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Continuous visual control of interception

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ABSTRACT

People generally try to keep their eyes on a moving target that they intend to catch or hit. In the present study we first examined how important it is to do so. We did this by designing two interception tasks that promote different eye movements. In both tasks it was important to be accurate relative to both the moving target and the static environment. We found that performance was more variable in relation to the structure that was not fixated. This suggests that the resolution of visual information that is gathered during the movement is important for continuously improving predictions about critical aspects of the task, such as anticipating where the target will be at some time in the future. If so, variability in performance should increase if the target briefly disappears from view just before being hit, even if the target moves completely predictably. We demonstrate that it does, indicating that new visual information is used to improve precision throughout the movement.

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1. Introduction

In general, people look at objects when they interact with them or intend to interact with them (Horstmann & Hoffmann, 2005; Johansson, Westling, Backstrom, & Flanagan, 2001; Land & Hayhoe, 2001; Mennie, Hayhoe, & Sullivan, 2007; Pelz, Hayhoe, & Loeber, 2001; Rothkopf, Ballard, & Hayhoe, 2007). This is also true when intercepting moving objects (Bahill & LaRitz, 1984; Brenner & Smeets, 2007, 2009; Mrotek & Soechting, 2007; Soechting & Flanders, 2008). However, the extent to which pursuing a target is essential for catching or hitting is not yet clear (Brenner & Smeets, 2010; Dessing, Oostwoud Wijdenes, Peper, & Beek, 2009; Sharp & Whiting, 1974, 1975). There are several reasons why it may be advantageous to keep one's eyes on the target (Wilmot, Wann, & Brown, 2006). The

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most obvious one is that doing so ensures that the resolution with which the visual information is acquired is maximal. We here evaluate whether this is the main reason for doing so.

Keeping the fovea directed at the ball ensures that one has access to the highest possible spatial resolution when localising the ball and judging its trajectory. This is probably particularly important if the ball's trajectory is not completely predictable, so that one must constantly consider whether one needs to adjust one's movement. If it is likely that the movement will have to be adjusted at a certain moment, such as occurs when one can anticipate that the ball will bounce off an uneven surface, people make sure to have their eyes on the ball at that moment (Land & McLeod, 2000). If the trajectory is predictable, it is probably less important to have the highest possible spatial resolution throughout the movement. Indeed, for reasonably predictable trajectories of a ball, it is not even necessary to see the entire trajectory in order to catch the ball (e.g., López-Moliner, Brenner, Louw, & Smeets, 2010; Whiting & Sharp, 1974). The extent to which vision at various moments is essential for successful interception is widely debated (e.g., Bootsma & van Wieringen, 1990; Dubrowski, Lam, & Carnahan, 2000; Marinovic, Plooy, & Tresilian, 2009; Müller & Abernethy, 2006; Sharp & Whiting, 1974; Teixeira, Chua, Nagelkerke, & Franks, 2006; van Soest et al., 2010; Young & Zelaznik, 1992). If there are moments at which visual information is not very important, it is also unlikely to be necessary to pursue the target at such moments.

We recently proposed that even for completely predictable target motion it is advantageous to keep one's eyes on the target throughout the movement (rather than only at the start), because if one maintains a high visual resolution, the accuracy with which one can predict where the target will be when one reaches it will keep increasing as the movement progresses (Brenner & Smeets, 2009). Directing one's gaze towards the target early in the movement helps ensure that the movement starts off more or less correctly, so that only modest adjustments are later needed, and keeping one's eyes on the target ensures that such modest adjustments are based on increasingly accurate estimates as the duration of the prediction decreases because the hand approaches the target. The first experiment of this study was designed to directly examine to what extent pursuing the target with one's eyes until one hits it is beneficial when intercepting targets that move in a completely predictable manner.

2. Experiment 1: eye movements

Virtual targets moved from left to right at a constant velocity across a surface. They were to be hit with a stylus. The stylus was initially at a starting point near the subject's body. When intercepting such targets, subjects tend to pursue the target with their eyes for most of the time (Brenner & Smeets, 2007, 2009). Even if subjects are explicitly instructed to fixate a static point, they cannot avoid following the moving target with their eyes just before hitting it (Brenner & Smeets, 2010). Moreover, even if we could train subjects not to pursue the target, adding such a second task could influence subjects' precision (Wilmot et al., 2006). We therefore wanted to influence the eye movements without any explicit instructions or constraints. To do so we compared interception in two slightly different tasks that required a similar spatial and temporal accuracy, but were designed to give rise to different eye movements: hitting a small target into a gap and hitting a target through a small gap.

We reasoned that subjects would want to direct their gaze towards the smallest relevant structure, which would be the small target when the task was to hit the moving target into the larger gap, but would be the small gap when the task was to hit through the static gap just as the larger target passes behind the gap. In these tasks the smallest structure was also the first one that the subject's hand encounters, which is also likely to encourage them to direct their gaze towards it. We expect this to have consequences for the precision of their hand movements, which we expect to be highest in relation to the structure that they are looking at.

2.1. Methods

2.1.1. Equipment

The setup and tasks are shown schematically in Fig. 1. Images were projected at 85 Hz and a resolution of 1024 by 768 pixels onto a back-projection screen that was 20 cm above a half-silvered

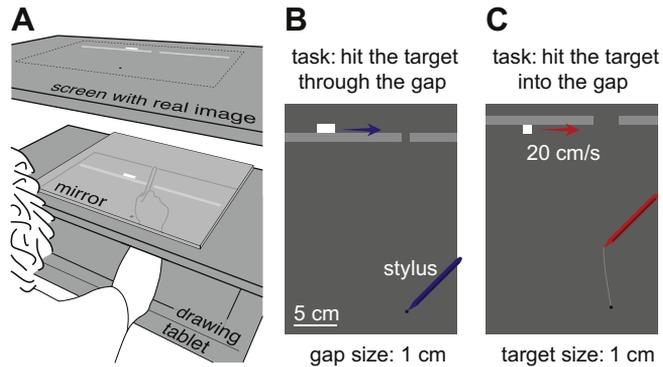


Fig. 1. Subjects had to intercept a moving target by sliding a stylus across the surface of a drawing tablet. The starting point, the target and a grey bar with a gap in it, were projected on a screen above a half-silvered mirror (A). The distance between the screen and the mirror was identical to that between the tablet and the mirror, so that the images appeared to be on the tablet. Subjects could see their hand through the mirror. The task was either to hit the target as it passed behind the gap, without hitting the bar (B), or to hit the target when it was in front of the gap (C). In both tasks it took the target 100 ms to cross the gap, there were two possible gap positions (left or right; 1 cm apart) and the target was midway across the gap at one of two possible times after it appeared (600 or 650 ms). The target always moved to the right at 20 cm/s.

mirror. There was a large (WACOM A2) drawing tablet 20 cm below the mirror, positioned so that it coincided precisely with the apparent position of the screen as seen through the mirror. Subjects intercepted the virtual targets by moving a stylus across the drawing tablet. The tablet determined the stylus' position at 200 Hz. Lamps between the half-silvered mirror and the drawing tablet (not shown) ensured that subjects could clearly see the stylus and their hand as well as the target. The setup was calibrated by having the experimenter align the tip of the stylus with small disks presented on the screen, allowing us to later present images of any desired dimensions at any desired position on the surface of the drawing tablet.

Movements of the subjects' eyes were recorded at 250 Hz using an Eyelink II (SR Research Ltd., Canada). Eye orientation was calibrated by having subjects follow jumping discs with their eyes before the session. We related distances between the horizontal and vertical positions on the screen to changes in the pupil positions reported by the Eyelink to later be able to determine the velocity of the eye. Head movements were not accounted for when calculating pursuit gain. Whenever we report where subjects were looking (rather than the eye's velocity) we account for the initial orientation of the head and for any drift in the Eyelink data on the basis of the subject's fixation of the starting point just before the trial (see Section 2.1.5).

Delays within our setup were accounted for, both when analysing the data and when providing feedback to the subjects. We considered the actual time at which the images were presented (considering rendering delays and delays in the projector) and the actual time at which the stylus was at a given position (considering the time it takes the tablet to measure the position and convey it to the computer) for everything except during the short interval just after the stylus hit the target. Since the interception was only registered 62 ms after it had occurred, the target moved on for 5 frames before the appropriate feedback could be presented. Subjects did not notice this, probably at least partly because the hand occluded the target at that moment.

