjects. We also determined the standard deviation in the five repetitions of each setting for each subject. When the subject's eyes were pursuing the ring, the average standard deviation (averaged across subjects and reference positions) was 1.12 cm when there was no visible background and 0.80 cm when there was one. When the subject's eyes were not pursuing the ring the average standard deviations were 0.56 and 0.17 cm.

Fig. 3 shows the average timing error for different velocities of ocular pursuit (solid triangles). The instruction was always to pursue the ring, which was always the only visible structure other than the flashed targets. The timing error increased slightly as the velocity of the eye decreased (i.e. as cycle duration increased). The solid circle depicts the average timing error from the comparable condition of experiment 1. This point appears to deviate from the trend in experiment 2 (a paired *t*-test comparing it with the average of the values for durations of 1.3 and 1.7 s was statistically significant: $t_3 = 3.8$, $P = 0.03$). The average gain of ocular pursuit in experiment 2 was between 0.985 and 1.006, so the discrepancy with experiment 1 cannot be explained by differences in pursuit gain. The averages of the standard deviations within the five repetitions of each setting were 1.45, 1.82, 1.59 and 1.82 cm for durations of 1.0, 1.3, 1.7 and 2.0 s respectively. Thus, the variability does not change systematically with pursuit velocity, but it is larger in experiment 2 than in the equivalent condition in experiment 1.

4. Discussion

We had hoped that allowing subjects to see the stimulus as often as they liked would reduce the variability in their settings. In fact, however, the average standard deviation when subjects pursued the ring without a background was about 1° in experiment 1, close to the variability in Hansen's (1979) hammer blows and in previous work with single presentations (Brenner & Cornelissen, 2000). It was even larger in experiment 2. In that sense the new method was no improvement.

Our subjects mislocalised the stimuli despite them being predictable. Thus our results indicate that the mislocalisation is not restricted to unpredictable stimuli. The timing error did not appear to depend on the target's position (Fig. 2), but did depend to some extent on the velocity of pursuit (Fig. 3). Why pursuit velocity influenced the timing error in experiment 2 is not clear. This was not so for the single subject in Mita et al. (1950). Moreover the data from our experiment 1 do not fit well in the trend found in experiment 2, although the data are for the same four subjects. Apparently other factors than a fixed timing error, such as the other conditions within the experiment, also play a role. Nevertheless, a timing error of slightly more than 100 ms accounts for most of the mislocalisation of the targets flashed in the dark during pursuit.

Adding a visible background decreased the magnitude of the mislocalisation substantially. Thus, although we still cannot explain why subjects made no systematic errors in Hansen's study, we now know that it was not due to the absence of a visible reference. When there is a visible background, subjects can localise flashed targets relative to structures in the background. It was easy to recognise individual configurations of background dots during the experiment. When judging the relative positions of simultaneously visible structures there is no need consider the direction of gaze (Brenner & Cornelissen, 2000). Nevertheless, although the errors became much smaller, they did not disappear altogether (open circles in Figs. 2 and 3). Perhaps subjects still relied to some extent on egocentric localisation. Alternatively, subjects may have misjudged the relative positions, in which case the remaining error has nothing to do with eye movements. Relative positions would be misjudged if it takes more time for retinal stimulation by a flashed target to result in a change in activity in the brain, than it does for retinal stimulation by a background that is permanently visible but moves across the retina (as found for flashed and moving targets with static eyes; Whitney & Murakami, 1998; Berry, Brivanlou, Jordan, & Meister, 1999).

Targets were hardly mislocalised if the eyes were not pursuing the ring. Thus the large errors during pursuit cannot be a direct consequence of the ring's motion on the screen (it has recently been shown that motion nearby can make subjects mislocalise flashed targets; Whitney & Cavanagh, 2000). They also cannot be caused by timing errors that are unrelated to eye orientation, such as errors in equating the time between a flash and a change in direction of the ring with the time between the change in direction and the next flash. We conclude that the mislocalisation is caused by retinal stimulation (the flashes) being combined with extra-retinal information pertaining to the eye orientation approximately 100 ms later.

