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RESEARCH ARTICLE

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Hitting moving targets

A dissociation between the use of the target's speed and direction of motion

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Abstract Previous work has indicated that people do not use their judgment of a target's speed to determine where to hit it. Instead, they use their judgment of the target's changing position and an expected speed (based on the speed of previous targets). In the present study we investigate whether people also ignore the target's apparent direction of motion, and use the target's changing position and an expected direction of motion instead. Subjects hit targets that moved in slightly different directions across a screen. Sometimes the targets disappeared after 150 ms, long before the subjects could reach the screen. This prevented subjects from using the target's changing position to adjust their movements, making it possible to evaluate whether subjects were relying on the perceived or an expected (average) direction to guide their movements. The background moved perpendicular to the average direction of motion in some trials. This influences the target's perceived direction of motion while leaving its perceived position unaffected. When the background was stationary, subjects hit disappearing targets along their trajectory, just as they hit ones that remained visible. Moving the background affected the direction in which subjects started to move their hand, in accordance with the illusory change in direction of target motion. If the target disappeared, this resulted in a hit that was systematically off the target's trajectory. If the target remained visible, subjects corrected their initial error. Presumably they did so on the basis of information about the target's changing position, because if the target disappeared they did not correct the error. We conclude that people do use the target's perceived direction of motion to determine where to hit it. Thus the perceived direction of motion is treated differently than the perceived speed. This suggests that the motion of an object is not broken down into speed components in different directions, but that speed and direction are perceived and used separately.

Keywords Visuomotor control · Interception · Direction of motion · Speed · Perception

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Introduction

Intercepting a quickly moving target, such as a spider that is running across a table, demands much of our visuomotor system. One cannot simply guide the hand to the present position of the target. It is necessary to take into account that the target is moving during the time that the hand's movement is planned and executed. We want to find out what information is used to determine where the target will be hit. Information that could be used, for a target moving across a frontal plane (such as the spider on the table), includes the target's changing position, its speed and the direction in which it moves.

Although speed is nothing but the rate of change in position over time, the perceptual system does not derive perceived speed from changing perceived position (for a review, see Nakayama 1985). Direction of motion is also perceptually dissociated from position. These dissociations can be demonstrated by presenting moving targets on a moving background and asking subjects to indicate the target's speed, it's direction of motion, and the position at which the target disappeared. Whereas the moving background does not affect the perceived position of the target, it does affect its perceived speed (Schweigart et al. 2003; Smeets and Brenner 1995a). If the background moves in the opposite direction to the target, the target seems to move faster than if the background moves in the same direction as the target. Similarly, a moving background systematically affects the target's perceived direction of motion, whereas it does not affect where subjects indicate that the target disappears (Smeets and Brenner 1995b).

Perhaps it is not surprising that if a moving background affects the perceived speed it will also affect the perceived direction. There are indications that our brain combines velocity components in two or more spatial directions to determine motion direction (Derrington and Suero 1991; Festa and Welch 1997; Stone et al. 1990). If so, anything that influences judgments of a velocity component can also influence the perceived direction. However, others claim that perception of speed and motion direction are fundamentally different. Matthews and Qian (1999) and Matthews at al. (2001) found that speed discrimination and direction discrimination could be altered independently of each other. Instead of determining direction of motion by combining velocity components, direction of motion could be determined by the same mechanism that processes orientation of static stimuli (Francis and Kim 2001; Geisler 1999; Westheimer and Wehrhahn 1994).

A way to distinguish between these two views on the perception of motion direction is to study whether perceived direction of a moving target influences interception movements in the same way as the target's perceived speed. Brouwer et al. (2002) found evidence that people do not use the target's perceived speed to determine where to hit it. If direction of motion is nothing more than the ratio of two velocity components, we expect that perceived direction is also not used in this task. It is not as self-evident as it may seem that subjects must use the perceived speed and direction of motion to guide the hand to a moving target. People could "guess" the speed and direction on the basis of previous targets. If the target does not move at that expected speed or in the expected direction, they could correct for the error that this introduces by continuously adjusting the movement to the most recent information about target position. Several studies indicate that subjects can adjust even fast interception movements on the way to a target if it suddenly changes its position or speed (Brenner and Smeets 1997; Brenner et al. 1998; Georgopoulos et al. 1981; Prablanc and Martin 1992; Soechting and Lacquaniti 1983).