2.1.2. Tasks and conditions

The two tasks were to hit a target as it passed behind a gap in a grey bar, and to hit a target into a gap in a bar (Fig. 1). The white target and the grey bar both always extended 1 cm in depth (the irrelevant dimension). The target always moved to the right at 20 cm/s. The path of the center of the target was 20 cm further from the subject than the center of the 5 mm diameter circular starting position. The bar was either closer than the target, so that the target moved just behind the bar, or beyond the target, so that the target moved just in front of the bar. Although the target and the bar both

extended 1 cm in depth, the analysis only considered the near surface of the target and the center of the bar. Thus we did not consider a target to be hit if the stylus entered it from the side, or a bar to be hit if the stylus grazed its corner but was between it and the other bar by the time the stylus was half way through the gap.

Within each task there were 4 conditions. The gap was either 5 mm to the left or 5 mm to the right of the center (where the bar was closest to the starting position). The moving target appeared 12 or 13 cm to the left of the gap, so that it reached the gap after either 600 or 650 ms (we will refer to this time as the 'urgency'). The different positions of the gap and the different urgencies were introduced so that visual information about the target's position and motion had to be used to perform adequately, while simply reproducing a stereotyped movement when the target appeared would lead to systematic errors.

When the task was to hit the target as it passed behind the gap, the gap was 1 cm wide and the target extended 2 cm laterally. Subjects were clearly instructed that they should hit the target without hitting the bar. If they hit the target, it shifted 1 cm away from the bar and stopped moving, and subjects heard a sound. If they missed the target, it continued moving. If they hit the bar, it turned red and the target continued moving (even if it had been hit). When the task was to hit the target into the gap, the target was a 1 cm square and the gap was 3 cm wide. Subjects had to hit the target while it was completely in front of the gap. If they did so successfully, it moved into the gap and stopped there, and they heard a sound. If they missed the target, it continued moving. If they hit the target while any part of it was in front of the bar, the bar turned red and the target continued moving along its original path.

In both tasks subjects had about 100 ms to successfully hit the target and had to hit within 1 cm, but in the first task this 1 cm was static while in the second it was moving. Assuming that subjects would try to optimize their performance by directing their eyes to where the highest resolution is needed, we predicted that this difference would give rise to different eye movements. Thus comparing these two tasks should let us compare performance for different eye movements without us having to explicitly constrain subjects' eye movements.

2.1.3. *Subjects and procedure*

Sixteen subjects took part in the experiment. They could adjust the height and position of the chair that they sat on as they pleased, to ensure that they could move comfortably, but could not move their head very far forward because of the mirror. The two tasks were performed in separate blocks of trials within a single session. Half of the subjects started with the task of hitting through the gap, while the other half started with the task of hitting into the gap. Each block started with 20 practice trials (5 for each condition) directly followed by the 100 trials that were later analysed (25 for each condition). Within each block the conditions were presented in random order. Subjects could rest at any moment by not placing the stylus at the starting point. As soon as they did place the stylus at the starting point a new target appeared. The stylus was considered to have been placed at the starting point if its tip was within the 5 mm diameter of the starting point and moved by less than 1 mm in 250 ms.

2.1.4. *Analysis*

Since subjects had to place the stylus exactly on a small disc (the starting point) to start the experiment, they had to direct their gaze towards that position before the trial. However, since the target and the bar with the gap only appeared after they had kept the stylus there for 250 ms, subjects often made a vertical saccade towards the region in which the target or gap will appear before they actually appeared. We were mainly interested in what the eyes were doing while the stylus was moving towards the target. We determined the horizontal eye velocity from the average displacement of the two eyes. The mean horizontal eye velocity during the last 200 ms before the hit was determined for each trial. The median of these velocities was determined for each subject and task (using the median eliminated the need to consider occasional saccades during that period).

In our analysis of the hand movements we only consider three times: the time the target (and bar with gap) appeared, the time the hand started to move, and the time of the hit. The hand is considered to have started moving when it moved 5 mm from where it was when the target appeared. The time at which the stylus reached the path of the near edge of the target is considered to be the time of the hit, even if the stylus did not actually hit the target. Linear interpolation was used to achieve a higher

resolution than provided by the sampling and presentation rates. The reaction time is the interval between when the target appears and when the hand starts to move. The movement time is the interval between when the hand starts to move and the time of the hit.

We evaluated whether subjects managed to hit the targets, but our main interest was in the variability (and systematic errors) across repetitions of the same kind of trials. When determining these measures we made no distinction between hits and misses. For each subject, task and condition (gap on left or right; target aligned with the gap after 600 or 650 ms) we determined the mean and standard deviation of 3 measures: the position of the target at the time of the hit, the position of the stylus at the time of the hit, and the position of the stylus relative to the target at the time of the hit. Our main interest is in possible correlations (across subjects and tasks) between the standard deviations in these measures and eye velocity. We predict that pursuing the target with one's eyes will increase the variability in the stylus' position (relative to the static surrounding) at the time of the hit, but will decrease the variability in its position relative to the target. To examine whether this is so we will correlate the subjects' differences in pursuit gain between the two tasks with the differences in the variability of the position of the stylus on the tablet at the time of the hit and with differences in the variability of the stylus' position relative to the target at the time of the hit.

2.2. Results

Of the 3200 trials (16 subjects; 2 tasks; 4 conditions; 25 trials each), 19 could not be analysed because the subject failed to move the stylus or lifted it off the tablet. Fig. 2 shows one subject's horizontal eye movements and stylus velocities for five consecutive trials of each task. When the task was to hit the target into the gap, this subject made a leftward saccade towards the target about 250 ms after the target appeared, and then pursued the target until it was hit (Fig. 2A). Thus the eyes were pursuing the target throughout the stylus movement (Fig. 2C). When the task was to hit the target through the gap, she made a smaller saccade, presumably towards the gap, about 250 ms after the target and gap appeared (Fig. 2B). The stronger tendency to pursue the target with the eyes when hitting into the gap was quite consistent across subjects, as was the higher velocity of the stylus for that task (see below). Comparing Figs. 2B and D we see additional velocity peaks when hitting into the gap. Subjects had periods during which they moved in different ways, but the additional peaks in the velocity profile are not characteristic for a certain task, because across subjects there were about as many trials with additional peaks for both the tasks.

Subjects hit more targets when the task was to hit through the gap (Fig. 3A) than when it was to hit into the gap (Fig. 3B; paired t -test: $t(15) = 2.6, p = .02$). In particular, subjects missed almost half the moving, 1 cm wide targets when trying to hit them into the gap (*missed moving target* and *place and time wrong* sectors in Fig. 3B), whereas they only missed the 1 cm wide gap on about a fifth of the trials when hitting through the gap (*missed gap* and *place and time wrong* sectors in Fig. 3A). As expected, subjects were more inclined to pursue the target with their eyes when hitting a small moving target into a large gap, than when hitting a large target through a small static gap (Fig. 3C; paired t -test: $t(15) = 5.5, p < .0001$). The average pursuit gain during the last 200 ms before the hit was about 0.2 when hitting through the gap and 0.7 when hitting into the gap.

