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Flashes are localised as if they were moving with the eyes

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Abstract

Targets that are flashed during smooth pursuit are mislocalised in the direction of the pursuit. It has been suggested that a similar mislocalisation of moving targets could help to overcome processing delays when hitting moving objects. But are moving targets really mislocalised in the way that flashed ones are? To find out we asked people to indicate where targets that were visible for different periods of time had appeared. The targets appeared while the subjects' eyes were moving, and were either moving with the eyes or static. For flashed targets we found the usual systematic mislocalisation. For targets that moved with the eyes the mislocalisation was at least as large, irrespective of the presentation time. For static targets the mislocalisation decreased with increasing presentation time, so that by the time the presentations reached about 200 ms the targets were not mislocalised at all. A simple model that combines smooth retinal motion with information about the velocity of smooth pursuit could account for the measured tapping errors. These findings support the notion that the systematic mislocalisation of flashed targets is related to the way in which people intercept moving objects.

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1. Introduction

The mechanisms by which people intercept moving objects are still far from being fully understood. One problem is that people must somehow anticipate where they will make contact with the object before the object reaches that position. This is necessary because the object is moving while the information flows through the visual and motor pathways to guide the limb to the interception point. This means that one must predict the object's future position. Such a prediction is relatively straightforward if one knows the object's velocity and how long it will take to reach the object's path. However, Brouwer, Brenner, and Smeets (2002) found that the perceived velocity of an object that one is trying to hit is not used to make such predictions. Nevertheless subjects can hit moving targets. Thus, they must account

for the distance that the object moves as the hand approaches it without using the perceived velocity. This raises the question of how to predict the object's displacement during the final part of the action, when no on-line corrections are possible because of neuronal and muscular delays. When people are pursuing the object with their eyes, a way in which the object's displacement during this time interval could be predicted is by misperceiving the object's position in a velocity-dependent manner. Such mislocalisation has often been reported (e.g. Hazelhoff & Wiersma, 1924).

The evidence that positions are mislocalised during pursuit comes from studies in which targets were flashed. Targets that are flashed during smooth pursuit are mislocalised in the direction of the pursuit (Hazelhoff & Wiersma, 1924; Mateeff & Hohnsbein, 1989; Mateeff, Yakimoff, & Dimitrov, 1981; Mita, Hironaka, & Koike, 1950; Mitrani, Dimitrov, Yakimoff, & Mateeff, 1979; Mitrani & Dimitrov, 1982; van Beers, Wolpert, & Haggard, 2001; Brenner, Smeets, & van den Berg, 2001). The critical assumption in using this finding to

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explain how people intercept moving targets is that the same mechanism of mislocalisation applies to moving targets that remain visible. The main reason to accept this assumption is that it would provide a functional explanation for the existence of such a systematic localisation error within the visual system.

If all objects were mislocalised in the direction in which the eyes move, we would encounter problems in avoiding surrounding static objects whenever we move our eyes to pursue a moving object. To avoid such problems the mislocalisation should only apply to the object that is moving. The information underlying the distinction between static and moving objects might be the motion in the retinal image. When the eyes move to pursue a target, that target's image is kept on the fovea, while most other objects' images move on the retina. Could the reason that flashed targets are mislocalised be related to the fact that their image does not move on the retina?

In order to test this hypothesis we examined whether "flashed" targets are mislocalised when their image does move on the retina. We presented targets for various time intervals. In order to be sure that the movement on the retina was critical, rather than the duration of presentation, we presented both static targets and ones that were moving with the pursuit disk. A complication that the longer presentation times introduce is that people may perceive the targets to be moving. We therefore asked our subjects to always indicate where the target first appeared. They indicated this position by tapping the screen.

2. Methods

2.1. Experimental set-up

Eight colleagues volunteered to take part in this study after being informed about what they would be required to do. Two of them were authors. The others were unaware of the hypothesis that was being tested. The research in this study is part of an ongoing research program that has been approved by the local ethics committee. Stimuli were projected onto a large screen (120×158 cm) that was tilted $20°$ with respect to horizontal. A CRT projector with fast phosphors (Sony, VPH 1271QM, 800×600 pixels, 120 Hz) projected the stimuli via a mirror from the rear onto this screen. The 800×600 pixels covered an area of 110 by 85 cm. The projector received its input from an Apple Macintosh G4. The subject was standing in front of the screen (Fig. 1). The room was dimly lit so that the subjects could see the screen and their hands. The screen itself was white with little structure on it except for a few stains and some dust. The edges of the screen and other objects surrounding the screen were clearly visible.
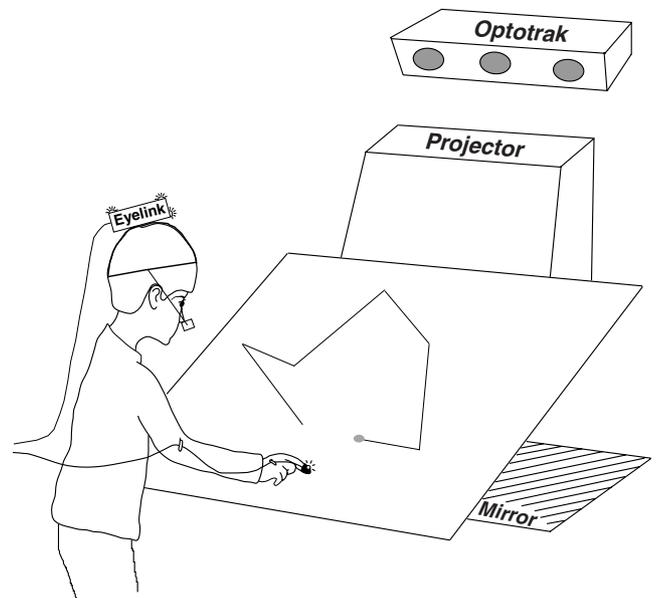

