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Spatial but not temporal cueing influences the mislocalisation of a target flashed during smooth pursuit

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Abstract. Human subjects misjudge the position of a target that is flashed during a pursuit eye movement. Their judgments are biased in the direction in which the eyes are moving. We investigated whether this bias can be reduced by making the appearance of the flash more predictable. In the normal condition, subjects pursued a moving target that flashed somewhere along its trajectory. After the presentation, they indicated where they had seen the flash. The mislocalisations in this condition were compared to mislocalisations in conditions in which the subjects were given information about when or where the flash would come. This information consisted of giving two warning flashes spaced at equal intervals before the target flash, of giving two warning beeps spaced at equal intervals before the target flash, or of showing the same stimulus twice. Showing the same stimulus twice significantly reduced the mislocalisation. The other conditions did not. We interpret this as indicating that it is not predictability as such that influences the performance, but the fact that the target appears at a spatially cued position. This was supported by a second experiment, in which we examined whether subjects make smaller misjudgments when they have to determine the distance between a target flashed during pursuit and a reference seen previously, than when they have to determine the distance between the flashed target and a reference seen afterwards. This was indeed the case, presumably because the reference provided a spatial cue for the flash when it was presented first. We conclude that a spatial cue reduces the mislocalisation of targets that are flashed during pursuit eye movements. The cue does not have to be exactly at the same position as the flash.

1 Introduction

It takes time for retinal stimulation to give rise to a neural response within the brain. This visual latency has consequences for localising moving objects. By the time a position has been determined, the object will have moved. To compensate for this, the visual system could predict the current position, as suggested by Nijhawan (1994) to explain a phenomenon called the flash-lag effect. However, there is behavioural evidence that such prediction is not responsible for the flash-lag phenomenon (Brenner and Smeets 2000; Eagleman and Sejnowski 2000; Whitney et al 2000). If one follows a moving object with one's eyes, its retinal image does not move but the eyes are rotating. In that case, the latency of the eye-orientation signal has consequences for localisation. Duhamel et al (1992) found neurons in lateral intraparietal cortex that start giving a response to a stimulus before an eye movement brings that stimulus into their receptive field. This suggests that efferent information about eye orientation may be involved in localising moving objects (Brenner et al 2001; Nijhawan 2001). Efferent information is different from afferent information in that it predicts a future eye orientation.

Given the considerations mentioned above, it is not surprising that mislocalisations are found in many different experimental settings involving moving targets. We will focus on position judgments during smooth-pursuit eye movements. Human subjects misjudge the positions of stimuli that are flashed during a smooth-pursuit eye movement. They also misjudge the position at which a pursued target disappears or changes brightness. The mislocalisation is in the direction of movement (Hazelhoff and Wiersma 1924; Mita et al 1950; Mitrani and Dimitrov 1982; Mateeff and Hohnsbein 1989; van Beers et al 2001; Brenner et al 2001). Hazelhoff and Wiersma (1924) assumed that this phenomenon was exclusively due to visual latencies and they called the mislocalisation expressed in time units the 'perception time' (Wahrnehmungszeit). They found that the perception time (on average 104 ms) was independent of the direction and speed of movement. Mita et al (1950) showed that the perception time depends on the retinal eccentricity of the flash and on the state of adaptation of the eyes. They also assumed that these mislocalisations were exclusively due to the visual latency in perceiving the flash, thus implicitly assuming zero latency for the eye-orientation signal. Mateeff et al (1981) showed that the position at which a moving target that is pursued by the eyes changes brightness is sometimes mislocalised against the movement direction, which would require a negative perception time. They explained this by introducing latencies for eye-orientation signals. A negative perception time arises when such latencies are longer than the visual latency.