Table 1 and Fig. 4 provide average values of various measures. A repeated measures analysis of variance (with factors task, urgency and gap position) on subjects' median reaction times revealed that reaction times were significantly shorter when there was more urgency ($p < .001$) and when the gap was on the right ($p = .04$), and that there was a significant interaction between urgency and gap position ($p = .03$). A similar analysis on the median movement times revealed that movement times were significantly shorter when there was more urgency ($p < .001$), when the gap was on the right ($p = .006$) and when hitting into the gap ($p = .03$), and a significant interaction between task and urgency ($p = .04$). Similar repeated measures analyses of variance revealed that the standard deviation in the *position of the target when hit* and in the *position of the target relative to the stylus at the time of the hit* were smaller when hitting into the gap than when hitting through the gap ($p = .04$ and $p < .0001$, respectively), whereas the standard deviation in the *position of the stylus at the time of the hit* was smaller when hitting through the gap ($p < .0001$). The only other significant effect for the three

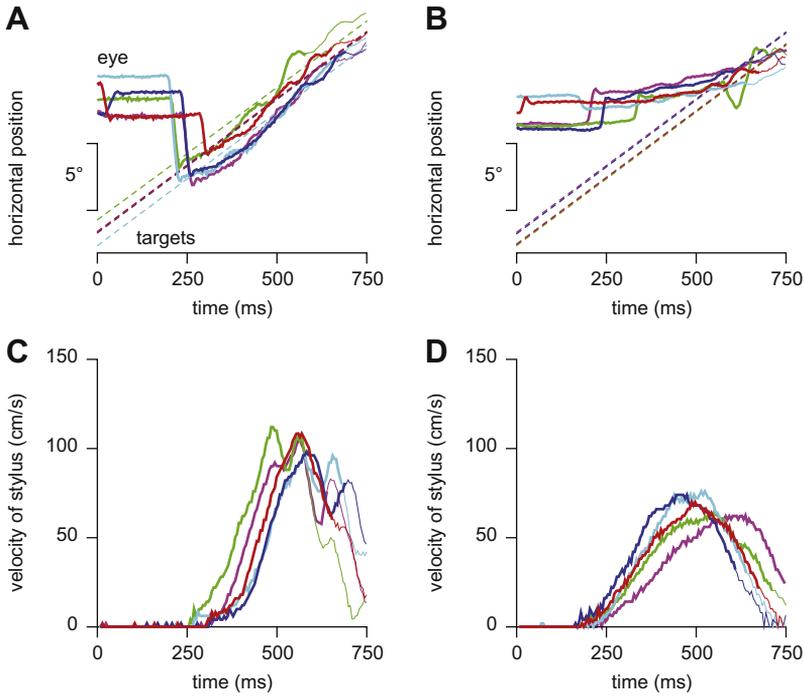


Fig. 2. Eye and stylus movements during one subject's 40–44th trial for each task. Time is measured from the moment the target appears. Upwards is to the right in A and B. The colors indicate the successive trials. The thin parts of the traces show how the movement continues after the stylus has reached the target. When hitting the target into the gap, the subject made leftward (downward in the figure) saccades to the targets after about 250 ms, and then pursued the targets (A). The targets' paths and the positions of the gaps varied across trials (4 conditions). When hitting the target through the gap (B), the subject made smaller saccades, presumably towards the gap (B). When hitting into the gap (C), the stylus started moving a bit later and moved a bit faster than when hitting through the gap (D).

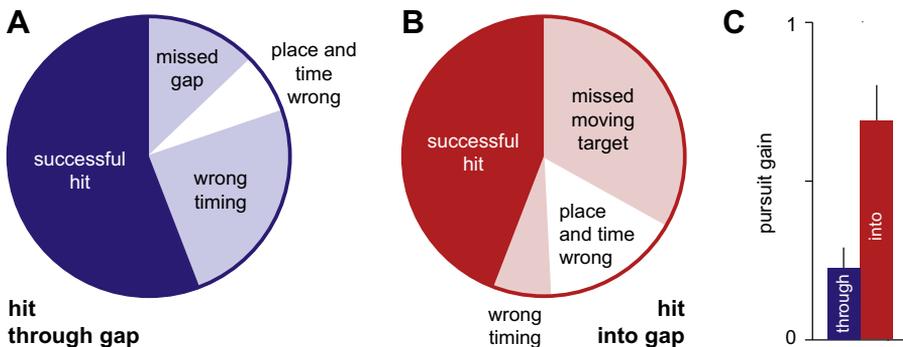


Fig. 3. Overall performance. (A) Fraction of trials in which the target was hit through the gap. Trials were unsuccessful if the stylus failed to pass through the gap (*missed gap* or *place and time wrong*) or if it reached the target's path too soon or too late so that it missed the target (*wrong timing* or *place and time wrong*). (B) Fraction of trials in which the target was hit into the gap. Trials were unsuccessful if the stylus missed the moving target (*missed moving target* or *place and time wrong*) or if it reached the target's path too soon or too late so that the target was still partly in front of the bar (*wrong timing* or *place and time wrong*). (C) Pursuit gain during the last 200 ms before the hit (mean and standard error across the sixteen subjects' median horizontal eye movements) when hitting through the gap (blue) and into the gap (red). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

The main parameters for each task, gap position and time for the target to reach the gap. Reaction and movement times are means of the individual subjects' median values. Systematic errors and standard deviations are means of the individual subjects' means and standard deviations. Positive errors are when the target has moved too far (position of target) or the stylus is too far to the right (other two measures).

Task	Hit through gap				Hit into gap			
	Left		Right		Left		Right	
Gap position								
Time for target to reach gap	600	650	600	650	600	650	600	650
Reaction time (ms)	272	283	275	280	295	312	292	299
Movement time (ms)	358	368	355	364	324	338	312	335
<i>Position of target</i>								
Systematic error (mm)	5.6	-0.3	5.0	-0.8	3.7	-0.7	0.6	-3.4
Standard deviation (mm)	7.3	7.3	7.3	7.9	6.4	6.8	6.9	6.8
<i>Position of stylus</i>								
Systematic error (mm)	1.9	1.4	0.3	0.1	5.6	3.4	2.3	-0.4
Standard deviation (mm)	3.2	3.1	3.0	3.0	5.0	5.4	5.5	5.1
<i>Relative position</i>								
Systematic error (mm)	1.9	4.0	1.8	3.0	-3.7	1.7	-4.8	0.9
Standard deviation (mm)	7.3	7.3	7.5	7.6	5.4	5.5	5.8	5.9

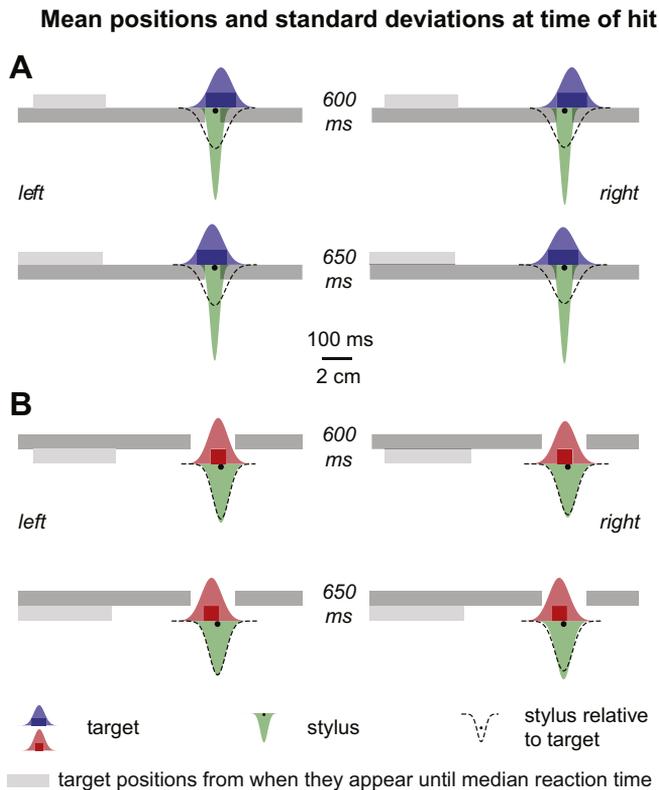


Fig. 4. Average systematic and variable errors (positions and widths of the Gaussian distributions are drawn to scale). The separate panels show performance for each of the four conditions (gap at left or right; to be hit after 600 or 650 ms) of each task ((A) hit the target through the gap; (B) hit the target into the gap). The light grey bars indicate the target's motion during the reaction time.

measures of variability was that the standard deviation in the *position of the stylus relative to the target* was smaller when the gap was on the left ($p = .03$).

Both pursuit gain and the various measures of precision differed considerably between subjects. Fig. 5 shows how the three standard deviations in positions at the time of the hit depend on the pursuit gain (all measures averaged across gap positions and urgencies; separate symbols for each subject and task). The standard deviation in the target's position (Fig. 5A) and in the stylus' position relative to the target (Fig. 5C) appear to decrease with increasing pursuit gain, whereas the standard deviation in the stylus' position in space appears to increase with increasing pursuit gain (Fig. 5B). This is consistent with the proposed role of pursuit in precision, but these differences confound influences of pursuit with differences between subjects and tasks. We therefore also compared individual subjects' differences between standard deviations and median pursuit gains in the two tasks. If the difference in pursuit is responsible for the difference in precision between the tasks, we expect the differences between individual subjects' standard deviations in the two tasks to depend on how differently subjects pursue in the two tasks.

