Journal of Motor Behavior, 1997, Vol. 29, No. 4, 297–310

Fast Responses of the Human Hand to Changes in Target Position

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ABSTRACT. If a target toward which an individual moves his hand suddenly moves, he adjusts the movement of his hand accordingly. Does he use visual information on the target's velocity to anticipate where he will reach the target? These questions were addressed in the present study. Subjects ($N = 6$ in each of 4 experiments) were instructed to hit a disk with a rod as soon as it appeared on a screen. Trajectories of the hand toward stationary disks were compared with those toward disks that jumped leftward or rightward as soon as the subject's hand started moving toward the screen, and with those in which either the disk or the background started moving leftward or rightward. About 110 ms after the disk was suddenly displaced, the moving hand was diverted in the direction of the perturbation. When the background moved, the disk's perceived position shifted in the direction in which the background was moving, but the disk appeared to be moving in the opposite direction. When hitting such disks, subjects adjusted their movement in accordance with the perceived position, rather than moving their hand in the direction of the perceived motion in anticipation of the disk's future displacement. Thus, subjects did not use the perceived velocity to anticipate where they would reach the target but responded only to the change in position.

Key words: arm movement, motor control, reaction time, spatial vision

Hitting, touching, or grasping a target takes time. Even if we try to hit a target as soon as we can, it takes several hundred milliseconds for our hand to start moving and another few hundred milliseconds for our hand to reach the target. In the meantime, the target could move. Such target motion is seldom predictable. Moreover, even if it is predictable, we do not make full use of that information to foresee where we will hit the target (Brenner & Smeets, 1994, 1996; Smeets & Brenner, 1995a). It is not surprising, therefore, that we can adjust the movement of our hand as it moves toward the target (e.g., Flash & Henis, 1991; Georgopoulos, Kalaska, & Massey, 1981; Prablanc & Martin, 1992; Soechting & Lacquaniti, 1983).

If a target that a subject is trying to touch is unexpectedly displaced, the trajectory of the subject's hand changes. For that change to take place, the subject needs neither to be able to see his hand nor to notice that the target has been displaced (Goodale, Pélisson, & Prablanc, 1986; Pélisson, Prablanc, Goodale, & Jeannerod, 1986; Prablanc & Martin, 1992). When the target is displaced, it is sufficient for the subject to quickly adjust his hand's trajectory on the basis of the target's new position. Sometimes, however, consideration of more information than the instantaneous position of the target might be advantageous.

Consider a moving target. If a person adjusts the movement of his hand only on the basis of the instantaneous target position, he will always move toward a position that the target had left some time earlier. How much earlier depends on the time it takes for visual information to influence his action. If the target's motion is also taken into account, he could anticipate where the target will be in the future and move directly toward that position. Of course, that makes sense only if the time it takes to respond to visual information is considerably less than the movement time (typically about 300 ms for hitting and about 600 ms for grasping).

Soechting and Lacquaniti (1983) found that it takes about 110 ms to respond to a change in target position if the direction of the change is known in advance. Van Sonderen, Denier van der Gon, and Gielen (1988) found that it takes more than 200 ms if the direction is not known in advance. In accordance with that difference, Paulignan, MacKenzie, Marteniuk, and Jeannerod (1991) found that subjects respond to an unpredictable displacement within 100 ms (by

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decreasing the acceleration of the wrist), but that they need about 275 ms to adjust the direction in which the wrist moves to the direction in which the target is displaced. Similar times were reported by Castiello, Paulignan, and Jeannerod (1991). Because 275 ms is close to the time it takes to hit a target, that lag implies that visual information about motion is of little use when the target one is trying to hit suddenly starts moving. Faster responses have also been reported, however. Prablanc and Martin (1992) found that it took only about 155 ms to respond adequately to an unpredictable displacement that took place during a saccade. Because the new target position could be detected only after the saccade had been completed, which they estimated to have taken place 40 ms after the displacement, those findings suggest that it takes only about 115 ms to adjust the movement of the hand. If a target is rotated as well as displaced, the hand starts to rotate to match the new orientation about 100 ms after the perturbation (Opitz, 1995). Such fast responses would enable visual information on motion to be used.

In the present study, we verified that subjects can respond to changes in target position within about 110 ms. We then examined whether they use visual information about the target's motion to anticipate where they will hit the target. We accomplished both objectives by determining how the moving hand responds to unpredictable changes in the visual information concerning the target's position. Those changes occurred as soon as the subject's hand started moving toward the screen.