Fig. 1. Schematic drawing of a subject performing the task. A moving pursuit disk is projected from the back onto the screen (via a mirror). An EyeLink measures the subject's eye movements. An Optotrak measures the subject's head movements and the position of the subject's finger. The grey disk in the drawing represents the red pursuit disk. The lines show part of the pursuit disk's path (subjects never saw these lines).

A red 15 mm diameter pursuit disk ($2 \, \text{cd/m}^2$) moved along a path of connected line segments. The subject was asked to pursue this disk with his eyes. At random moments a green disk was shown. The subjects were instructed to quickly tap the position of this green disk with their index finger. We call these green disks tapping targets. The average interval between two tapping targets was 4.5 s (the range was 2–9 s). The tapping targets were never presented close to the moment that the pursuit disk changed direction, or close to the edge of the screen. The duration of the line segments in which a tapping target was shown was chosen at random from between 800 and 1200 ms. The tapping target appeared after the pursuit disk had followed the line segment for a random interval between 300 and 500 ms. The direction in which the pursuit disk moved was chosen at random from all possible directions. The pursuit disk's velocity was chosen at random from between 16 and 32 cm/s. The pursuit disk's initial position on such segments was not constrained, but if the combination of the randomly drawn interval and direction would place the tapping target outside the central (84×41 cm) part of the screen a new interval and direction were chosen at random. If necessary, this was repeated until an appropriate interval and direction were found.

The tapping targets were green 30 mm diameter disks ($8 \, \text{cd/m}^2$). They were presented for various durations: about 1, 43, 93 or 193 ms (1, 6, 12 or 24 frames at 120 Hz). When they were presented for more than one

frame they were either stationary, so that they gave rise to movement of the retinal image, or moved with the pursuit disk, so that there would be little retinal movement if the gain of pursuit was close to one. In all cases the tapping targets were initially centred at the position of the pursuit disk, so that flashed targets and ones that moved with the pursuit disk looked like a bright green ring surrounding the red pursuit disk. The targets that were stationary were also initially centred at the position of the pursuit disk, but of course the pursuit disk moved away from this position. We instructed the subjects that if the tapping target moved they had to tap the position at which it first appeared. There were 15 tapping targets in each of the seven categories. The experiment was divided into five blocks of trials that took about 1.5 min each, with a short break between the blocks. The tapping targets of each category were distributed evenly across the blocks.

2.2. Measurements

The position of the tip of the subject's right index finger was measured at 250 Hz by a movement analysis system (Optotrak 3020; Northern Digital) that tracked an infrared emitting diode (IRED) that was attached to the nail of the subject's index finger. On one of its analogue input channels the Optotrak measured the blue video signal from the computer. This was done in order to be able to synchronise the measured IRED positions with the moments that the tapping targets were visible: the tapping targets were drawn in green as well as in blue, but only the green output was connected to the projector.

Eye movements were measured with an EyeLink system (EyeLink I; SensoMotoric Instruments, Teltow, Germany). This is a fast video-based eye tracker with cameras attached to the subject's head with a headband (van der Geest & Frens, 2002). In order to prevent the headband from slipping relative to the head we attached a bite board to the headband. Three IREDS were attached to the EyeLink's headband, so that we could measure the head's position and orientation in space using the Optotrak. This was needed to convert the EyeLink's (eye in head) data into gaze positions on the screen (i.e. to determine where the subject was looking).

The Eyelink provides information about the orientation of the eyes in the head. Since our subjects were free to move their heads this information has to be combined with measured head movements if we want to determine where the subject is looking (i.e. gaze position). In order to be able to do so a calibration procedure was conducted before each experiment. First, we determined the position of the eyes relative to the head (i.e. relative to the IREDS attached to the headset). We did this by asking the subjects to position their head so that they could look through three small tubes, first with their left eye and then with their right eye. We knew the position at which the lines through these tubes intersect, so the measured positions of the headband when subjects could see through all three tubes gives us the positions of the eyes relative to the headband. We next performed the Eyelink's standard 9-point calibration procedure, on a monitor that was part of the Eyelink system. After this calibration, the Eyelink gave us gaze positions on that monitor (assuming that the subject's head never moved). Since we knew where the monitor was during the calibration we could convert the output of the Eyelink into directions of gaze. With information about the position and orientation of the head, from the markers on the headband, and knowing where the screen is, the directions of gaze could be converted into positions on the screen. To confirm that these calculations revealed where the subject was looking, we presented a dot at the calculated position and asked the subjects to look around the screen while moving and turning their heads. All subjects reported that the dot remained near where they thought they were looking, but some reported a small systematic offset. We did not try to correct for such offsets because we were mainly interested in the direction and speed of the eye movements, rather than the precise direction of gaze, so small systematic offsets hardly matter.