For every subject we subtracted the values when hitting through the gap from those when hitting into the gap. The points in panels D–F of Fig. 5 show how the standard deviation differs in relation to how pursuit gain differs across subjects for the two tasks. The distributions of the points in panels D–F confirm that the effects that we saw in panels A to C are a consequence of the eye movements, and not of differences between subjects or tasks. When there was little difference in pursuit gain (values close to zero on the horizontal axis) there was little difference between the standard deviations (values close to zero on the vertical axis). As the difference in gain increases, so does the difference between the standard deviations. This is evident in a negative correlation between *the difference in pursuit gain*

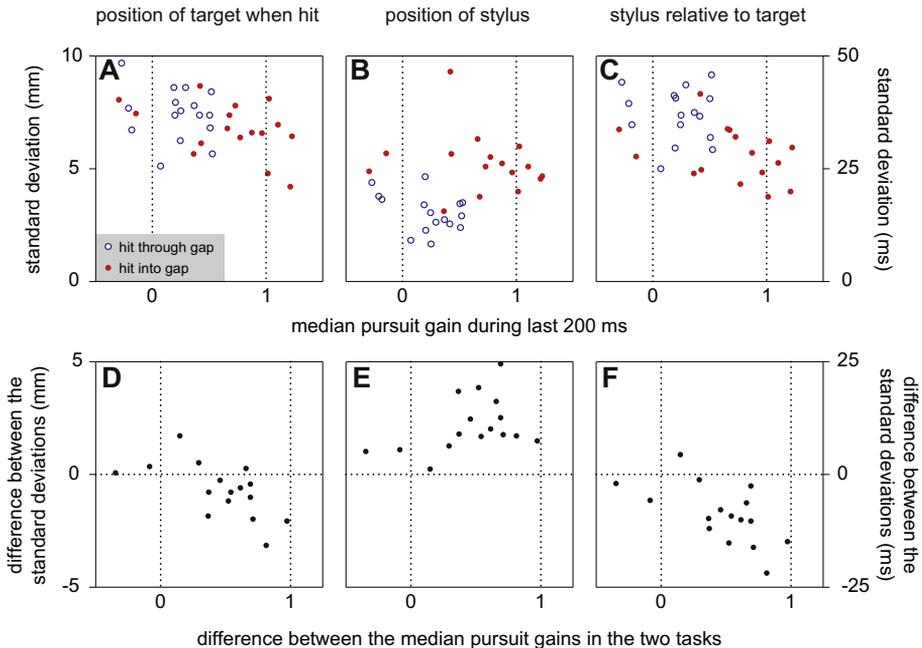


Fig. 5. Relationship between individual subjects' eye movements and three measures of their precision: variability in the position of the target at the time of the hit (A,D), in the position of the stylus at the time of the hit (B,E), and in the position of the stylus relative to the target at the time of the hit (C,F). (A–C) Standard deviations (averaged across conditions) in the positions when hitting the target through the gap (open blue symbols) or into the gap (solid red symbols) as a function of the median horizontal pursuit gain during the last 200 ms before the hit. (D–F) The difference between each subject's data for the two tasks: standard deviations and pursuit gain when hitting through the gap were subtracted from the corresponding values when hitting into the gap.

and the difference in the standard deviation in both target position ($r = -.62$; $p < .01$; Fig. 5D) and the stylus' position relative to the target ($r = -.62$; $p < .01$; Fig. 5F). The difference in the standard deviation of the stylus' position in space appears to increase when the difference in pursuit gain increases, but the positive correlation is not statistically significant ($r = .41$; $p = .12$; Fig. 5E).

There are also systematic errors in the position of the target at the time of the hit. Fig. 6 summarizes such systematic errors by comparing them with what one would expect if subjects either always hit when the target reaches a fixed position in space (independent of where the gap is on that trial) or always hit a certain time after the target appeared (independent of when it reached the gap on that trial). When hitting through the gap subjects appear to largely base their timing on some kind of average of the time that it took the target to reach the gap on previous trials: less than half of the 50 ms difference in urgency between trials is compensated for. When hitting into the gap subjects rely less, but still considerably, on such an average. When hitting into the gap they also tend to hit when the target reaches a fixed position in space (approximately at the overall average gap position). This is not because they fail to judge the gap position until the stylus is close to the gap when pursuing the target, because the mean direction in which the hand started moving (the first cm of displacement) depended on the position of the gap: a median difference across subjects of 1.4° for a 2.9° difference in the direction to the gap (paired t -test: $t(15) = 3.4$, $p = .004$; when hitting through the gap the median difference was 1.6° ; $t(15) = 6.3$, $p < .0001$).

2.3. Discussion

As we expected, pursuit gain was generally higher when hitting a small moving target than when hitting through a small static gap. Thus our assumption that subjects would tend to look towards the smallest object was correct. However, there was considerable variability in pursuit gain across subjects. Some of this variability may be due to the fact that we measured eye orientation relative to the head. We did so because measuring head movements is cumbersome in our setup, and in previous studies we found that head movements contributed quite little to the overall shifts in gaze (Brenner & Smeets, 2007, 2009). Nevertheless we think that the consistently negative pursuit gain of two of our subjects must be due to head movements (translation as well as rotation) combined with a stable gaze.

Fig. 3 shows that when hitting through the gap, subjects were about as likely to miss the gap when they got the timing right (missed on 19% of such trials) as when they got the timing wrong (missed on 22% of such trials), but when hitting into the gap, subjects were clearly less likely to miss the target

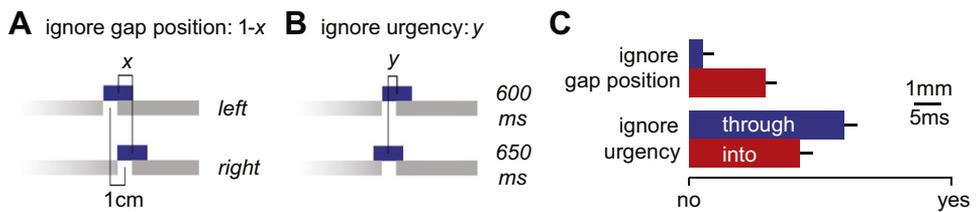


Fig. 6. Interpretation of systematic errors. (A) If subjects would ignore the position of the gap altogether they would (on average) reach the target's path when the target was at the same position when the gap was on the left as when it was on the right ($x = 0$ cm). If they fully considered the gap position they would reach the path when the target was 1 cm further to the right when the gap was 1 cm further to the right ($x = 1$ cm). The extent to which subjects ignored the gap is therefore $1 - x$. (B) Similarly, subjects would make systematic errors if they hit the targets a fixed time after the targets appeared ($y = 1$ cm, because the target moves 1 cm in 50 ms) rather than hitting targets 50 ms later if they reach the gap after 650 ms than if they reach the gap after 600 ms (so that $y = 0$). The extent to which subjects ignored the urgency is therefore y (if y is expressed in cm, or $y/50$ if y is expressed in ms). (C) Bar lengths (with standard errors across subjects) indicate the extent to which subjects tended to hit the target when it was at a fixed position in space (ignoring the fact that the gap could be on the left or the right) and the extent to which they hit a fixed time after the target appeared (ignoring the fact that it could take either 600 or 650 ms for the target to be aligned with the gap). The scale runs from no systematic error (*no*) to relying completely on the average value (*yes*). Blue bars: hit the target through the gap. Red bars: hit the target into the gap. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

when they got the timing right (missed on 43% of such trials) than when they got the timing wrong (missed on 70% of such trials). Both the finding that subjects failed to hit the 1 cm wide moving target more often than they failed to pass through the 1 cm wide static gap, and the finding that subjects missed a considerably larger proportion of the 1 cm wide targets when they got the timing wrong, can be understood if the hand is controlled within a static reference frame (rather than one that moves with the target or the eye) so that getting the timing wrong influences the accuracy relative to the moving target but not relative to the static gap.