The study by Brouwer et al. (2002) indicated that people use an expected (average) speed to anticipate where a target will be hit, rather than the perceived speed. Subjects had to hit simulated spiders which ran at different constant speeds across a background. By making the spiders invisible before the subjects could reach them, subjects were prevented from using the target's changing position to adjust their hand's movement. This made it possible to evaluate whether subjects were relying on the actual speed of the target. Subjects hit too far ahead of the disappearing point of slow spiders and not far enough ahead of fast spiders. This finding supports the idea that the target's changing position and an expected, average speed were used. In the same set of experiments, the movement of the background was manipulated in order to affect the perceived speed of the running spider while leaving the perceived positions unaffected. The subjects hit equally far in front of the spider's disappearing point when the background was moving in the opposite direction to the spider's motion than when it moved in the same direction. Again this indicates that the perceived speed is not used, but that subjects hit moving targets by using an expected speed and the target's changing position.

In the present study, we investigated whether people likewise only use an expected (average) movement direction of the target in addition to the target's changing position to anticipate the hit position, ignoring the target's perceived movement direction. An indication to the contrary comes from a study by Smeets and Brenner (1995b). They found that the starting direction of the hand when hitting moving targets is affected by a moving background in a way that is consistent with the direction illusion caused by this moving background. This contrasts with the finding that illusory speed caused by a moving background does not affect the hand's starting direction (Smeets and Brenner 1995a).

The paradigm we used here is similar to that used by Brouwer et al. (2002). We asked subjects to hit virtual discs which moved across a screen in one of five slightly different, constant directions. Sometimes the targets disappeared from view before the subjects could reach the screen; sometimes the background moved.

If subjects only use position and an expected (average) direction to determine the hit position, they should underestimate the differences in direction when they hit the disappearing targets. There should be no effect of the moving background, since the background only influences the target's perceived direction of motion and not its perceived position.

If subjects use the target's perceived direction of motion, they should hit somewhere on the disappearing target's path, just as they do for targets that remain visible (provided that the time that the targets are visible is long enough to detect the direction). There should be an effect of the moving background, as this influences the perceived direction of motion.

Materials and methods

A schematic view of the setup is shown in Fig. 1. Subjects hit targets using a 22-cm-long Perspex rod. The rod's diameter was 1.8 cm. It was held like a darts arrow, between fingers and thumb. The targets were presented on a monitor with a protective, transparent 43×34 cm Macrolon screen in front of it. The screen was tilted 30° from the vertical. The images were made to appear to be situated on this screen by having the subjects wear liquid-crystal shutter spectacles and presenting different images to the two eyes. To make sure that subjects could see the stimuli on the screen clearly, we darkened the room. Subjects could adjust the chair's height to find a comfortable posture so that they could make natural hitting movements.

We attached two infrared markers (IREDs) to the rod and three to the shutter glasses to measure the position of the subject's hand and head. The positions of these IREDs were recorded by a movement-analysis system at 250 Hz (Optotrak 3010; Northern

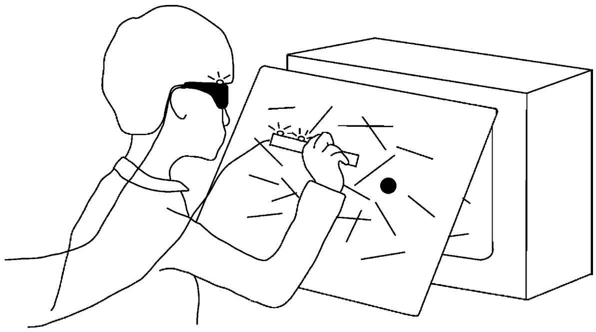

Fig. 1 A schematic view of the experimental setup. The subject sits in front of a monitor on which the images are presented. Shutter spectacles make the images appear to be on a protective screen in front of the monitor. IREDs attached to the rod and the spectacles make it possible to monitor the position of the hand and head