The first way we examined whether subjects use visual information about a target's motion to predict where they will hit it was by comparing their responses to abrupt target displacements with their responses to targets starting to move. To assure that responses could be directly compared, we chose target velocities that brought the targets to approximately the same positions—before being hit—that the abrupt displacements did. If subjects respond only to the instantaneous target position, the response to target motion should be more gradual than that to abrupt displacements, because, in the former case, the change in position increases gradually. In contrast, if subjects anticipate where they will hit the moving target on the basis of its motion, they should immediately redirect their hands toward the new location; thus, the adjustments should be very similar in both cases.

A second way one can examine whether subjects use a target's motion to anticipate where it will be hit is by moving the background. Moving the background gives an illusion of target motion in a direction opposite to the one in which the background is moving (e.g., Duncker, 1929), without a change in the target's actual or perceived position (e.g., Smeets & Brenner, 1995a). A response to such illusory information on target motion would therefore provide direct evidence that subjects use the target's motion to adjust their actions.[1]

In the two main experiments reported on in this article, subjects had to hit an object lying on a background. They were asked to hit the targets as soon as they appeared. The use of simulated, rather than real, targets and backgrounds enabled us to control the motion of target and background very precisely. We conducted two additional experiments to show how the moving background influences perception. The findings from a choice reaction-time experiment in which the same stimuli were used confirmed that the moving background gives rise to perceived motion in the opposite direction. A position-matching experiment with the same stimuli surprisingly showed that the moving background displaced the perceived position of the target in the opposite direction: the direction in which the background had moved.

EXPERIMENTS 1 AND 2

Method

Subjects and Instructions

The same 6 subjects participated in both experiments: the authors and 4 of their colleagues. The only special instructions subjects received was that they should hit the targets as fast as they could (a prize was awarded to the subject who hit the targets fastest). We imposed no restrictions on how subjects should sit or move during the experiment except that they had to be able to start with the rod in the starting position.

The Target and Background

The target and its background were both presented on a computer monitor (Silicon Graphics GTX-210 computer and HL69SG monitor). The monitor (34 × 27 cm; 1,280 × 492 pixels; tilted backward at an angle of about 11°) was protected by a transparent screen that was tilted backward at an angle of about 30° (Figure 1; the distance between the center of the monitor and the protective screen was about 8 cm). The protective screen was necessary because subjects were encouraged to hit the targets as quickly as possible. The tilt made the movement more comfortable. Images were presented at a rate of 120 Hz. Liquid crystal shutter spectacles ensured that alternate frames were presented to the left and right eyes. Predominantly red stimuli were used because the liquid crystal shutter spectacles work best at long wavelengths (about 33% transmission when open and 0.3% when shut). The room was dark so that subjects would not be able to see anything except for the image on the screen.

The target was a red disk with a diameter of 2 cm (as seen on the protective screen) and an effective luminance of 0.8 Cd/m^2. The disk appeared to lie on a background of about 42 orange lines. The lines forming the background were distributed at random within a 20-cm × 16-cm area on the protective screen and were oriented at random (with the limitation that they should not be within 30° of horizontal). They were 4 cm long (simulated length on the protective screen). To mask the appearance and disappearance of lines at the borders of the background (when it moved), we decreased the intensity of the lines in the leftmost and rightmost 4 cm of the background area.