Brenner et al (2001) suggested that mislocalisations arise because incoming retinal signals are combined with outgoing oculomotor commands, without considering neural delays. However, other studies show that there are more factors involved than just constant latencies. For instance, Mitrani and Dimitrov (1982) and van Beers et al (2001) found that the mislocalisation of a target flashed during pursuit was smaller when the flash was presented behind than when it was presented in front of the pursued target, which is not so easy to explain by visual or eye-orientation-related latencies. Two studies reported results that are particularly hard to explain with constant latencies: Mitrani et al (1979) and Mateeff et al (1981). In both studies, subjects were asked to report the position along a ruler at which a pursued target disappeared. In both studies, the mislocalisations were smaller near the end of the ruler. This was interpreted as an effect of expectancy: the closer the target comes to the end of the ruler the more certain the subject becomes that it will soon disappear. It has been shown that being able to predict where a flash will occur reduces the error in relative localisation in the flash-lag effect (Brenner and Smeets 2000; Baldo et al 2002). Whether this is also so when the eyes are moving, rather than the retinal image, is not yet known. In the Mitrani et al (1979) and Mateeff et al (1981) studies it is not certain that expectancy was the critical factor, because the presence of a reference can also influence the extent of mislocalisation (Mateeff and Hohnsbein 1989; Brenner et al 2001), and the end of the ruler may have served as such a reference when the target flashed nearby. Moreover, the subjects may have been reluctant to specify positions near or beyond the end of the ruler. In the experiments described here, we re-investigated the influence of expectancy on the amount of mislocalisation during pursuit.

We manipulated expectancy in a number of ways. We distinguish between giving the subjects information that emphasises *when* or *where* the flash would appear. Information about when the stimulus would appear was given by presenting either visual or auditory warning signals before the flash. Information about where the flash would appear was given by showing the whole stimulus twice. Although the when and where of a moving stimulus are obviously related, we reasoned that presenting warning signals at regular intervals primarily indicates when the target will appear, while having seen the target before will primarily cue a certain position as being a likely place for the target to appear.

2 Experiment 1

2.1 *Methods*

Subjects were eleven members of our department, including two of the authors. We told them all that the purpose of the warning signals and the repeated presentations was to make the appearance of the flashed target more predictable. They were seated in front of a computer monitor in a dark room. On each trial, a pursuit disk appeared moving at a constant velocity from left to right across a light-grey background and disappeared. The subjects were instructed to follow this pursuit disk with their eyes.

At a random position on its trajectory a target was flashed. The flashed target surrounded the pursuit disk (figure 1). Such a sequence of the pursuit disk travelling across the screen with a target flashed somewhere along its trajectory will be called a motion sequence. After a motion sequence the subjects indicated the position of the flashed target with a computer mouse. They could take as much time as they wanted.

Four different conditions were used (figure 1). In the NORMAL condition, the subjects saw the motion sequence once. In the TWICE condition, they saw precisely the same motion sequence twice. The mouse pointer was only presented after the pursuit disk had traversed the screen for the second time. The target was flashed at the same position both times. In the THIRD condition, two red warning flashes that surrounded the pursuit target preceded the target flash at 500 ms intervals. In the BEEP condition, the target flash was preceded by two warning beeps at 500 ms intervals. These preceding warnings could be used to anticipate the moment of the flash.