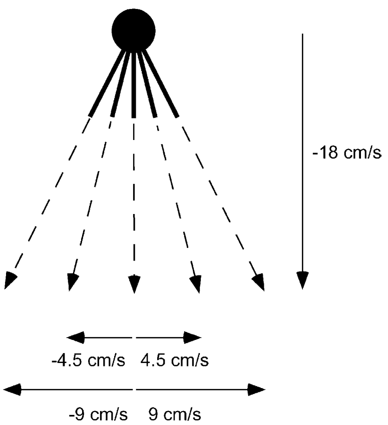

Fig. 2 Scaled overview of the directions in which the disc could move. *Solid lines* indicate the parts of the paths in which the disc was always visible. The disc's vertical speed was always 18 cm/s downwards. The horizontal speed could be 9 cm/s or 4.5 cm/s, either leftwards or rightwards, or 0 cm/s. This resulted in directions of motion relative to the vertical of 27°, 14° and 0°

Digital). Information about the position of the head was used online to adjust the images on the screen to the head's movement. Information about the position of the rod was used online to guide the subject's hand to a starting area and to give the appropriate feedback. The delay in adjusting the images to the movements of the subjects was 21±3 ms.

The targets were yellow discs with a diameter of 1.8 cm which could move in five different directions from top to bottom. The starting position of the disc was always 9 cm above the starting position of the hand. The discs moved across a background of 4 cm red lines which were placed at random within a circle of 30 cm around the center of the screen. At the edges of the circle the intensity of the lines faded. After each trial a new background was generated.

Design

The discs moved in one of five different directions, as illustrated in Fig. 2. The speed in the vertical, downward direction was always 18 cm/s. The speed in the horizontal direction was 9, 4.5, or 0 cm/s. This resulted in overall speeds of 20.1, 18.6, and 18 cm/s. The resulting directions of motion were −27°, −14°, 0°, 14°, and 27° relative to the vertical (with negative values indicating motion to the left). The disc disappeared after 150 ms in half of the trials. In the remaining trials, the disc was visible throughout the duration of the trial. Furthermore, in half of the trials the background moved either to the left or to the right at 6 cm/s. In the remaining half, the background remained static. Thus, we had 5 different directions of motion, 2 presentation times and 3 types of background motion, giving a total of 30 different conditions. Each subject hit 240 targets. The background was static on 120 trials; it moved to the left on 60 trials, and it moved to the right on the remaining 60 trials. The different directions and presentation times were divided equally over these trials. The trials were presented in random order.

Subjects and procedure

The present experiment is part of an ongoing research program that has been approved by the local ethics committee. Fifteen colleagues volunteered to take part in this study after being informed about what they would be required to do. Four were the authors. The remaining 11 were naive about the purpose of the experiment. One of these subjects was excluded from the analysis because too much of his data was missing due to occluded IREDs.

The subjects were instructed to hit the discs as quickly and accurately as possible. The subjects rested about 15 min after the first 120 trials. They could take additional short breaks whenever they liked by not immediately returning to the starting area after a hit.

Before the start of a trial, messages on the screen guided the hand to within 5 cm of a point 40 cm away from the center of the transparent screen. A line pointing out of the screen indicated the direction to the point at which the tip of the rod was to be held. Once the rod was within this area, the trial started.

In the conditions in which the discs disappeared, it reappeared as soon as the subjects hit the screen. At that time, the disc gave subjects feedback about their performance in that trial in all conditions. If the center of the disc was within 1.8 cm of the center of the rod when it had reached the screen, the disc was scattered in several unequal pieces. If the distance between the center of the disc and the center of the rod was more than 1.8 cm, the disc moved away from the rod in the direction opposite to the error.

Analysis

From a total of 3,360 trials of the remaining 14 subjects, only 8 trials were excluded due to occluded IREDs or because the subject did not react within 700 ms.

Reaction time was defined as the time until subjects moved the rod faster than 10 cm/s, from the moment that the stimulus appeared on the screen. Movement time was the time between when the rod first moved faster than 10 cm/s and when the rod reached the screen. The hand's starting direction was the angle in degrees between the direction to the screen and the line through the hand's starting position and the position measured at the moment that the hand had moved 5 cm in the direction of the screen.

The hit position was the position on the screen that was hit by the center of the rod. The target position was the position of the target on the screen at the time that the rod hit the screen. To calculate the distance error, we subtracted the distance between the hit position and the disappearing point from the distance between the target position and the disappearing point (see Fig. 3). For trials in which the disc remained visible, we took the position of the target after it had been moving for 150 ms instead of the disappearing point. If subjects hit too far ahead of the disc's center, the error was negative. If they did not hit far enough, the error was positive.