To determine the temporal relationship between the EyeLink's measurements and those of the Optotrak we used a pulse generator. The pulses from the pulse generator were measured by one of the analogue input channels of the Optotrak and via the parallel port of the "operator PC" of the EyeLink system. The relative timing of these synchronisation signals was determined using a model eye: a cylinder with a hole (simulated pupil) in it. The model eye was connected to a potentiometer. Rotating the model eye (by hand) changed the voltage over the potentiometer. An analogue input channel of the Optotrak measured this voltage. At the same time, the EyeLink measured the changing position of the simulated pupil. The data measured by the EyeLink was shifted in time by various amounts and correlated with the data measured by the Optotrak. The shift of the EyeLink data that gave the highest correlation coefficient told us how to synchronise the measurements. We found that the data point at the moment of the pulse in the Optotrak file corresponded to the data point 5 ms after the pulse in the EyeLink data file.

2.3. Data analysis

We defined the tapped position as the first position after the start of the movement at which the IRED was less than 2 cm from the screen (the finger was almost touching the screen because the IRED was attached to the nail). In a few cases, no tapped position could be

determined because the subject did not move (presumably because he did not notice the tapping target) or because the subject turned his hand so that the IRED on the finger could not be seen by the Optotrak. To quantify the mislocalisation we calculated one-dimensional tapping errors: the distance along the direction of pursuit from the initial position of the tapping target to the position that was tapped. We divided this distance by the pursuit disk's velocity to express the tapping error in time units. The error in time units indicates how long it would take for the pursuit disk to move to the tapped position. This kind of mislocalisation has generally been reported in time units. Originally, Hazelhoff and Wiersma (1924) did so because they assumed that the error reflected "perception time". Later this was done because most authors assumed that it has something to do with neural delays. Moreover, the error has been found to be less dependent on pursuit speed if it is expressed in time units (Mita et al., 1950). To check whether this is also the case in our experiment, we compared the slopes of the regression between the errors and the velocity of the pursuit disk when the errors are expressed in spatial units and when the errors are expressed in time units (all conditions were included in this analysis).

We determined the position of gaze on the screen for both the left and the right eye, and then averaged them. Occasionally the gaze position could not be determined, either because the subject turned his head so that the Optotrak could not see one of the IREDS on the headset, or because the EyeLink could not determine the eye orientation (presumably because the subject blinked). In both these cases the missing parts of the gaze path were not used in the analysis, but parts that were not missing were used.

In order to find out what kind of eye movements the subjects made we characterised the gaze movement that was made between 100 ms before and 500 ms after the onset of a tapping target. To get a measure of the direction and speed of the gaze movement, the gaze positions were convoluted with the first derivative of a normalised Gaussian, with a width of 8 ms. This gave us smoothed gaze velocity vectors. We used the length of these vectors to separate saccades from smooth pursuit.

We defined saccades as changes in gaze position that involve angular gaze velocities exceeding 40°/s (in any direction). If the period in which the angular eye velocity was above 40°/s was shorter than three samples (at 250 Hz) it was considered to be noise. If not, we added 8 ms of eye movement before and after the periods during which the angular velocity exceeded 40°/s to be sure to include the beginning and end of the saccade, and consider the total change in gaze during this period as the saccade. To calculate the mean smooth pursuit component of the eye movement at a certain moment (relative to tapping target onset) we averaged all remaining eye movements. For both saccades and smooth pursuit

we report the component of the eye movement in the direction in which the pursuit disk moved.

3. Results

The tapped position could be determined for 98% of the tapping targets. On average, the finger tapped the screen 629 ms after the tapping target appeared. The average errors are shown in Fig. 2. When the tapping error was expressed in temporal units it did not depend significantly on the velocity of the pursuit disk for any of the subjects. On average, the tapping error decreased by 0.7 ± 1.3 ms (mean $\pm$ SE) for every cm/s increase in the velocity of the pursuit disk (mean slope of the regression described in the previous section; the decrease was not consistent across subjects $t_7 = 0.5$; $p = 0.62$). When the tapping error was expressed in spatial units it depended significantly on the velocity of the pursuit disk for four of the eight subjects ($p < 0.05$). On average, the tapping error increased by 1.1 ± 0.3 ms for every cm/s increase in the velocity of the pursuit disk (the increase was consistent across subjects $t_7 = 3.9$; $p = 0.006$). This justifies our choice to express the errors in time units.