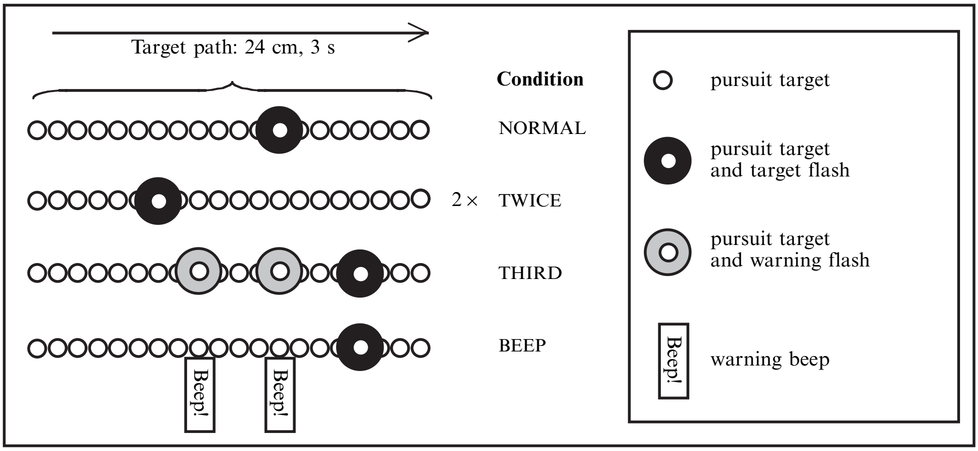

Figure 1. Schematic representation of the stimuli in experiment 1. In the NORMAL condition, the pursuit disk moved at a constant velocity across the screen. A flashed target surrounding the pursuit disk was shown at a random position. In the TWICE condition, the pursuit target moved across the screen twice with the flashed target both times at the same position. In the THIRD condition, two red warning flashes spaced at equal intervals preceded the target flash. The BEEP condition was similar to the THIRD condition but now two warning beeps, instead of flashes, preceded the target flash. In all cases, the mouse cursor used by the subject to indicate the position of the target flash was identical to the pursuit disk with the flashed target. Note that not all frames are represented in this figure.

The stimuli were presented on a computer monitor (392 mm $\times$ 293 mm; 815 $\times$ 611 pixels; 120 Hz). Subjects viewed the monitor from a distance of 60 cm (1 cm on screen $\approx$ 1 deg visual angle). The trajectory of the pursuit disk was 24 cm long and it was traversed in 3 s. The pursuit disk was white and had a diameter of 3 mm (47 cd m^{-2}). The target flash was a black, 8 mm diameter disk. The warning flashes were red, 8 mm diameter disks (9 cd m^{-2}). The background was grey (30 cd m^{-2}). Flashes were presented for one frame. The pursuit disk occluded their centre so that the subjects saw the flash as a ring surrounding the pursuit disk. Target flashes were presented at random positions between 8 and 20 cm along the trajectory. The mouse cursor with which the subject indicated a position was identical to the target flash with the superimposed pursuit disk but remained visible until a judgment was made. The mouse cursor appeared at a random position. A head-and-chin rest restricted head movements. Horizontal movements of the left eye were monitored with an Ober 2 (Permobil, Meditech) at 1100 Hz. The eye-movement recordings were used to ensure that the subjects made no saccades during a 400 ms interval centred on the moment of the target flash.

If they made a saccade, the trial was discarded and the subject was notified of this by a beep. If the subject did not know where she/he had seen the target flash, she/he could discard the trial herself/himself by pressing the right mouse button. Discarded trials were repeated later during the experiment.

Data were collected in three sessions of approximately 15 min. The first session consisted of the conditions NORMAL, TWICE, and THIRD. In the second session the TWICE condition was replaced by the BEEP condition, so it consisted of conditions NORMAL, THIRD, and BEEP. The third session was a repetition of the first. For each condition there were 30 trials, so each session had 90 trials. These 90 trials were presented in a random order.

Localisation bias was defined as the difference in horizontal position between the subjects' response and the target flash (a bias in the direction of pursuit is defined as positive). It was expressed in time units by dividing this difference by the velocity of the pursuit disk.

Our analysis started by checking whether individual settings were approximately on the target's trajectory, and whether the pursuit during 400 ms around the flash was good. Settings that deviated vertically by more than 3 cm were discarded, as were settings from trials where the gain of the pursuit deviated by more than 50% from the subject's mean gain in that session.

The next step in our analysis was to exclude subjects whose bias depended on the position on the screen at which the target was presented. We reasoned that the data of such subjects were influenced by some other factor than that under study, which might itself be influenced by our manipulations. We checked for an influence of the position on the screen by checking whether the slope of the regression of the error against the target flash position was significantly different from zero (at $\alpha = 0.05$). If it was, that subject's data were discarded.