4.1. A possible explanation

We certainly cannot yet explain the differences between the studies, and do not even know for sure what factors are involved. Nevertheless, there are a number of more or less consistent findings across studies. Foremost is the fact that the mislocalisation is always in the direction of pursuit. Our study suggests that when subjects are forced to rely on extra-retinal information about eye orientation, they combine the retinal stimulation with an eye orientation about 100 ms later. The magnitude of the error differs between studies, but our estimate of 100 ms is not exceptionally large in comparison with other studies.

Although 100 ms may not seem very long, we argue that it is extremely long in this context. Our stimuli were well above detection threshold. Under optimal conditions, 100 ms is about what it takes to initiate an eye movement in response to such visual stimuli (Fischer & Ramsperger, 1986; Gellman, Carl, & Miles, 1990). Thus 100 ms is presumably enough time for retinal stimulation to result in activity within the brain *and* for activity within the brain to result in movement of the eyes.

If subjects localise flashed targets by combining the brain activity caused by the flash with brain activity in response to proprioceptive signals about eye orientation, the delays will partly cancel each other. To explain the 100 ms error we find, proprioceptive signals would have to take 100 ms shorter than retinal signals to reach the brain (so that they indicate an eye orientation 100 ms after the flash). Since we have just argued that retinal signals take less than 100 ms to reach the brain, proprioceptive signals would have to have a negative delay. Of course it is possible that retinal signals are further delayed *within* the brain before being combined with proprioceptive signals about eye orientation, but why should the brain actively introduce systematic errors in this manner?

In contrast to proprioceptive signals, which only become available after a neural delay, the signals that drive the eyes can provide information about the orientation of the eyes before their orientation changes. Since the eyes are seldom subjected to unexpected forces, such signals provide a reliable prediction of their subsequent orientation. There is considerable support for the notion that the brain combines incoming retinal input with outgoing oculo-motor commands (see Matin, 1986). We propose that this takes place without any attempt to compensate for the associated delays. Thus, that brain signals resulting from visual stimulation some time earlier are combined with brain signals that will result in an eye movement some time later.

This can explain a timing error of about 100 ms. In order to follow a moving object with one's eyes, the oculo-motor signals must constantly specify a position that is slightly ahead of the instantaneous viewing direction, and thus of the moving object, because otherwise the object's image would not remain on the fovea. Thus, at the moment that the brain detects the flash, the oculo-motor signals must specify a position that is ahead of the viewing direction at that time, which in turn is ahead of where the eyes were directed when the flash stimulated the retina. Combining incoming retinal input directly with outgoing oculo-motor commands will make flashed targets appear to be displaced by about the distance that the subjects' gaze shifts during the sum of the sensory and motor delays. We have already seen that this sum amounts to about 100 ms.

Our proposal is consistent with the notion that experimental manipulations that increase retinal delays will increase the extent to which flashed targets are mislocalised. That the timing error is not completely independent of pursuit speed may mean that the time between there being brain activity related to an eye orientation and the eye actually having that orientation depends on the velocity of pursuit.

4.2. Comparison with mislocalisation just before saccades

An attractive aspect of the proposal is that it is very simple, both conceptually and in terms of the neuronal processing that would be required to implement it. Moreover, our proposal need not only apply to smooth pursuit. It also predicts visual mislocalisation just before saccades. In accordance with the proposal, there are quite a number of studies that report spatial mislocalisation before saccades. When a target is flashed two or more times at a single position, just before a saccade, the flashes are perceived at different locations (Jordan & Hershberger, 1994; Matin, Matin, & Pola, 1970; Schlag & Schlag-Rey, 1995). More generally, targets flashed just before saccades tend to be mislocalised in the direction of the impending eye movement (Mateeff, 1978; Honda, 1991, 1993; Dassonville, Schlag, & Schlag-Rey, 1992; Schlag & Schlag-Rey, 1995; Cai, Pouget, Schlag, & Schlag-Rey, 1997).