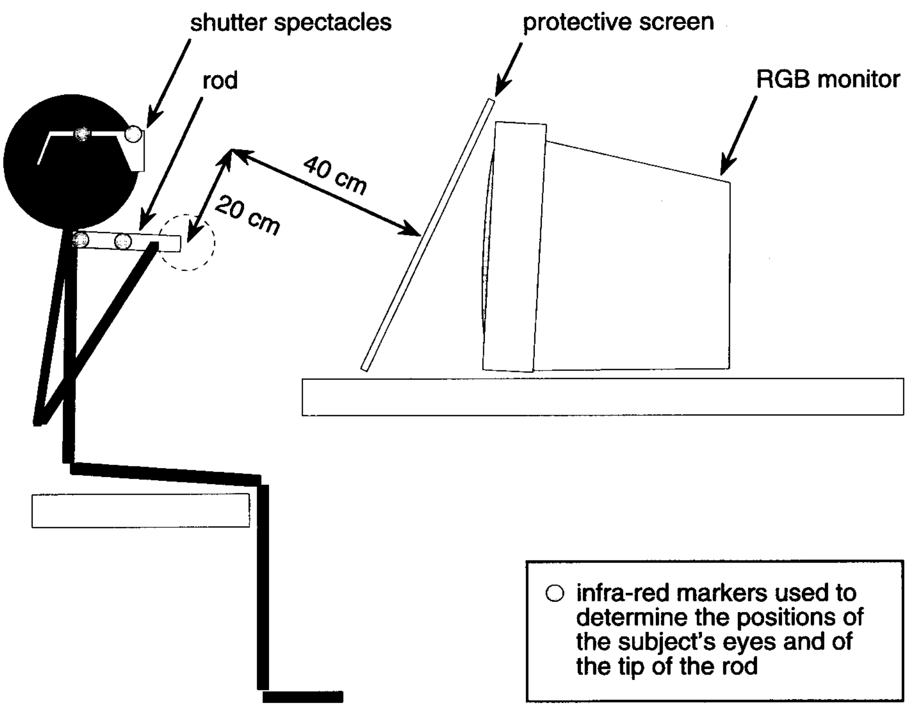

FIGURE 1. The experimental setup used in the first two experiments. Subjects saw 42 randomly oriented lines forming a plane that corresponded with the protective screen. That was achieved by presenting different images on the monitor for the two eyes (liquid crystal shutter spectacles). Because the subjects were free to move their heads, all positions on the monitor had to be calculated for each frame (120 Hz) on the basis of the desired perceived position on the protective screen, the position of the monitor, and the momentary position of the subject's eye (delay was about 34 ms). To start a trial, subjects had to place the tip of the rod within 5 cm of a fixed position in space (dashed circle). At some unpredictable moment, a red disk appeared exactly in front of the tip of the rod. The subject's task was to hit the red disk as quickly as possible.

There was no restriction on head movements (restriction of head movements has been shown to impair both hand and eye movements [Biguer, Prablanc, & Jeannerod, 1984; Collewijn et al., 1992]). Whenever subjects moved their heads, the position of the structures' images had to be changed on the computer monitor so that the structures would appear to remain at the same position on the protective screen. On each frame, we calculated new positions for each structure (lines and target), taking into account the positions of the subjects' eyes at that moment (see below; note that we accounted for the position of the eye in space, not its orientation in the head).

Measuring the Subjects' Movements

On the basis of active infrared markers, we recorded the positions of the subject's head and hand with a movement analysis system (Optotrak 3010, Northern Digital Inc.). The markers for measuring movements of the hand were attached to a perspex rod (22 cm long, 1 cm radius) with which the subject was to hit the targets. The wires attached to the markers were long, thin, and flexible so as not to restrain the subject's movements. Hereinafter, we sometimes describe our data in terms of the position and movement of the hand, although, strictly speaking, we will always be reporting on the position and movement of the tip of the rod. That position was determined by extrapolation from the measured positions of two markers at fixed positions on the rod's central axis. Two more markers were aligned horizontally on the right earpiece of the shutter spectacles so that movements of the head could be measured. The resolution of the position measurement was better than 0.1 mm (in all three dimensions). Position data were collected at 300 Hz for 1.5 s per trial.

We determined each eye's position from the positions of the markers on the spectacles and the distance between the subject's eyes. Because we used only two markers on the spectacles, we could account for all changes caused by translations of the head, but only for the influence of rotations around two axes. Rotations of the head around the third axis were ignored. Subjects did not notice errors arising from such rotations. Neither did they notice the delay (about 34 ms) in adapting the visual image to changes in the positions of the eyes.

Synchronization

Although we wanted subjects to see a red target, the computer was sometimes programmed to draw a purple one (red and blue). We used the blue component of the image generated by the computer to synchronize the information on the position of the rod (300 Hz) with the appearance and change in position of the target on the screen (120 Hz). That signal never reached the monitor (therefore, the target was always red) but was fed to one of the analog input channels of the Optotrak. In that manner, we were able to determine the moment that the target actually appeared on the screen (blue signal on) and the moment that the change occurred (blue signal off)—for example, when the target started to move—with the 3-ms resolution with which the positions of hand and head were determined. That also allowed us to determine the delay between the onset of movement of the rod and the first moment that the target appeared at a new position. That delay was 34 ± 7 ms (mean and standard deviation). A substantial part of the delay (about 21 ms) was caused by the time it took to "draw" and present a new image on the monitor.

Procedure

The target appeared only if the tip of the rod was less than 5 cm away from the starting position: 40 cm straight out and 20 cm downward from the center of the protective screen (dashed circle in Figure 1). That left the subjects quite free in choosing how to hit the targets while ensuring that the target would appear on the background. Instructions on the screen helped subjects to place the tip of the rod within the required region. Once that was accomplished, the instructions disappeared and subjects saw the plane of randomly oriented lines. After some time (2–4 s), the red disk appeared. To allow us to average the trajectories, we made sure that the disk always appeared at the same position relative to the tip of the rod (20 cm above its orthogonal projection on the protective screen). Subjects did not notice that. What they did notice was that the target did not always appear at the same position on the screen. The subjects' task was to hit the disk with the rod as quickly as possible.