It appears that getting the timing right is a bit harder when hitting through the gap (32% errors) than when hitting into the gap (23% errors; *wrong timing* and *place and time wrong* sectors of Fig. 3A and B). This suggests that pursuing the target improves the precision in timing the hit as well as maximizing the spatial resolution with which the moving target's position can be judged. In accordance with this interpretation, the standard deviation in the position of the target at the time of the hit decreased with increasing pursuit gain (Fig. 5D). This is not a trivial consequence of a better spatial resolution, because when fixating the small gap subjects have to judge the motion of the target as its image shifts towards the fovea, and when pursuing the small target they have to judge the position of the gap as its image shifts towards the fovea, so in terms of retinal signals the tasks are approximately equivalent. The equivalence is not complete because the actual retinal eccentricities and speeds depend on the precise direction of gaze. Moreover the retinal images of the gap when pursuing the target and of the target when fixating the gap are on opposite sides of fixation and are moving in opposite directions. Nevertheless, considering the way in which individual subjects' performance depends on pursuit gain (Fig. 5) and the fact that we previously found no difference in performance when hitting targets moving leftwards and rightwards (Brenner & Smeets, 2007), we consider information related to the pursuit eye movement to most likely be responsible for the improved precision in timing the hit when pursuing the target. We attribute the difference to being able to time the hit better when pursuing the target because oculomotor information helps judge the moving target's position and velocity (Wilmot et al., 2006). If this is true, then people probably move their eyes to improve timing estimates as well as to improve the critical spatial resolution.

We found a difference in systematic errors between the two tasks (Fig. 6). When hitting *into* the gap, subjects relied on the position of the gap on previous trials to time their hit. They probably compared an extrapolation from where they were looking based on the target's apparent speed with this remembered position. When hitting *through* the gap they knew where the gap was, because they were fixating it. Instead of relying on its position on previous trials they had an even stronger tendency to hit a fixed time after the target appeared. Presumably, varying the time and place by 50 ms and 1 cm across trials is not enough to make it pointless to rely on information from previous trials. The fact that our subjects relied on such information implies that our measures of precision do not only depend on variability in sensory and motor processes, but also on expectations based on previous trials. If our subjects' expectations did not change much between trials, then relying on expectations could have increased precision (by supplementing sensory information), but if every trial influenced the expectation for the next trial substantially (see de Lussanet, Smeets, & Brenner, 2001), the expectations themselves will have varied a lot so that relying on them could even have decreased precision.

In the introduction we anticipated that differences in pursuit gain would lead to differences in precision because keeping one's eyes on a structure throughout the movement allows one to continuously control the movement relative to that structure. The results in Fig. 5 are consistent with this explanation: precision relative to the moving target increases (smaller standard deviations) and precision relative to the static target decreases (larger standard deviations) when the eyes follow the moving target (higher pursuit gain). Attributing the improved timing (smaller standard deviation in the position of the target relative to the gap) when pursuing the target to the additional oculomotor information during pursuit is also consistent with such continuous control.

In order to pursue the moving target subjects initially direct their eyes away from the gap, towards where the target has appeared (Fig. 2A). By doing so they increase the visual resolution near the target and decrease the visual resolution near the gap. Thus the data of Experiment 1 could also be accounted for without continuous control and improved judgments of the target's motion during pursuit. If the visual resolution at the moment that the stylus starts to move is critical, then the decrease in precision with increasing pursuit gain in Fig. 5B may be due to the larger eccentricity of the gap when initially

directing one's eyes at the target in order to pursue it. The increase in precision with respect to the target with increasing pursuit gain (Fig. 6A and C) may be due to the smaller eccentricity of the target when initially directing one's eyes closer to it. To check whether the direction of gaze is really important throughout the stylus' movement (to control the ongoing movement), and not just near its onset (to plan the movement) and at the time of the hit (to obtain reliable feedback), we explicitly tested this in a second experiment.

3. Experiment 2: continuous estimates

One reason to favor an interpretation in terms of continuous control is that the resolutions of visual estimates of target position (van Beers, Sittig, & Denier van der Gon, 1998) and target speed (de Bruyn & Orban, 1988) are too poor to predict the time and place of interception at movement onset (Brenner & Smeets, 2009). However, this reasoning would not apply if performance were based directly on relative positions (Lee, Georgopoulos, Clark, Craig, & Port, 2001; but see Brenner & Smeets, 2003; Brouwer, Brenner, & Smeets, 2003), or if the speed of the pursued targets were judged more precisely when the hand starts to move than one would expect from comparing sequentially presented 100 ms intervals of retinal motion (the stimuli used in de Bruyn & Orban, 1988), or if several sources of information were combined to provide better estimates than any could provide on its own (Ernst & Bühlhoff, 2004). It is easy to be mistaken about what information is used for a given task (see de Grave, Brenner, & Smeets, 2004; Smeets & Brenner, 2008), so the second experiment was designed to directly examine whether it is important to update the estimates that guide one's movements on the basis of new visual (and possibly oculomotor) information throughout the movement.

To evaluate the importance of providing visual information during the last stages of a movement we removed such information for various durations and examined how this affected performance. The task was to hit targets that moved at a constant velocity into a gap. The target sometimes disappeared briefly, just before it reached the gap. This was achieved by giving a section of the background exactly the same color as the target so that the target was not visible when it was within that section (Fig. 7). The target was partly visible as it entered and left the section. By varying the size of the section we could remove information about the position and motion of the target for different amounts of time while the target still seemed to move smoothly. Subjects could anticipate when the target would disappear from the beginning of each trial, so they could plan their movements in accordance with the time that the information will be available.

If it is important to continuously consider new visual information during the movement, we expect the precision to decrease if the target disappears shortly before it is hit. In the Appendix we describe a simple model that we developed to get a rough idea of the extent to which we can expect the precision in the stylus' position relative to the target and in the target's position relative to the gap to improve during the movement. The model relies on people updating their estimate of when the target will reach the gap throughout the movement. The difference between the improved estimate and the original one is used to guide the moving stylus to where it will hit the target, rather than to adjust the stylus' speed to ensure that it hits the target when it is aligned with the gap.

3.1. Methods

The same equipment was used as in Experiment 1. The task was to hit the target into a gap. All details were identical to those for the same task in the first experiment unless mentioned otherwise. The main difference was that there was a static rectangle of the same color as the target (white) immediately to the left of the gap on some trials (Fig. 7). The left edge of the gap in the bar, the rectangle's right edge and the starting point were aligned laterally. The rectangle extended 3 cm from the bar in depth. The target was 2 cm wide. We did not measure eye movements.

3.1.1. Conditions

There were 24 conditions. Targets moved at one of three velocities: 20, 30 and 40 cm/s. Their starting positions were varied to ensure that the center of the target would reach the left edge of the gap

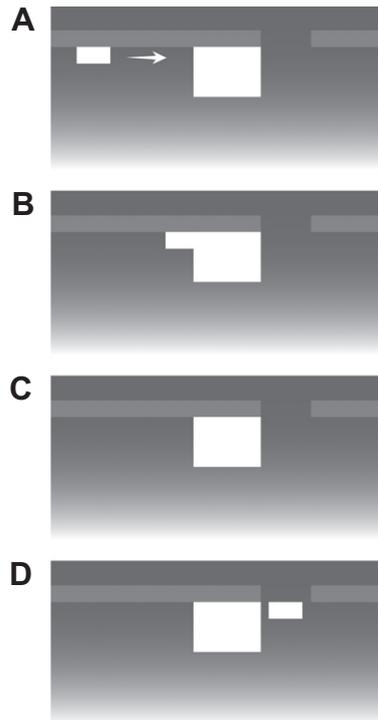


Fig. 7. The target moves rightwards at a constant velocity as in the first experiment (A), but on some trials it has to pass a rectangle before reaching the gap. The target and rectangle are both white, so one cannot see the border between them when the target and rectangle overlap (B), and no new information about the target is provided from when they fully overlap (C) until the target reappears at the other side (D). One could also consider this as the target moving behind the rectangle.

after one of two intervals: 650 or 750 ms. We will refer to this as the urgency despite the slightly different definition (in Experiment 1 we used the time until the target reached the *center* of the gap; here we were limited by not wanting the rectangle to block the gap and also wanting to more or less equate the times at which the targets disappeared). The gap's width depended on the target's velocity so that subjects always had a 50 ms interval during which they could successfully hit the target into the gap. For each velocity and urgency there were four conditions that only differed in the presence and size of the rectangle on the target's path. There could either be no rectangle, a 2 cm wide rectangle (so that some part of the target was always visible), or a rectangle with a width that makes the target completely invisible for 100 or 200 ms. The width that makes the target completely invisible for 100 or 200 ms depends on the target's speed: for a target moving at 30 cm/s that is completely invisible for 200 ms, the rectangle would be 8 cm wide.