For the remaining subjects we calculated the mean localisation bias for each condition. Subjects' mean localisation biases and pursuit gains in the different conditions were compared with those in the NORMAL condition with paired t-tests.

2.2 *Results*

3% of all settings were discarded because they deviated vertically by more than 3 cm or the pursuit gain differed by more than 50% from the mean gain. Five of the eleven subjects had biases that depended on the position on the screen, so we excluded these subjects from further analysis. These excluded subjects all had positive slopes.

The mean localisation biases of the six remaining subjects are shown in figure 2. A positive bias is in the direction of pursuit. In all conditions, subjects misjudged the target position in the direction of pursuit. The localisation biases in the TWICE condition are significantly smaller than those in the NORMAL condition ($p = 0.01$). The other two conditions were not different from the NORMAL condition ($p = 0.97$ and $p = 0.79$ for conditions THIRD and BEEP, respectively).

The differences in localisation bias are not caused by differences in eye movements because the gain of the pursuit did not differ between the NORMAL condition and the TWICE condition ($p = 0.31$).

2.3 *Discussion*

The slopes of the localisation bias against the flash position were significantly different from zero for five of the eleven subjects. They all had positive slopes, opposite to the findings of Mitrani et al (1979) and Mateeff et al (1981) who found negative slopes. Our experiments were aimed at getting a clearer view on the influence of expectancy. Since we did not use a visible ruler, we thought that in our case the position on the screen was not important, and therefore we randomly selected positions on the screen for each trial. Not having the same positions for the different conditions made us

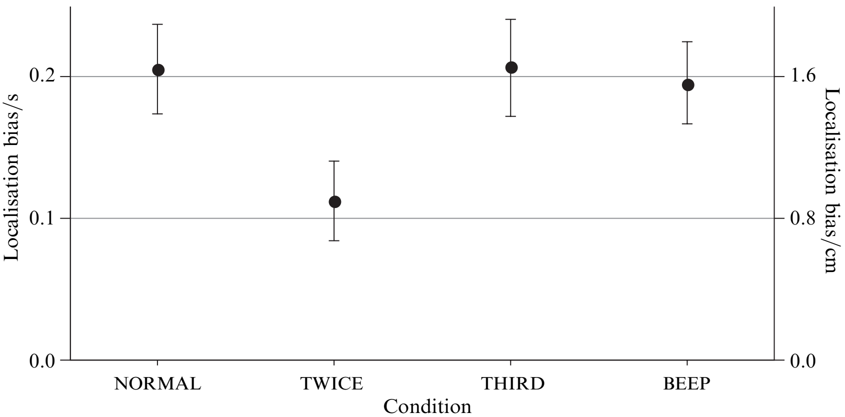

Figure 2. The average (and standard error) of the mean localisation biases of six subjects. Only the mean localisation bias in the TWICE condition differs significantly from that in the NORMAL condition.

reluctant to compare biases across conditions for subjects whose bias depended on the position. However, including all the subjects does not change our main result that the bias in the TWICE condition was about half the size of that in the three other conditions. The average bias was, however, smaller for the excluded subjects. Presumably they were using an additional source of information that reduced the bias, but which depended on the position on the screen.

The results show that making the appearance of the flash more predictable does not necessarily reduce the mislocalisation. The mislocalisation decreased significantly only in the TWICE condition. In that condition exactly the same stimulus was shown twice. The lack of effect in the other two experimental conditions (THIRD and BEEP) argues against predictability in general being critical. Apparently warning subjects that the flash is about to occur does not make any difference. Only cueing subjects as to where the flash would appear made a difference. Thus apparently it is not the raised expectancy that reduces the bias, but the fact that the second target in condition TWICE appears at a spatially cued position. This is interesting since the cue is presumably misperceived, because it arises from a motion sequence which is identical to that in condition NORMAL. This suggests that the cue does not have to be at the same position as the flash.