The tapping target that was only visible for 1 ms was mislocalised by 175 ms in the direction of the pursuit. In spatial units this was 4.4 cm. The initial positions of the tapping targets that moved with the pursuit disk were mislocalised to about the same extent, except for the ones that were visible for a very long time (193 ms) which were mislocalised even further. The tapping targets that did not move with the pursuit disk were mislocalised less,
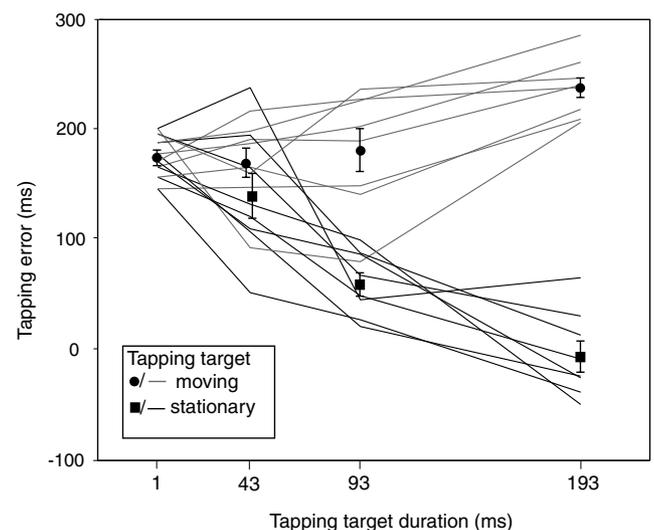

Fig. 2. The tapping error as a function of the tapping target duration. The black symbols show the overall mean tapping error and the error bars indicate the between-subjects standard error. The thin lines connect the mean tapping errors of the individual subjects.

especially if they were visible for a long period of time. The stationary tapping targets that were visible for 193 ms were not mislocalised at all.

The eye movements that were made in the different conditions differed in several respects. The average pursuit gain is shown in the central parts of each panel in Fig. 3. The lengths of the components of the saccades that were in the direction of pursuit are shown in the lower parts of each panel in Fig. 3. The hand velocity (top part of each panel) is also shown to illustrate the relation between the eye movements and the hand movements. When the tapping target was stationary the smooth pursuit gain started to drop about 100 ms after the tapping target appeared. When the tapping target moved with the pursuit disk the pursuit gain remained high until after the tapping target disappeared.

Up to about 150 ms after the tapping target appeared most saccades were *forwards*, in the direction of pursuit (positive saccade lengths in bottom part of each panel in Fig. 3). These are presumably catch-up saccades that compensate for a too low gain of smooth pursuit. Their occurrence is independent of the duration of the flash (Fig. 4a). Most saccades that started later were *backwards*, in the opposite direction than pursuit, presumably redirecting gaze to the perceived position of the target in anticipation of the upcoming tap. The transition from *forward* to *backward* saccades occurred 100 ms later if the tapping target moved with the eyes. When the tapping targets were stationary, *backward* saccades appeared earlier and there were more of them (see Fig. 4b). The difference is particularly clear when comparing the two kinds of targets that were visible for 193 ms.

Targets that are presented shortly in the temporal proximity of a saccade can be mislocalised in very complicated ways (for reviews see Schlag & Schlag-Rey (2002) or Ross, Morrone, Goldberg, & Burr (2001)). To determine whether the tapping errors are specifically related to smooth pursuit, or whether pre-saccadic mislocalisation is also important, we checked whether the *catch-up* saccades shortly after target onset influence the tapping errors. To do so we split the trials into ones with and ones without a *catch-up* saccade starting less than 152 ms after target onset (*catch-up* saccades started within this period in about 20% of the trials, see Fig. 4a). The presence of a *catch-up* saccade closely after target onset appears to have no influence on the errors (see Fig. 5a). Thus it appears that the errors are not influenced by saccades and do not depend on the total displacement of gaze after target onset. When a *catch-up* saccade was made the average displacement of gaze was 183% of the average displacement during this period when no *catch-up* saccade was made.

Comparing the percentage of *backward* saccades in Fig. 4b with the errors in Fig. 2 shows that the errors were smaller in the conditions in which the percentage of *backward* saccades was higher. One might therefore think that the presence of these *backward* saccades is responsible for the difference in the tapping errors. To examine this possibility we split the trials into ones with and ones without such saccades (between 152 ms and 500 ms after the onset of the tapping target). Fig. 5b shows the tapping errors (as in Fig. 2) split by whether or not a *backward* saccade was made in that trial. Whether subjects made *backward* saccades appears to have no influence on the tapping error (see Fig. 5b). It also had no influence on the timing of the tap: the interval between the flash and the tap was not different when subjects made a *backward* saccade than when they did not (paired *t*-test: $t_{49} = 0.93$, $p = 0.36$).

4. Discussion

We confirmed that targets that are presented for short periods of time (i.e. *flashed*) during smooth pursuit are mislocalised in the direction of the eye movement. Moreover, we show that if the target is visible at a single position for a longer period of time, the amount of mislocalisation is reduced. If the target is visible for the same period but moves with the pursuit disk, its initial position is mislocalised at least as much as flashed targets are. This shows that the reduced mislocalisation is not caused directly by the duration of target presentation.