Figure 3 also shows how the direction error was determined. It is the angle between the target's direction of motion and a line through the hit position and the position of the target after it had been moving for 150 ms (which is the disappearing point in half of the trials). If subjects hit too far to the left, the angle was negative. If subjects hit too far to the right it was positive. If subjects hit in

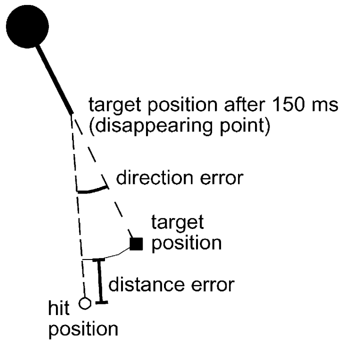

Fig. 3 Definition of the distance error and the direction error. The distance error is the distance between the hit position and the disappearing point subtracted from the distance between the target position and the disappearing point. When the disc remained visible, we took the position of the target after 150 ms presentation time instead of the disappearing point. The direction error is the angle in degrees between the direction of motion of the target and a line through the position of the target after 150 ms presentation time (i.e., the disappearing point in half of the trials) and the hit position. When the hit position was to the left of the target position, as in the example here, the direction error was considered to be negative

the correct direction, the direction error was zero. Note that this does not necessarily mean that subjects hit the disc perfectly. They could still hit too far behind or ahead of the disc.

For the statistical analysis, we included both hits and misses. Differences between conditions were evaluated using repeated-measures analyses of variance with direction of the target's motion (−27°, −14°, 0°, 14°, 27°), background motion (leftward, rightward, static), and presentation time (disappearing or visible) as factors. We took P=0.05 as the level of significance. All significant effects are mentioned.

Results

Timing

The average reaction time was 247 ms, with no significant influence of the direction of target motion, visibility, or background motion. There was a significant but unsystematic interaction between presentation time and direction of motion ($F_{4,52}$=3.22, p=0.02). The reaction times, averaged across presentation time and direction of motion, varied between 243 and 253 ms.

The average movement time was 216 ms, with a marginally significant influence of direction ($F_{4,52}$=2.55, P=0.05). Subjects hit targets moving in a rightward direction slightly faster than they did targets moving in a leftward direction. The maximal difference between the average movement times for each direction of motion was less than 4 ms. Subjects tended to hit the disappearing discs slightly faster than the discs that remained visible. The average difference was less than 3 ms and was not statistically significant ($F_{1,13}$=4.34, P=0.06). Background motion had no effect on movement time.

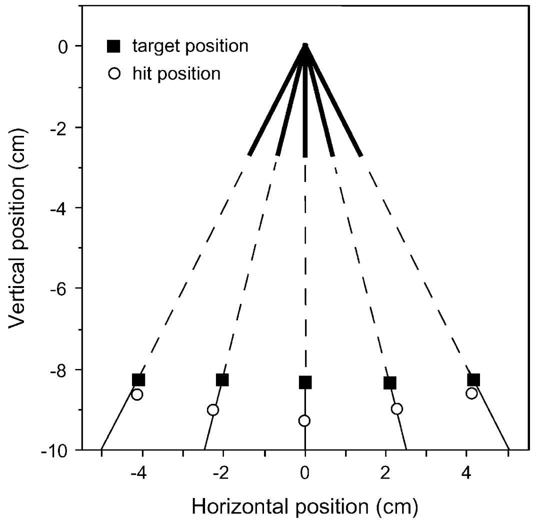

Fig. 4 Scaled overview of the target's directions of motion, the average target positions and the hit positions in the disappearing conditions (averaged across the three types of background motion). The *fat solid lines* indicate the part of the path during which the disc was visible. The *dashed lines* indicate the part of the path during which the disc was invisible. The *thin solid lines* are extrapolations of the targets' paths, drawn to make it easier to see the deviation of the hit position from the target's direction of motion

Starting direction and hitting errors: effects of the target's direction of motion

Not surprisingly, the direction of motion influenced the hand's starting direction ($F_{4,52}$=216.16, P<0.01). This indicates that subjects adjusted their hand's starting direction to the target's direction of motion or to its position at the hand's movement onset.