To evaluate the suggestion that spatial cueing influences the bias even if the cue is not at exactly the same position as where the target was, we conducted a second experiment in which the trial was not shown twice, but a cue was given at a slightly different position than the flashed target. To emphasise the relevance of the cue, we asked subjects to report the separation between two sequentially presented positions: that of a static reference and that of a target flashed during pursuit. We compared a condition in which the static reference was shown first followed by the flash during pursuit, with a condition in which the reference was shown after the flash during pursuit. The subjects had to indicate the separation between the two sequentially seen positions. We reason that, if the flash during pursuit is shown first, it will be mislocalised to the full extent. Therefore a similar bias as in the NORMAL condition in experiment 1 should be apparent in the separation judgments. If the flash during pursuit is shown after the static target, so that subjects are cued about where the flash would occur, the misjudgment should be smaller (as in the TWICE condition).

3 Experiment 2

3.1 *Methods*

Subjects were eleven colleagues including one of the authors. All subjects except for this author were naïve with respect to the aim of the experiment. The experimental setup was the same as in the first experiment. The subjects had to indicate the distance between two targets. One of the targets was presented very briefly during pursuit, like the flashed target in experiment 1. The other was a static target that was presented for 1 s, giving the subjects enough time to fixate it. There was a 500 ms interval between the two presentations. Two conditions were compared, the PURSUIT-FIRST and the STATIC-FIRST conditions (figure 3). In the PURSUIT-FIRST condition the target that was flashed during pursuit was presented first. In the STATIC-FIRST condition the static target was presented first. Otherwise the two conditions were identical.