Asking subjects to localise moving targets always introduces complications, because it is difficult to separate timing errors from spatial errors. We asked subjects to indicate where the target appeared. A possible explanation for the difference between the responses to the moving and the static targets could be that subjects did not tap the initial position of the target. The reason for that might be that the lack of movement of the retinal image removed the sense that the position changed over time (Mack, 1970), so that subjects judged the position at a later time than target onset. However even the most extreme possibility, that subjects tapped the position at which the targets disappeared, could not account for the difference between the mislocalisation of the stationary and the moving targets (Fig. 6). To make the difference disappear we would need to assume that subjects judged positions beyond the position of target offset.

In the introduction we predicted a difference in tapping error between static and moving targets on the basis of the proposal that targets are only mislocalised if no retinal motion is detected. In Fig. 2 one can see that for a 93 ms presentation of a stationary target subjects make an error that is about half of the magnitude of the error that is made when there is hardly any retinal motion (93 ms presentation of a moving target). This argues against our simple proposal, because we expect the retinal motion either to be detected or not. However,
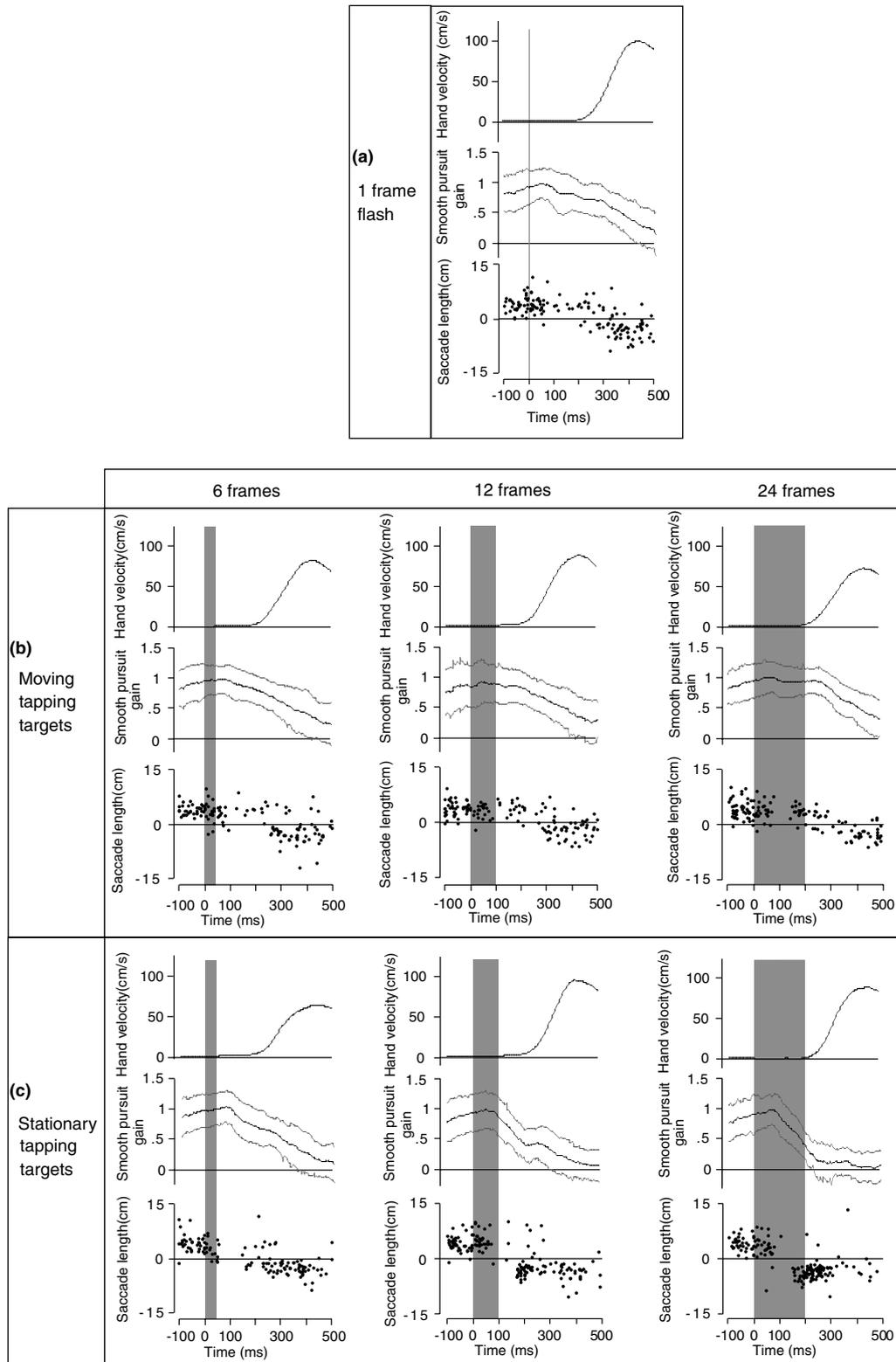
Fig. 3. The hand velocity, the gain of smooth pursuit (black trace: average; grey traces: average plus or minus one standard deviation) and the lengths of the saccades, all as a function of the time relative to the moment that the tapping target appeared. The shaded area indicates the period when the tapping target was visible. Data for the 1 ms tapping targets (a), the tapping targets that were visible longer and were stationary (b), and the tapping targets that were visible longer and moved with the pursuit disk (c).