Figure 4 depicts the average hit positions and target positions for the short presentation time. The target's directions of motion and disappearing points are also indicated to give a global idea of the subjects' performance. Note that, whenever the distance between the target position and the hit position was less than 1.8 cm, the feedback indicated that the target was hit correctly.

In Fig. 5 we plot the distance error for each direction of motion and presentation time. The average distance errors have negative values, which means that subjects generally hit below the center of the target (as was already evident for the disappearing targets from Fig. 4). They do this more in the middle direction of motion than in the outer ones, as indicated by a significant effect of the target's direction of motion on distance error ($F_{4,52}$=9.01, P<0.01). This is consistent with subjects ignoring the difference in velocity between the targets. The effect was weaker when the disc remained visible than when it disappeared (interaction between presentation time and direction of motion, $F_{4,52}$=4.29, P<0.01), presumably because subjects adjusted their movement on the basis of the perceived position in the former case.

Figure 6 shows the direction error for each direction of motion and presentation time. The direction error was

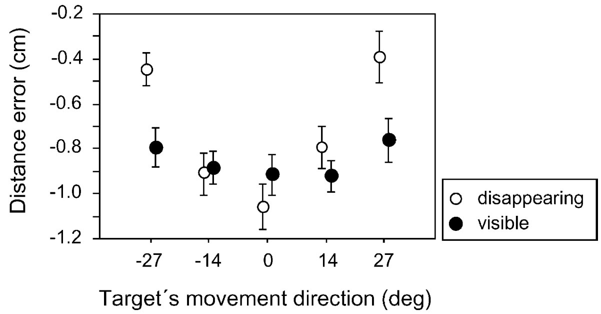

Fig. 5 Average distance error for each direction of motion and each presentation time (averaged across the three types of background motion). *Error bars* indicate standard errors between subjects. The distance errors are negative, which means that subjects generally hit below the center of the disc. The distance error depends more strongly on the target's direction of motion when the discs disappeared than when the discs remained visible. This pattern is in accordance with the use of changing position and an average speed

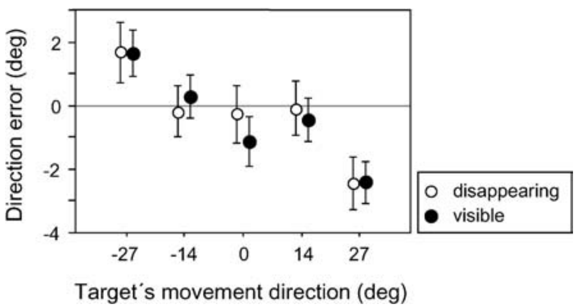

Fig. 6 Average direction error for each direction of motion and each presentation time (averaged across the three types of background motion). *Error bars* indicate standard errors between subjects. The direction error depends on the target's direction of motion, but this dependency is the same for disappearing discs and discs that remain visible. This indicates that subjects used the perceived direction of motion and not an expected direction of motion

influenced by the target's direction of motion ($F_{4, 52}$=4.13, P<0.01). The effect was the same for discs that remained visible as for discs that disappeared (no interaction between presentation time and direction of motion, $F_{4, 52}$=0.37, P=0.83).

Starting direction and hitting errors: effects of the moving background

Figure 7 shows the hand's starting direction for each background motion and presentation time. In line with the perceived direction of motion of the target, subjects started by moving their hand more to the left if the background moved to the right, and more to the right if the background moved to the left (effect of background motion on the hand's starting direction, $F_{2, 26}$=14.67, P<0.01). As may be expected for a variable that is measured at the beginning of the movement, the effect is

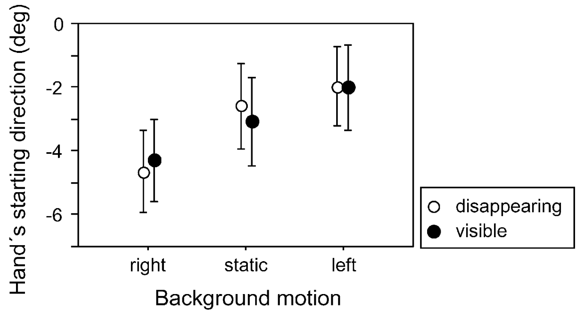

Fig. 7 Average starting direction of the hand for each background motion and each presentation time. *Error bars* indicate standard errors between subjects. Subjects start moving more to the left (i.e., a more negative starting direction) when the background is moving to the right, and more to the right when the background is moving to the left. There is no difference between the two presentation times. These results are in accordance with the use of the perceived direction of motion