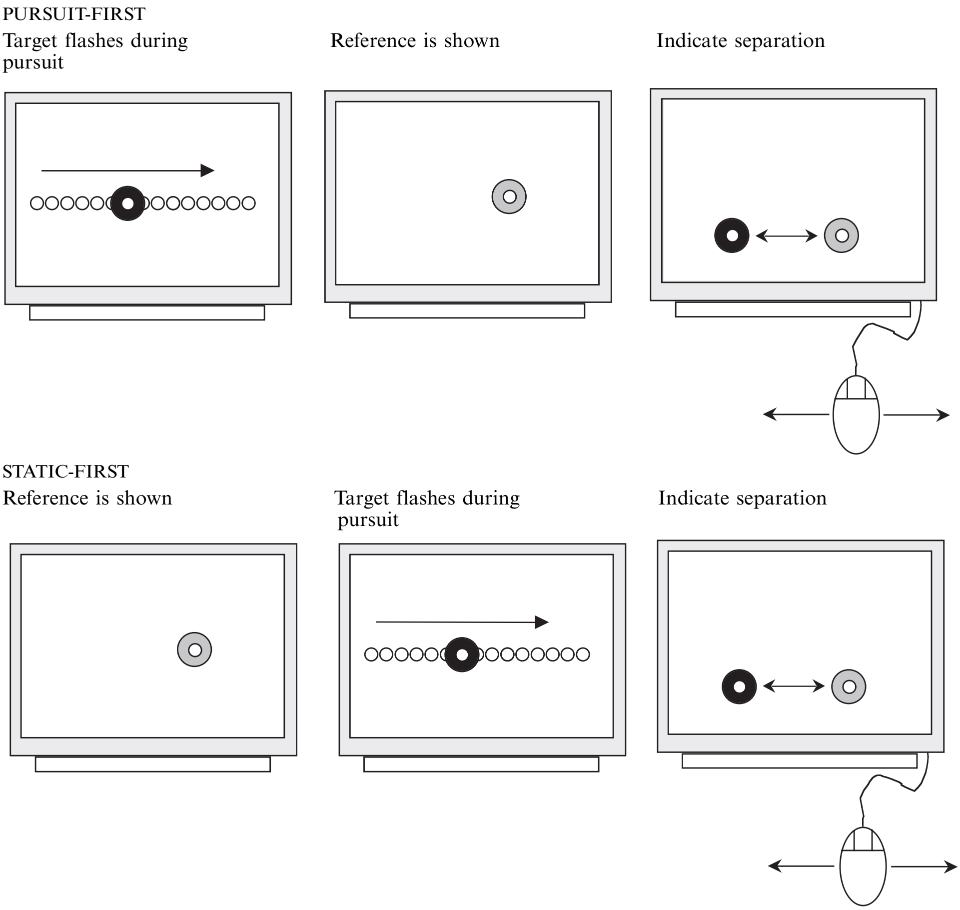

Figure 3. Schematic representation of the stimuli in experiment 2. In the PURSUIT-FIRST condition subjects saw a flashed target during a pursuit eye movement followed by a statically presented target (reference). They then had to indicate the separation. In the STATIC-FIRST condition the statically presented target was shown first and the flashed target second. Otherwise the two conditions were identical.

The static target had the same dimensions as the target that was flashed during pursuit, but it was red instead of black. Presenting a flashed target during pursuit was done in exactly the same way as in the NORMAL condition in the first experiment. The position of the flash was chosen at random from within the same range as in experiment 1. Because subjects mislocalise the flashes in the direction of pursuit, the static targets were presented at positions a little further in the direction of pursuit. The position of the static target was chosen at random from the range of positions that the pursuit disk would reach between 100 ms before and 250 ms after the flash. After the subject had seen both targets, two disks (a black one and a red one, both with a white centre) were presented at the centre of the screen, below the actual trajectory. Moving the mouse moved them by the same amount in opposite directions. The subject had to indicate the distance between the targets, taking into account which one was shown further to the left. The black disk was identical to the target presented during pursuit, and the red disk was identical to the static target. When the subject thought she/he had replicated the separation between the targets, she/he pressed the left mouse button. Eye movements during pursuit were checked in the same way as in the first experiment, and subjects could discard trials of which they were not sure by pressing the right mouse button. Discarded trials were presented again later in the experiment.

Our measure of performance, distance bias, was the difference between the signed separation set by the subject and the real separation (setting the flash too far to the right is considered a positive bias). It was expressed in time units by dividing this difference by the velocity of the pursuit disk.

Our analysis started by checking whether the gain of the pursuit did not differ too much from the subject's mean gain. Settings from trials in which the gain of the pursuit eye movement deviated more than 50% from the mean gain were discarded.

We again excluded subjects whose distance bias depended on the position of the screen (for the same reason as in experiment 1). This was done by checking whether the slope of the regression of the distance bias against the position on the screen was significantly different from zero (at $\alpha = 0.05$).

For every subject, we calculated the mean distance bias for each condition. The biases and pursuit gains in the two conditions were compared with a paired t-test.

3.2 *Results*

5% of all settings were discarded because the pursuit gain differed by more than 50% from the mean gain. Four of the eleven subjects had biases that depended on the position on the screen, so we excluded these subjects from further analysis. They all had positive slopes, indicating that they misperceived the flash in a similar way as the subjects that were excluded in experiment 1.

The mean distance bias, averaged over the remaining seven subjects, is shown in figure 4. All biases are positive, consistent with a misjudgment of the flash in the direction of the pursuit. The bias is smaller in the STATIC-FIRST condition than in

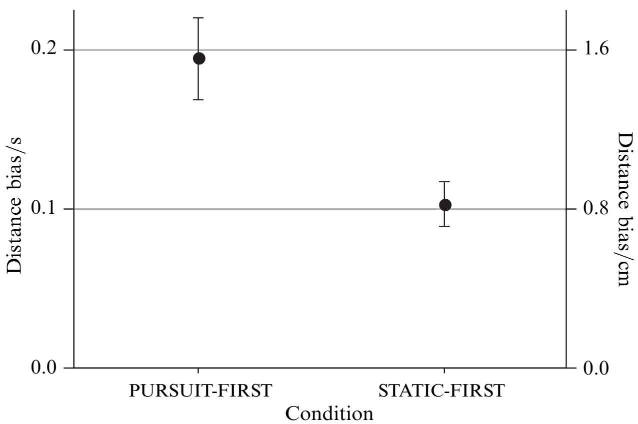

Figure 4. The average (and standard error) of the mean distance biases of seven subjects. The difference between the two conditions is significant.

the PURSUIT-FIRST condition ($p = 0.01$), indicating that the spatial cue not only works for judging position but also for judging separations. The distance bias did not depend on the real separation for any of our subjects, confirming that the spatial cue need not be at precisely the same position.