since this is an average value, it could be that the retinal motion is close to the threshold so that subjects some-

times do and sometimes do not detect it. If so, the distribution of errors for this condition should be bimodal.
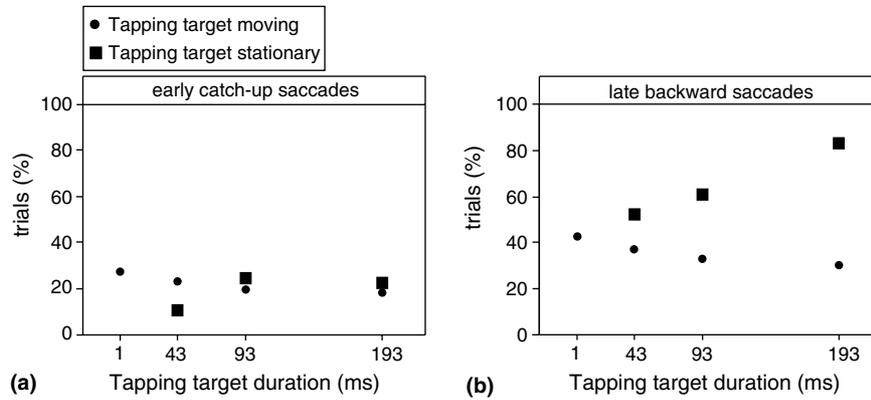
Fig. 4. The percentage of trials in which a *catch-up* saccade started less than 152 ms after the onset of the tapping target (a) and the percentage of trials in which a *backward* saccade started between 152 and 500 ms after the onset of the tapping target (b), both as a function of the duration of the tapping target. 100% corresponds to 120 trials.
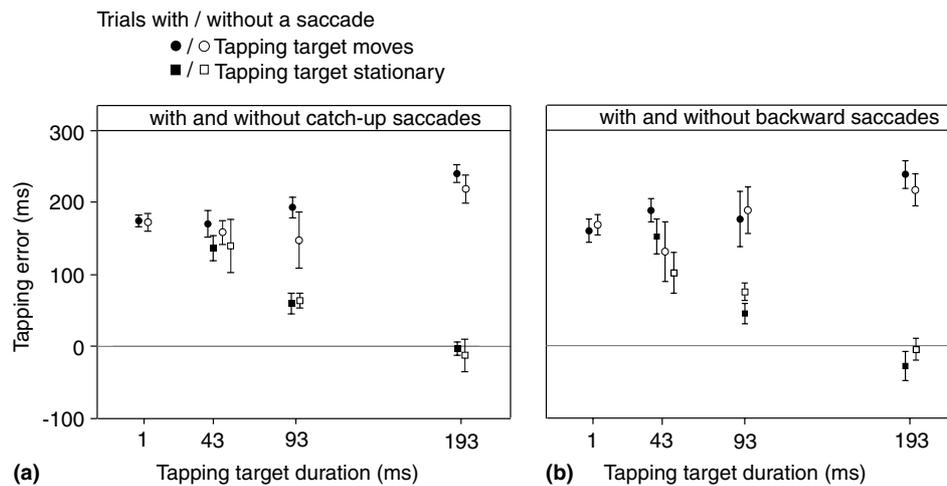

Fig. 5. The tapping error as a function of tapping target duration, shown separately for trials with and without *catch-up* saccades that started less than 152 ms after target onset (a) and shown separately for trials with and without *backward* saccades that started between 152 ms and 500 ms after target onset (b). The error bars indicate between-subjects standard error.

Fig. 7 shows this not to be the case. Thus the dependence of the mislocalisation on the retinal motion is unlikely to be a matter of detecting the presence or absence of motion.

Even when fixating a stationary point people can make systematic errors. These errors depend on the retinal eccentricity of the target's image. Both compression towards the fovea (Müsseler, van der Heijden, Mahmud, Deubel, & Ertsey, 1999; van der Heijden, van der Geest, de Leeuw, Krikke, & Müsseler, 1999) and expansion away from the fovea (Bock, 1986; Enright, 1995; Henriques, Klier, Smith, Lowy, & Crawford, 1998) have been found. Kerzel (2002) proposed that since the eyes move past the final position of a pursued target, compression towards the fovea might explain the forward mislocalisation of the final position. In our experiment the eyes also moved on after target onset, and the retinal eccentricity of the position that had to be tapped changed differently in trials with than in trials without a backward saccade. However, in Fig. 5b we saw that it did not matter for the tapping error whether a *backward* saccade was made after target onset or not. From this we can conclude that the retinal eccentricity of the position that one is tapping (just before or at the moment of the tap) is irrelevant. As we saw in Fig. 5a, the presence of catch-up saccades shortly after target onset did not matter either. This suggests that the smooth pursuit component of the eye movement is critical for the localisation error, rather than the total shift of gaze.