Targets can be mislocalised even if they are flashed more than 80 ms prior to saccade onset (Honda, 1991, 1993; Dassonville et al., 1992; Jordan & Hershberger, 1994; Morrone, Ross, & Burr, 1997). The amplitude of the mislocalisation can be up to 93–104% of the amplitude of the subsequent saccade (see table 2 of Dassonville et al., 1992). However, this is certainly not always the case. There are again large differences between studies, both in methodology and in results. Dassonville et al. (1992) had subjects localise flashed targets with saccades. Miller (1996) had them do so by pointing manually. Honda (1991) had them do so with a visible marker. Jordan and Hershberger (1994) had them do so by reporting the position relative to other flashed stimuli. Cai et al. (1997) by reporting the position relative to a reference that was visible until the flash. Mateeff (1978) by reporting the position relative to a reference that was visible throughout the presentation. In most cases the flash had to be closer to target onset than the 100 ms predicted in Section 4.1 and the magnitude of the mislocalisation was only between quarter and half of the amplitude of the subsequent saccade.

Flash luminance and state of retinal adaptation appear to influence the extent of the mislocalisation just before saccades (Bockisch & Miller, 1999), just as they do for mislocalisation during pursuit (Mita et al., 1950). The larger errors in Dassonville et al.'s (1992) study than in many others may be related to the fact that subjects only took about 440 ms to respond in that study. In Honda's (1991) study, for instance, the marker for indicating the perceived location of the flash only appeared 1.4 s after the flash. If our explanation for the mislocalisation is correct, the errors may be more prominent for quick responses because they depend on motor efference being used for judging eye orientation. Motor efference is presumably the first source of information about the saccade to become available. Later, visual and proprioceptive information may provide independent judgements that are not prone to the same errors.

Whether the localisation can be done relative to other visible structures also makes a difference. When experiments were conducted in the dark, the mislocalisation was the same for targets flashed at various positions (Dassonville et al., 1992; Honda, 1993; Schlag & Schlag-Rey, 1995). When there was a visible background, the mislocalisation was still in the direction of the saccade (Honda, 1993), but it was smaller (Honda, 1993), and its time-course and amplitude were no longer the same for all positions (Honda, 1993, 1995). Under some conditions subjects even perceived targets that were flashed just before saccades near the endpoint of the saccade, irrespective of where they really were (Morrone, Ross, & Burr, 1997). Moving a background to simulate the retinal stimulation during saccades also gives rise to localisation errors, but these errors are clearly different from those before real saccades (Honda, 1995; Morrone et al., 1997). Thus, visible structures other than the targets themselves influence the spatial localisation of targets flashed just before saccades, just as they do the spatial localisation of targets flashed during pursuit. Moreover, as we would predict, the mislocalisation was larger and less variable in the dark. However, as for pursuit, the influence of having visible structures is so dependent on details that differ between studies, that a direct comparison between the influence on the two kinds of eye movements is not yet meaningful.

Jordan and Hershberger (1994) asked subjects for verbal reports of the relative positions of stimuli presented in rapid succession. This allowed them to judge the rate at which the perceived position shifts during individual trials. Their data suggest that the shift is quite abrupt, in accordance with the abrupt nature of the saccades themselves. However, contrary to the proposal, most other studies support a gradual shift (Honda, 1991; Dassonville et al., 1992; Schlag & Schlag-Rey, 1995; Bockisch & Miller, 1999).

Thus, most factors that influence the mislocalisation during pursuit also appear to influence the mislocalisation just before saccades (target detectability, availability of a visible reference, way of responding). Moreover, many aspects of the mislocalisation are consistent with our proposal. However, it is evident that our simple scheme cannot explain the bewildering variability in the results reported in the literature. What it does explain is why flashed targets are almost always localised considerably too far in the direction of the (impending) eye movement.

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