3.1.2. Subjects and procedure

Three subjects took part in the experiment. Each took part in six sessions. Each session started with 30 practice trials (5 for each velocity and urgency; no white rectangle), directly followed by the 240 trials that were later analyzed (10 for each condition). The latter trials were presented in random order.

3.1.3. Analysis

Performance was clearly worse for the first session, so we did not include the first session in the further analysis. The data of the remaining five sessions were combined (excluding the practice trials) to give 50 trials per subject and condition. For each subject we determined the number of trials in

which they successfully hit the target into the gap, the median reaction and movement times, and the systematic and variable errors in the position of the target at the time of the hit and in the position of the stylus relative to the target at the time of the hit. These parameters were determined in the same manner as in the first experiment. On the basis of the results of the first experiment we could expect to see some systematic biases, but our main interest is in the variability. Since we had many conditions and few subjects, we evaluated performance for which we could clearly predict the influence of the condition with rank correlation tests (after averaging across subjects). In the figures we also present the variability between subjects.

3.2. Results

Except for removing the data of each subject's first session, no trials were excluded from the analysis. As one might expect, subjects were more successful at hitting slower targets into the gap (Fig. 8A). More surprisingly, subjects were also more successful when there was *less* time between when the target appeared and when it was aligned with the gap (650 rather than 750 ms). When there was only 650 ms until the target reached the gap, subjects started moving about 13 ms earlier (Fig. 8B) and moved faster (movement time was about 53 ms shorter) than when they had 100 ms longer to reach the target. Subjects also started moving later (Fig. 8B) and moved faster if the target was moving faster (average movement times of 433, 418 and 401 ms for targets moving at 20, 30 and 40 cm/s, respectively). When there was 750 ms until the target reached the gap, subjects systematically hit too early: they hit further to the front of the target (Fig. 8C) when the target had not yet reached the center of the gap (Fig. 8D).

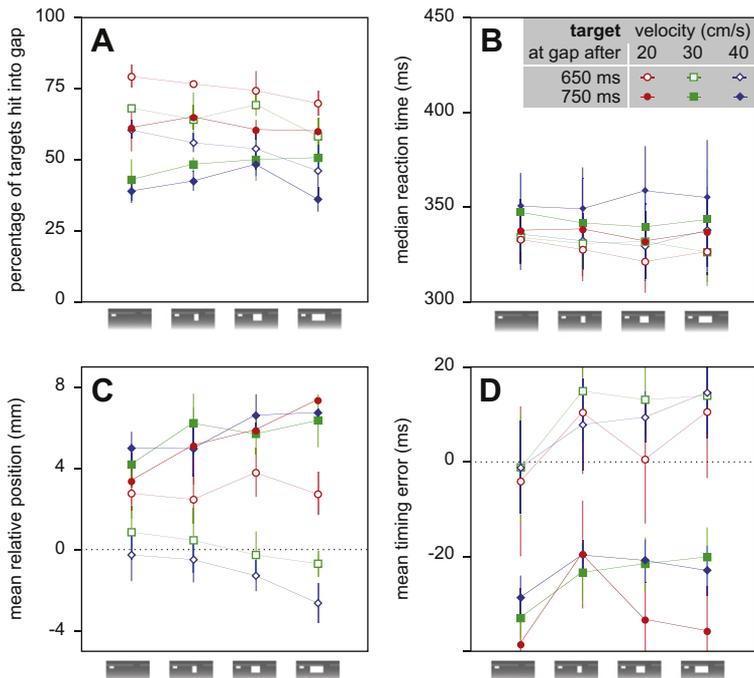


Fig. 8. Average performance in the 24 conditions (with standard errors across the three subjects). The horizontal axis represents rectangle size: no rectangle (continuous vision), a 2 cm wide rectangle (some part of the target always visible), a rectangle that occludes the target completely for 100 ms, and one that does so for 200 ms. The panels show the percentage of targets that were successfully hit into the gap (A), the median reaction time (B), and the mean position of the stylus relative to the target (C) and of the target relative to the gap (D) at the moment of the hit.

The systematic timing error hardly depended on the target velocity (Fig. 8D). The approximately 34 ms difference in mean timing error for the different urgencies is consistent with subjects relying for 34% on the average timing on previous trials to time their hits (as in Experiment 1; Fig. 6). The systematic errors in the position of the stylus relative to the target at the time of the hit (Fig. 8C; also see Brouwer, Brenner, & Smeets, 2002) can largely be accounted for by the same systematic timing errors. Unless one varies where one aims to hit the target with the urgency, which one is unlikely to do because the gap was always at the same place, hitting targets systematically too early (negative values in Fig. 8D) means that one hits ahead of the target (positive values in Fig. 8C).

A timing difference of 34 ms corresponds with 7, 10 and 14 mm for targets moving at 20, 30 and 40 cm/s. That the difference between the spatial errors for targets reaching the gap at different times (separations between open and solid symbols of the same color in Fig. 8C) is larger for faster targets is therefore consistent with a temporal origin of the errors. However, the spatial errors are smaller than one would expect for a 34 ms temporal error. They are also smaller the longer the target is visible: the average difference between the open and solid symbols in Fig. 8C depends on the rectangle size (Kendall rank correlation; $\tau = 1$; $p = .04$; one sided test) with more than double the difference for the condition with the largest rectangle than for that with no rectangle. Thus, timing errors are partly compensated for on the basis of new spatial information during the movement. The average difference between the open and solid symbols in Fig. 8D also depends on the duration of target occlusion (Kendall's $\tau = 1$; $p = .04$), but the difference between the two extreme conditions is only about 23%.

The above interpretation of the systematic errors implies that visual information during the last part of the movement is used to reduce spatial errors (and to a lesser extent timing errors). This is consistent with an analysis of the standard deviations in the timing of the hit and of the position of the stylus relative to the target at the time of the hit. The spatial variability clearly increases as more and more of the trajectory is occluded (Fig. 9A). It is also larger for faster targets, as expected if part of the variability has a temporal origin. The temporal variability hardly depends on how much of the trajectory is occluded (Fig. 9B). Fig. 9C and D shows our rough prediction for the data in Fig. 9A and B, based on Eqs. (1) and (2) of the Appendix respectively, and the measured median movement times for each condition (averaged across subjects). For the position of the stylus relative to the target the correlation between the prediction and the data is quite good ($r = .89$; $p < .0001$; Fig. 9E). For the position of the target relative to the gap the overall correspondence is not bad, but the correlation is less impressive ($r = .55$; $p < .01$; Fig. 9F).

The systematic errors suggest that people rely on prior experience as well as on visual information. To determine the extent to which our subjects relied on the *directly preceding* trial, we calculated the difference between the mean timing errors for trials in which the target reached the gap after 650 or 750 ms on the *previous* trial. Values were first calculated for each subject and condition separately and then averaged across subjects and conditions. If the target only reached the gap after 750 ms on the previous trial, subjects hit 7 ms later (paired t -test: $t(2) = 15.8$, $p = .004$) and 1 mm further to the back of the target ($t(2) = 8.2$; $p = .01$) than if it reached the gap after 650 ms on the previous trial. The 7 ms effect of the previous trial is clearly less than the 34 ms difference shown in Fig. 8D, so subjects clearly did not just (or even mainly) rely on the immediately preceding trial. Subjects also hit 5 ms later (and 1 mm further to the back of the target) if the previous target was slow (20 cm/s), than if it moved at one of the other two speeds (only hitting later when the previous target moved at 20 cm/s than when it moved at 30 cm/s was statistically significant; $t(2) = 5.8$; $p = .03$).