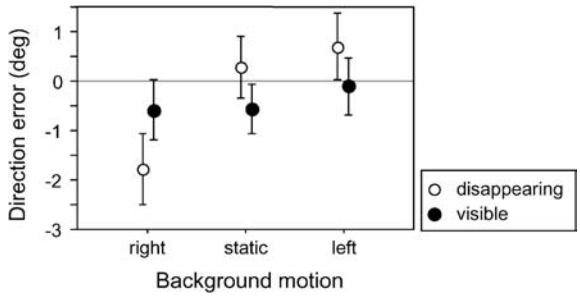

Fig. 8 Average direction error for each background motion and each presentation time. *Error bars* indicate standard errors between subjects. In the disappearing conditions, subjects hit too far to the left when the background moved to the right and too far to the right when the background moved to the left. This is consistent with an illusory direction of motion effect caused by the moving background, which also affected the hand's movement at the start. In the conditions where the disc remained visible, subjects were apparently able to correct for the error caused by the moving background; in these conditions background motion did not affect the hitting error

the same for the discs that disappear and the ones that remain visible (no interaction between background motion and presentation time).

In Fig. 8, we plot the direction error for each background motion and presentation time. A significant interaction between background motion and presentation time on direction error ($F_{2, 26}$=3.47, P=0.046) shows that the effect of background motion was not the same for both presentation times. Figure 8 indicates that the effect was stronger when the discs disappeared than when they remained visible. A separate repeated-measures analysis on the data in which the discs disappeared revealed a strongly significant influence of background motion on direction error ($F_{2, 26}$=5.72, P<0.01).

Interactions between background motion and direction of motion

There were significant interactions between background motion and direction of target motion on the hand's starting direction ($F_{8,\ 104}$=3.11, P<0.01), distance error ($F_{8,\ 104}$=2.60, P=0.01), and direction error ($F_{8,\ 104}$=3.11, P<0.01). There was also a significant three-way interaction between background motion, direction of target motion, and presentation time on direction error ($F_{8,\ 104}$=2.69, P=0.01). These may all have to do with the way in which the moving background influences the perceived motion of targets moving in different directions.

Discussion

If subjects had only used the target's position and an expected, average direction to determine where to hit the screen, they would have hit straight below the disappearing point of a shortly presented disc. This would have resulted in direction errors of 27°, 14°, 0°, −14°, and −27° for the targets with directions of motion of −27°, −14°, 0°, 14°, and 27°, respectively. Figure 6 shows that this is not the case. The errors were very small, even when the target had been visible for only 150 ms. Nevertheless the effect of direction of motion on the direction error was significant. Subjects did not extrapolate the target's direction of motion perfectly, but systematically hit a bit too far toward the center of the screen, as would be expected if subjects had partly used an average direction, or if subjects had not perceived the direction of motion correctly. Perception of motion direction is known to depend on the axis of movement. Observers are better at discriminating motion directions around the cardinal than around the oblique axes (Ball and Sekuler 1987; Matthews and Welch 1997). More specifically, Loffler and Orbach (2001) found a systematic bias in the perceived direction of motion of dots moving toward −26.6° and 26.6° (following our definition of motion direction). Subjects perceived them to move in a direction that was biased toward the vertical axis. The error was about 2.5°, which is qualitatively and quantitatively similar to our direction errors at −27 and 27° (see Fig. 6).

Irrespective of whether the error arises from partly using an average direction or from misjudging the direction, the error should have been larger when more extrapolation was needed. This was not the case: the effect of direction of motion on direction error is not larger when the discs disappeared than when they remained visible (no interaction between direction of motion and presentation time on direction error). The effect of direction of motion on direction error is more likely to be caused by subjects not being willing to move their hand further to the left or the right than necessary: the error did not have to be absolutely zero for a successful hit. It seems that subjects perceived the direction of motion more or less correctly and used the perceived direction of motion to determine where to hit.