We rejected the proposal that the mislocalisation depended on whether retinal motion was detected or not. Could the mislocalisation depend on the retinal motion in a more complicated way? Our new proposal is that the perceived position depends on the sum of the pursuit signal and the retinal motion, integrated over some time. We reasoned that there is no need to explicitly detect whether targets are stationary, because stationary targets will yield retinal motion that exactly matches the
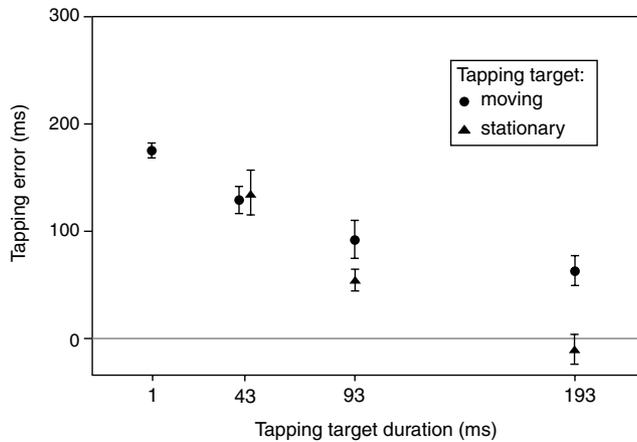
Fig. 6. The tapping error when it is calculated relative to the final position of the tapping target as a function of the tapping target duration. The error bars indicate the between subjects standard error. Note that the task was to indicate the target's initial position. For stationary targets it makes no difference whether the error is calculated relative to the initial or the final position, but we reproduce the errors here for comparison.
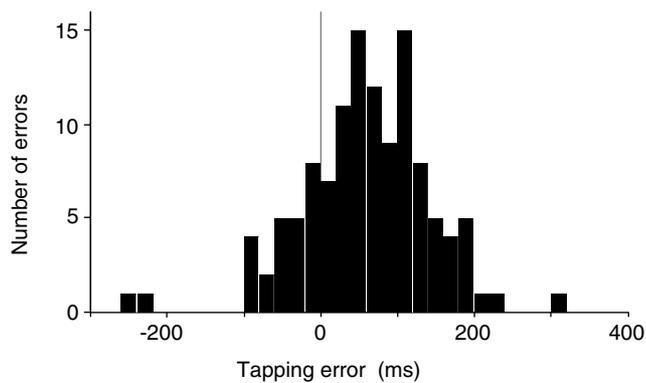

Fig. 7. Histogram of tapping errors when tapping the position of a stationary target that was presented for 93 ms. The distribution is clearly unimodal (bin width: 20 ms).

pursuit signal but with an opposite sign. Integrating the retinal motion and the pursuit signal over time gives an estimate of the target's displacement over the integration period. This is very similar to using a velocity signal, and is therefore suitable for predicting future target positions.

This new hypothesis is qualitatively consistent with our results. Flashed targets and ones that are moving with the eyes produce little retinal motion. Consequently, their position is misperceived by an amount that depends on the speed of pursuit, because the pursuit signal is integrated over some time, and there is no retinal motion to cancel it. Stationary targets do produce retinal motion that counteracts the integrated pursuit signal, but this only cancels the integrated pursuit completely if the target remains visible during the whole integration time.

Quantitatively, this hypothesis predicts that the tapping error is the sum of the gaze displacement caused by pursuit and the displacement of the retinal image during some time interval. We tried to predict the tapping errors by integrating the sum of those two signals for different periods of time. Because we found that the errors did not depend on whether or not a saccade was made closely after target onset we assume that the error only depends on the smooth pursuit signal and on retinal motion when the eyes move smoothly. Thus, our model has two components the integrated smooth pursuit and the integrated smooth image movement. Both of these can be extracted from our data. We started the integration at the moment of target onset. It turned out that the error was predicted best if we integrated over 200 ms. The integration was done according to the following equation:

$$\text{error} = \int_0^{200} (G_p V_{pd} + V_r)\, dt$$

In this equation V_{pd} is the pursuit disk's velocity and G_p is the gain of smooth pursuit, so their product is the velocity of the smooth displacement of the gaze direction. V_r is the velocity of the target's image across the retina. Integrating these values gives the total smooth change in gaze and displacement of the retinal image during the 200 ms after target onset. The velocity of the retinal motion (V_r) is considered positive if the image moves in the direction in which the retina is moving, so that during pursuit it is negative for stationary targets (and the two components of the equation cancel each other). It is zero when no target is visible or when the retinal motion is extremely fast (i.e. during saccades).