3.3. Discussion

Altogether, the subjects' performance suggests that getting the timing right is difficult. Subjects tended to hit targets that reached the gap in 750 ms too early, and to hit ones that appeared 650 ms before they reached the gap too late, which is what one would expect if prior experience influenced their timing judgments. The standard deviation in their timing was about 30 ms (Fig. 9B). The way in which the spatial errors depend on how long the target's path is occluded (Figs. 8C and 9A, and the comparison with the prediction in Fig. 9E) suggests that with no occlusion, initial temporal errors are partly compensated for by continuously updating the anticipated position of the hit on the basis of new visual information. This continues until neuromuscular delays make it impossible to use new

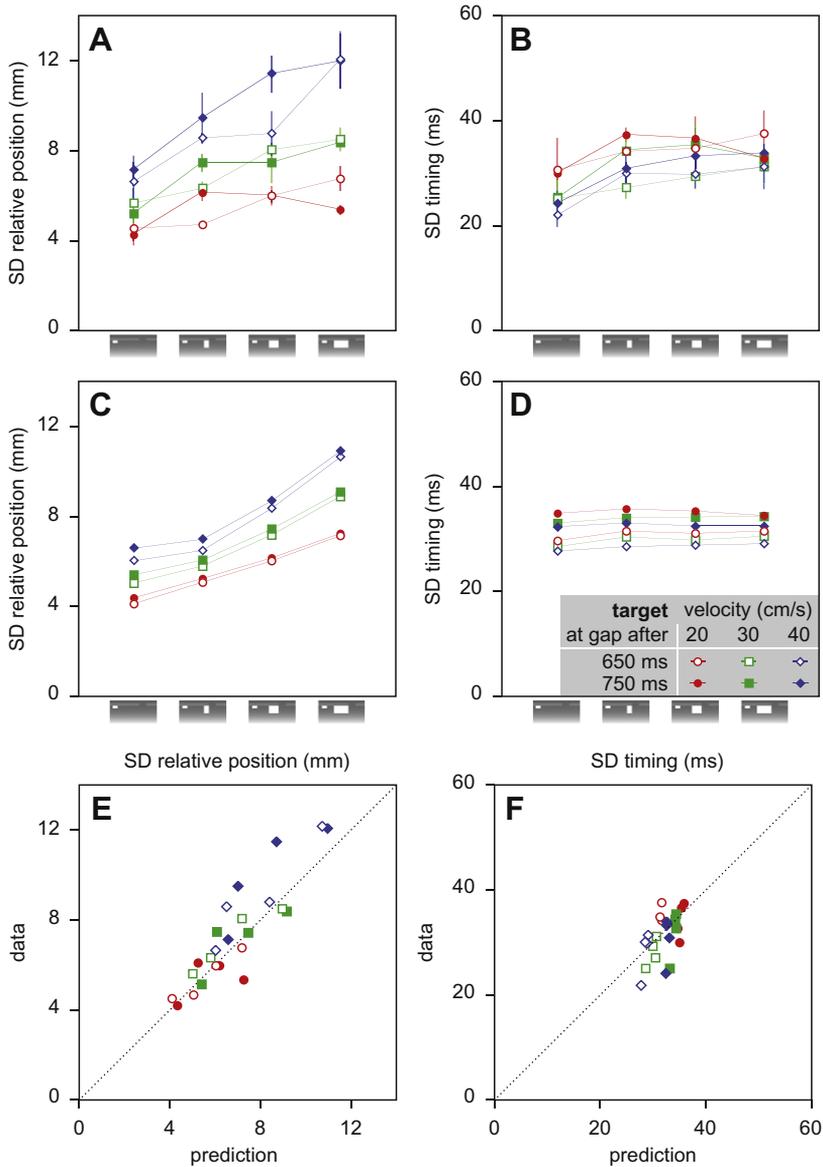


Fig. 9. Standard deviations in the position of the stylus relative to the target (**A,C and E**) and of the target relative to the gap (**B,D and F**) at the moment of the hit. The three subjects' average performance in the 24 conditions (**A,B**), predictions based on Eqs. 1(C) and 2(D) of the Appendix, and the relationship between the standard deviations and the predictions (**E,F**). Further details as in Fig. 8.

visual information. Our analysis suggests that such continuous control is used to guide the hand (stylus) to the target, but not to adjust the timing of the hit. We did not measure eye movements in the second experiment, but pursuit gain is likely to decrease when the target is occluded (Becker & Fuchs, 1985). The fact that subjects appear to hit slightly later when the target is occluded (Fig. 8D) could be related to this, which would be consistent with our earlier claim that oculomotor signals contribute directly to judgments of target velocity. If oculomotor signals contribute directly to performance, then more variability in such signals could also contribute to the poorer performance during occlusion.

Although the predictions in Fig. 9C and D are similar to the data in Fig. 9A and B in many ways, there are some clear discrepancies. One such discrepancy is that we did not predict that subjects would be so much more precise when there was no white rectangle. A possible explanation for the smaller standard deviations when there was no rectangle than when there was a 2 cm wide rectangle is that we underestimated the influence of occluding part of the target. For the predictions we considered the target to be occluded while its front edge was crossing the rectangle. In terms of the available information, we considered that this might even overestimate the effective occlusion, because part of the target was always visible. However, it is possible that the target's position and velocity cannot be estimated with the same precision when its borders are not *all* clearly visible, so the effective occlusion may be longer than we considered for our predictions whenever there was a rectangle. Another possible explanation is that the distance to the gap looks a bit larger with a white rectangle on the path (as in the Oppel-Kundt illusion; e.g., *Deregowski & McGeorge, 2006*), which would also explain why subjects seem to hit a bit later when an occluding rectangle is present (Fig. 8D).

Increasing the size of the white rectangles not only increased the time across which the motion of the target had to be predicted, but it also decreased the time for which the motion of the target was visible before it disappeared. Judgments of velocity become more accurate with increasing presentation duration (*Snowden & Braddick, 1991*; *van Donkelaar, Lee, & Gellman 1992*), but this is unlikely to be responsible for the change in precision because each step in rectangle size corresponded with a change of 100 ms in presentation duration, which is equivalent to the difference in presentation duration between targets that reach the gap after 650 and 750 ms. Thus if decreasing presentation duration were responsible for the increase in the standard deviation with rectangle size in Fig. 9A, the open symbols would systematically be higher than the solid symbols; they would have the same value as the 'next' solid symbol. This is clearly not the case.

Performance in Experiment 2 was generally better when subjects were given less time. This appears to imply that performance is suboptimal, because having access to more information should not be harmful. Why did subjects not simply wait 100 ms longer before starting to move if the target appeared 100 ms earlier? In fact they only waited 13 ms longer (Fig. 8B) and then took 53 ms longer to reach the target, so that they hit it 34 ms earlier with respect to when the target was in front of the gap (Fig. 8D). Perhaps waiting long enough to reliably judge when they should start moving would have made them start too late, especially on trials in which they only had 650 ms to get to the target, so that starting before being certain about the urgency gives a better overall performance (although starting later would have led to better performance on some trials if subjects had been able to identify such trials in time).

If subjects often started moving before they could tell how quickly they should move, they must have adjusted their velocity to the remaining time after having started to move. As in previous studies (e.g., *Brouwer, Brenner, & Smeets, 2000*; *Brouwer, Smeets, & Brenner, 2005*), subjects move faster when hitting faster targets. They were not free to adjust their velocity in response to the speed of the target after having started to move (as in *Brenner, Smeets, & de Lussanet, 1998*), because timing was constrained by the need to reach the target when it was aligned with the gap. Thus they had to have longer reaction times for faster targets (Fig. 8B); which is the opposite of what is found if the task is to respond as quickly as possible; e.g., *Smeets & Brenner, 1994*) in order to move faster to hit them. This suggests that they did have some idea of how quickly they should move before they started to do so, although the longer reaction times for faster targets may also be caused by a larger eccentricity, so no firm conclusions can be drawn on this matter.