The effects of the moving background also indicate that subjects used the perceived direction of motion to guide their hand to where they hit the screen. Figure 6 shows that subjects started to move their hand in accordance with the target's illusory direction of motion. If they had only used information about the target's position and an expected direction of motion, there would have been no effect, since the moving background does not affect perceived position. When the target disappeared, the moving background caused systematic direction errors as is shown in Fig. 7. When the target remained visible, subjects were able to correct their initial error (interaction background motion and presentation time on direction error).

Other studies have also indicated that visual illusions affect a hand's movement more at the start than at the end of the movement (Glover and Dixon 2001, 2002; Westwood et al. 2001). Glover (2002) explains this by postulating that illusions affect the planning of action but not the control. We prefer to explain this by postulating that different sources of information are used simultaneously (Smeets et al. 2003; for a review, see Smeets et al. 2002). In this experiment, subjects use the (correctly) perceived position and the (illusory) perceived direction of motion to estimate where they will hit the target. During the movement they continuously update this estimate so that the effect of the illusion becomes increasingly smaller (as long as the changing position information remains available).

As it takes time to adjust the hand's movement to the new target position, one would expect to find a small, illusory effect of the moving background on the direction error in the conditions in which the disc remains visible as well. We did not find this. Maybe the effect was just too small to be measured. Alternatively, the perceived position of the target that subjects used for updating their hand's movement may not have been the current position of the target but a position that is shifted a bit further in the actual direction of motion. There is evidence that observers perceive a target's position a certain time ahead. One line of evidence comes from studies about representational momentum. Representational momentum is the finding that observers remember the final position of a moving target further in its direction of motion (for a review, see Hubbard 1995). This displacement varies with target speed; the final position of a faster target is perceived as further ahead than that of a slow target. It is debated whether this effect is related to eye movements (cf. Kerzel 2002 with unpublished work by Hubbard). Another line of evidence comes from studies in which the position of a dot that is flashed while the eyes are moving is misperceived in the direction of the eye movement (Mita et al. 1950; Mitrani et al. 1979). Brenner et al. (2001) and Schweigart et al. (2003) propose that the perceived position of a target is determined by the efference copy of the eye position. Thus, a moving target's position will be perceived a certain time ahead if you (intend to) pursue it. As ocular pursuit is quite accurate, also with moving backgrounds (Kowler et al. 1984; Schweigart et al. 2003), this misperception may serve as a prediction of the future position of the target. If the visuomotor delay approximately equals the time that the perceived target position is shifted further ahead, using the (mis)perceived position will compensate for the small illusory effect that we mentioned in the beginning of this paragraph (for a similar suggestion, see Smeets et al. 1998).

The use of a target position that is shifted further ahead could also explain that subjects can hit targets correctly by only using the target's position and an average speed, as well as the small effect of actual speed on the distance that subjects hit in front of the disappearing point of a moving target (Brouwer et al. 2002). The use of average speed is shown again in the present experiment. Subjects generally hit the bottom of the invisible disc, but they hit significantly further from its center if the disc was moving slightly more slowly (the middle direction of motion) than if it was moving slightly faster (the outer directions). This is in accordance with using an average instead of the actual speed to determine the hit position. Actual speed hardly seemed to have an effect in the present experiment. If the hit position were only determined by the average speed, there would be a difference of 7 mm (in the distance error) between hits toward the slowest targets and the fastest targets (the difference between the time that the disc was invisible times the fastest speed and the time that the disc was invisible times the slowest speed). The difference is 6 mm. This means that the distance that subjects hit ahead of the disappearing point was (almost) exclusively determined by the average speed. In the present experiment, the target speeds may have been too small to be easily detected, so the use of an average speed is not surprising. However, the use of an average speed was also found in the experiments by Brouwer et al. (2002), in which the speeds ranged from 6 cm/s to 18 cm/s. These differences must have been detected because target speed influenced movement time (see also Brouwer et al. 2000).

In the present study, we found that subjects use the perceived direction of motion to guide their hand to the hit position. Conversely, subjects use an expected, average speed (instead of the perceived speed). Thus, speed and direction of motion are treated differently in determining the hit position of a moving target. This suggests that the motion of an object cannot be broken down into speed components in different directions, but that speed and direction are perceived and used separately.

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