The difference in distance bias is not caused by differences in eye movements because the subjects' average gains in the STATIC-FIRST condition were not different from those in the PURSUIT-FIRST condition ($p = 0.10$).

3.3 *Discussion*
We have excluded four subjects from our analysis for the same reason as in experiment 1. Again, including these subjects does not make a difference for our main result that the error was smaller in the STATIC-FIRST condition; it only affects the absolute values. The average bias was again smaller for the excluded subjects.

We found that the separation between two sequentially presented targets was misjudged. The misjudgment was consistent with the way in which the positions of the flashes shown during pursuit were misjudged in experiment 1. The misjudgment was smaller in the STATIC-FIRST condition, in which the approximate location of the flash was cued before the flash during pursuit was shown. We conclude that the mislocalisation of the position of a target that is flashed during pursuit can be reduced by cueing the approximate position where the flash will appear.

4 General discussion
In both experiments we excluded subjects whose settings depended on the position on the screen at which the flash was presented. We did so because we reasoned that they were influenced by other factors than those that we were manipulating. For all these subjects the dependence on screen position was opposite to that found by Mitrani et al (1979) and Mateeff et al (1981). Since we could not explain the dependence on screen position, we felt reluctant to average the errors over the screen, so we excluded these subjects. However, including all subjects does not influence the differences between the conditions. It only affects the absolute values.

We found that subjects mislocalise the position of a target that is flashed during a smooth-pursuit eye movement in the direction of pursuit. Giving warnings shortly before the moment of the flash did not reduce this bias. Showing the same stimulus twice did. We interpreted this as an indication that it is not the ability to anticipate the flash that influenced the performance, but the fact that the second flash came at a spatially cued position. This was supported by our second experiment. There we asked subjects to judge the position of a flash seen during pursuit relative to a reference seen either before or afterwards. We found that subjects made smaller errors when they had to judge the separation between the flash and a reference seen before, than when they had to judge the separation between the flash and a reference seen after the flash. So again subjects made smaller misjudgments when the approximate position of the flash was cued.

Our second experiment might look a bit like the sequential localisation experiment in van Beers et al (2001). In that experiment van Beers et al show that, when subjects have to null the distance between two flashes seen sequentially during a single pursuit eye movement, the duration of the first flash influences the error while that of the second one does not. The first flash was always shown in front of the pursued disk while the second one was always presented behind it. Since they just showed in their second experiment that flashes behind a pursued disk are hardly mislocalised, it is not surprising that they do not find an effect of prolonging the duration of the second flash. That they do find an effect of showing the first flash longer is consistent with flashes in front of the pursuit disk being mislocalised (as shown in their second experiment), and with a reduction of such mislocalisation when showing a flash for a longer duration (as shown in their fourth experiment). So, our explanation of their results is that all that is happening is that the first flash is mislocalised less when it is shown for a longer duration, probably owing to the additional information from the retinal slip. Such an explanation cannot account for the results from our second experiment, since we only presented the target for a long duration when it was static.

Our two experiments differed from each other in two important aspects. First, while in the TWICE condition of the first experiment the reference was exactly at the position of the flash, it was only in its vicinity (ranging from -0.8 cm to 2.0 cm) in the STATIC-FIRST condition of the second experiment. Second, the first experiment was a localisation task while the second was a distance estimation task. The fact that the results were so similar suggests that neither of these differences was important. We conclude that spatial cueing reduces the amount of mislocalisation of a flash presented during smooth pursuit.

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