4. General discussion

We conclude that new visual information is used throughout interceptive movements to update the estimate of where the target should be hit. The first experiment showed that eye movements are important for this, not only because spatial precision at the target is higher when gaze is directed towards the target, but probably also because pursuing the moving target with the eyes improves the estimate of its velocity. We found systematic differences in performance for the two tasks and between subjects that could be related to the differences in eye movements. The second experiment

showed that the precision of the hit deteriorates if we remove information about the target's position and motion during the last part of the hitting movement. It does so in about the way that we would expect on the basis of an analysis of the resolution of the various components of the task. Together the results imply that our visual estimate of where the target will be at a selected time is continuously improved during the movement, and the movement is adjusted accordingly, and that gaze is directed in a manner that supports this goal (but that the eye and hand are not strictly coupled).

In both experiments subjects clearly relied on expectations based on previous trials as well as on direct visual information. We attribute most systematic errors to expectations about timing (Figs. 5, 8C and 8D; also see de Azevedo Neto & Teixeira, 2009) and about the position of the gap (Fig. 6). Brouwer et al. (2002) interpreted systematic errors when hitting disappearing targets in terms of not being able to account for the target's velocity. Although this seems a very different conclusion, in both cases subjects partially reverted towards average values on previous trials (de Lussanet et al., 2001). Apparently the spatial and temporal resolutions of visual estimates of the relevant parameters are so poor, or the parameters take so long to judge reliably, that it is worthwhile relying on information from previous trials. The current study shows that this is even so in the relatively simple case of lateral motion at a constant velocity. Continuously adjusting the movement on the basis of the latest visual information compensates for errors that relying on incorrect expectations introduces (smaller systematic errors with less occlusion in Fig. 8C) as well as increasing precision (smaller variable errors with less occlusion in Fig. 9A).

It is quite obvious that the quality of visual information can influence performance. It is also clear that removing information at a time at which it is normally used can disrupt performance (e.g., Marinovic et al., 2009; Müller & Abernethy, 2006; Whiting & Sharp, 1974). We interpret the poorer performance when visual information is removed (Experiment 2) or when its resolution is reduced by looking elsewhere (Experiment 1) as evidence that new visual information is used throughout the hitting movement. This implies that using such information is beneficial. One possible limitation in drawing this conclusion from the data is that it may only apply for movements performed under time pressure. We found that even when reliable visual information was constantly available subjects were willing to use their experience on previous trials to guide their action. Perhaps the time that we gave our subjects was too short to make and combine all the judgments, so they partly relied on expectations. If we had always given them more time they may have performed better, using more of the available visual information. However, the fact that subjects clearly did not perform better when given more time in Experiment 2, and the reasonable agreement between the data and the predictions in Fig. 9E and F, although time pressure is not considered for the predictions at all, suggest that time pressure is unlikely to be the main factor limiting performance.

The subjects' eye movements in the two tasks of Experiment 1 (Fig. 3C), the influence of the different eye movements on performance (Fig. 5), and the influence of removing visual information in Experiment 2 (Fig. 9), all suggest that continuous visual updating is important to achieve a high spatial resolution. This was examined here for the condition in which there is little uncertainty about the target's motion because it always moved at a constant velocity. Moreover the conditions were ideal for judging distances and velocities because the target moved laterally at a fixed distance. Visual judgments are likely to be poorer for motion in depth, which would have to be judged from changes in retinal image size and binocular disparity. Moreover, for motion in depth the instantaneous resolution is likely to increase as the target approaches, so there would be even more reason to continuously update one's judgments on the basis of new visual information. When the target's motion is more variable it is obviously also more important to constantly update one's movements. Thus we can conclude that whenever accuracy is an issue, continuous visual control is indispensable.

Appendix A. A simple mathematical model

To quantify our expectations we distinguish between variability arising from spatial errors when bringing the stylus to an anticipated interception point ($\sigma_{spatial}$), variability arising from errors in timing the stylus' arrival at an anticipated interception point (σ_{time_stylus}), and variability arising from errors in judging when the target will reach an anticipated interception point (σ_{time_target}). The

appropriate interception point in our experiment is directly in front of the gap. For simplicity, we assume that the timing of the stylus' arrival at the interception point is determined before the hand starts to move, so the position directly in front of the gap is the relevant interception point for that judgment. The anticipated interception point that guides the stylus' path is adjusted during the movement to ensure that the stylus hits the target (even if it does so at the wrong time), so it is constantly changing. For the judgment of when the target will reach the anticipated interception point either this changing position or the position directly in front of the gap could be used; for simplicity we will use the position directly in front of the gap.

We assume that whenever it is available, visual information is used to update the anticipated interception point that is used to guide the stylus. The advantage of seeing the target longer is that errors in judging when the target will reach the anticipated interception point become smaller as the anticipated time of the interception approaches (and the target comes closer to the interception point). Deviations from the initial estimate of when the target will reach the interception point are converted into changes in the stylus' destination, so that the position of the stylus relative to the target at the time of the hit only depends on the final timing error. The variability in this timing error (σ_{time_target}) is multiplied by the target's velocity (v) to obtain a spatial measure of variability. Since the timing uncertainty decreases during the movement the spatial uncertainty does as well. Information provided during the last 110 ms before the hit cannot be used to predict the interception point due to neuronal delays (Brenner & Smeets, 1997), so for the condition with no white rectangle we use the estimate of σ_{time_target} 110 ms before the stylus reached the target (estimates based on this value may be slightly too optimistic because some attributes take longer to respond to; Brenner et al., 1998). For the other conditions we determine the interval between when the target first hits the white rectangle and when its center is exactly aligned with that of the gap (which was always more than 110 ms, so we can assume that there was always enough time to respond to the last provided information), and use the estimate of σ_{time_target} at this time before the stylus reached the target.

To estimate the standard deviation in the stylus' position relative to the target at the time of the hit (σ_{rp}), we consider all the above-mentioned sources of variability. We defined the sources of variability in a manner that ensures that they are independent, so:

$$\sigma_{rp} = \sqrt{\sigma_{spatial}^2 + \sigma_{time_stylus}^2 v^2 + \sigma_{time_target}^2 v^2} \quad (1)$$

The standard deviation in the position of the stylus (relative to the gap) when hitting through the static gap in Experiment 1 is about 3.1 mm (Table 1). We use this value as our estimate for the spatial error ($\sigma_{spatial}$). For estimating the precision of judging when the target will reach the gap (σ_{time_target}), we assume that (at any time t) the time until the target reaches the gap (t_t) is judged by dividing the judged separation (s_t) by the judged velocity (v_t): $t_t = s_t/v_t$. If this is true, and the two judgments have independent variability, then:

$$\frac{\sigma_{time_target}^2}{t_t^2} = \frac{\sigma_s^2}{s_t^2} + \frac{\sigma_v^2}{v_t^2}$$

Since σ_s/s_t and σ_v/v_t are Weber fractions for judging separation and velocity, both of which are approximately constant with values of about 5% (McKee & Welch, 1989), we use $\sigma_{time_target} = 0.07t_t$ to estimate the uncertainty about timing at time t_t . In this context, t_t is determined by the last moment at which useful new visual information is available (as explained above). Finally, we assume that σ_{time_stylus} is a fixed fraction of the movement time (MT). We use a fraction of 3% (estimated from the right side of Fig. 4 of Wing & Kristofferson, 1973), so $\sigma_{time_hit} = 0.03MT$.

The timing of the hit (i.e., where the target is relative to the gap at the moment of the hit) only depends on the estimate of when the target will be in front of the gap (with variability σ_{time_target}) and how accurately one can reach the target at that time (with variability σ_{time_stylus}). If we assume that the timing of the movement is based on estimates at the reaction time (i.e., assuming that the timing is not modified during the movement and ignoring delays in using such information during the reaction time), the overall standard deviation in the timing of the hit (σ_t) is:

$$\sigma_t = \sqrt{\sigma_{\text{time_stylus}}^2 + \sigma_{\text{time_target}}^2} = \sqrt{(0.03MT)^2 + (0.07MT)^2} = 0.076MT \quad (2)$$

Applying Eqs. (1) and (2) to the data for hitting into the gap in Experiment 1 gives values of 5 mm ($\sigma_t = 25$ ms) and 3.1 mm (σ_{rp}) for the position of the target when hit (Fig. 5A) and the position of the stylus relative to the target (Fig. 5C), respectively. These values are both about as good as the best subjects' performance.

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