This model is consistent with the measured errors (Fig. 8). Note that the model is not equivalent to saying that the subjects tapped where they were looking 200 ms after target onset. Firstly, the model does not consider saccadic eye movements, but only smooth eye movements. Secondly, in addition to the smooth *eye* movement, smooth *retinal* movement is also considered. The fact that a model that ignores saccadic eye movements reproduces the tapping errors so well suggests that the brain uses prior knowledge that objects in our surroundings never move at saccadic speeds. This is probably an essential part of predicting the target's future position on the basis of short periods of retinal motion and eye movements. It ensures that (catch up) saccades will not result in sudden perceived displacements, and eliminates the necessity to deal with the stringent temporal requirements, and the high retinal speeds, which would otherwise make it difficult to evaluate motion signals near the fast and abrupt changes that are characteristic of saccades.

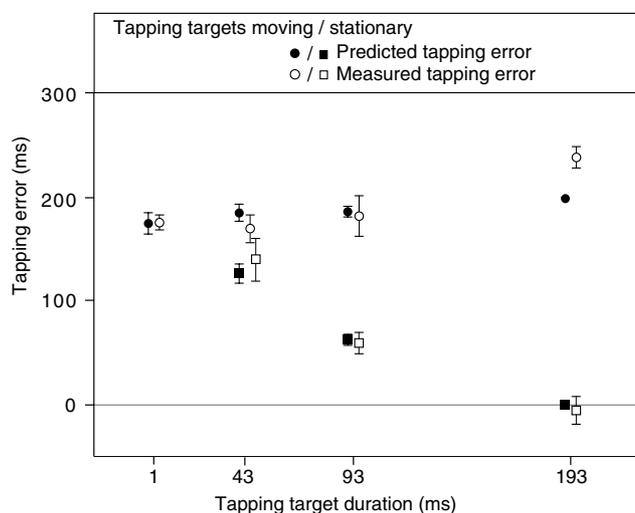The duration of 200 ms is longer than most of the times that were previously suggested. Early studies that

Fig. 8. The tapping error as predicted by adding gaze displacement caused by smooth pursuit and smooth retinal motion for 200 ms after target onset. To make it easy to compare the prediction (solid symbols) with the measured errors, we reproduced the latter as open symbols (data from Fig. 2). The prediction was based on individual trials, so we can also give an error measure that is equivalent to that for the measured data.

measured the length of the error in time units called this the "perception time" (Hazelhoff & Wiersma, 1924; Mita et al., 1950). Later studies suggested that the mislocalisation was related to the way in which retinal information and information about eye orientation are combined (Mateeff et al., 1981; Brenner et al., 2001), and examined factors that can influence the mislocalisation (Mateeff & Hohnsbein, 1989; Mitrani & Dimitrov, 1982; Rotman et al., 2002). Various factors can do so. The value of 200 ms in our model is not directly equivalent to the mislocalisation in time units, because our model predicts less mislocalisation if the eyes follow the target with a combination of smooth pursuit and catch-up saccades. However, it is not likely that there were many saccades in the mentioned studies, because the experimenters carefully tried to evoke smooth pursuit eye movements. Therefore, the value of 200 ms is probably not fixed, but depends on the experimental conditions.

Our main conclusion is that flashes are mislocalised because they produce no retinal motion. The evidence for this is that our subjects mislocalised the flashed targets in the same way as they did the other targets that produced no retinal motion: the moving targets. Stationary targets did produce retinal motion, and they were not mislocalised if they were present long enough. A simple model that combines the smooth retinal motion with a pursuit signal can account for the tapping errors quite well. According to the model these signals are integrated during a short interval (about 200 ms) to predict the target's position a fixed time later. The model implies that *any* target that moves relative to oneself will be mislocalised in its direction of motion, because when

a target moves there must be either a pursuit signal or retinal motion. When the subject does not pursue the target, there is retinal motion that will be integrated for 200 ms after target onset, and when the subject does pursue the target, there is a pursuit signal that will be integrated for 200 ms after target onset. The only instance in which the model predicts no mislocalisation is when the target is stationary (and visible for longer than the integration period). In that case there is either no motion at all, or else the pursuit signal and the retinal motion are equal in magnitude and opposite in sign so that they cancel each other.

It has often been suggested that when the eyes are not moving, targets that are moving are judged to be further in the direction of their motion than they really are (giving rise to the flash-lag effect; Nijhawan, 1994). The flash-lag effect has been shown to depend on the (retinal) motion after the flash (Brenner & Smeets, 2000). The onset of motion is also often judged to have occurred further in the direction of motion than it really had (e.g. Fröhlich, 1923). When targets are flashed during smooth pursuit they are generally mislocalised in the direction of pursuit. We here show that during pursuit, subjects misjudge the positions at which moving targets appeared in a similar manner. We propose that not only the initial position is misperceived, but that moving targets are constantly judged to be further along their path than they really are. This proposition is supported by the finding that the flash-lag effect disappears when the moving target is pursued (Nijhawan, 2001). We propose that this is because the flash and the pursued target are then both mislocalised. Such localisation errors could be useful, because the control of any fast action that is aimed at a moving target must include some mechanism for dealing with neuronal and muscular delays. The existence of such a mechanism presumably gives rise to the mislocalisation of flashed targets that we (and others) have found. This would provide a functional significance for the mislocalisation, which would explain why such a systematic error has not been corrected during evolution or during the individual's development.

Acknowledgments

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