In the first experiment, the target sometimes jumped to the left or to the right when the rod started moving. The rod

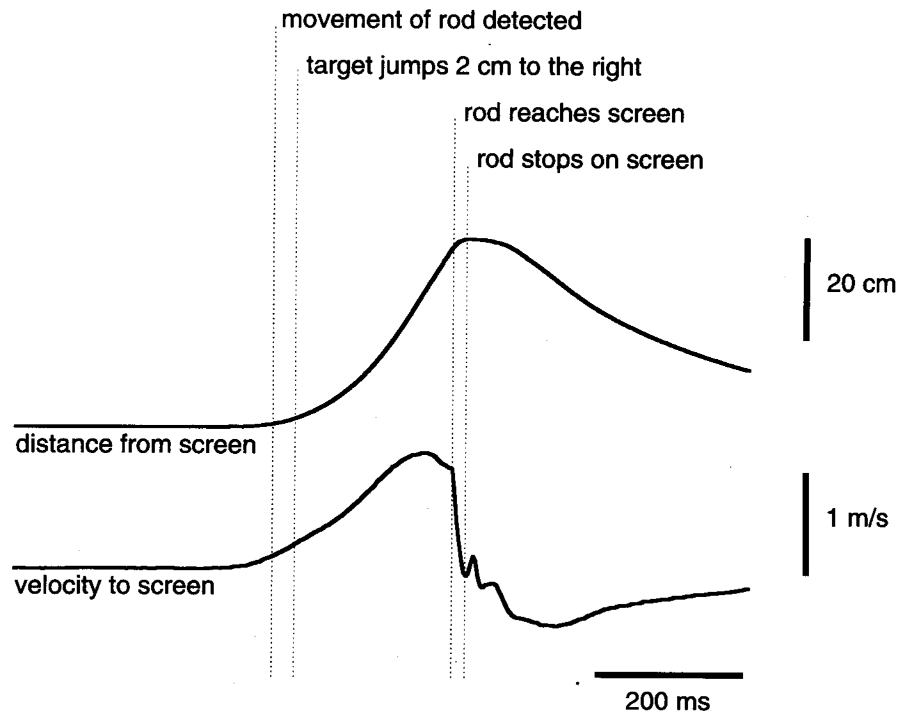

FIGURE 2. Example of a single movement toward the screen (Subject EB). The rod started moving toward the screen about 360 ms after the target appeared. About 34 ms later, the target jumped to the right. After another 220 ms, the rod hit the protective screen. It took another 20 ms for the rod to stop moving forward altogether because the screen was slightly flexible. Note the constant acceleration until just before the rod hit the screen.

was considered to have started moving once its position was 0.5 mm closer to the screen than the average position during the preceding second. Because of the above-mentioned delay (see *Synchronization*), the jump occurred about 34 ms after the rod was considered to have started moving (Figure 2). Most subjects did not notice the fact that the timing of the jump had anything to do with their own movement. There were 30 trials on which the target jumped 4 cm to the left, 30 on which it jumped 2 cm to the left, 30 on which it remained at the same position, 30 on which it jumped 2 cm to the right, and 30 on which it jumped 4 cm to the right.

In the second experiment, which was conducted several weeks later, there were 22 trials in each of the seven conditions. The target either did not move or else it started moving to the left or to the right at 12 or 24 cm/s (velocities at which the targets, on average, moved about 2 and 4 cm before being hit). Moreover, rather than the target, the background could start moving to the left or to the right at 24 cm/s. In those last two conditions, the target did not move.

Within each experiment, trials of different conditions appeared in random order, so it was impossible for the subjects to predict what would happen. A few trials were discarded because subjects did not react within 750 ms of the moment the target appeared or because the infrared markers were hidden from view for longer than 10 ms.

Subjects received feedback on their performance. The target broke into four unequal pieces if we considered it to have been hit; that is, if the center of the rod was within 1.8 cm of the center of the disk. If subjects hit to the left of the target, the target moved away to the right. If they hit to the right, it moved away to the left. Moreover, subjects could vaguely see the rod's (and their hand's) contour because parts of the image were occluded when the rod was close to the screen. For the feedback, we did not determine the moment that the rod stopped on the screen (see Figure 2) but considered subjects to have hit the screen as soon as the tip of the rod was less than 5 mm from the screen.

Analysis of the Trajectories

To calculate average trajectories for each subject and experimental condition, we determined the lateral position of the tip of the rod (using linear interpolation) when it was at various distances (steps of 3 mm) from the screen. Those lateral positions were then averaged (for each distance from the screen).

The position of the tip of the rod was determined approximately every 3.3 ms (300 Hz). We calculated the average velocity during the interval between two measurements by dividing the displacement of the tip of the rod by the 3.3 ms between the measurements. To obtain the velocity at the moment that the position of the tip of the rod was determined, we used the average of the velocities during the intervals before and after that moment. To obtain the acceleration, we took the difference between these velocities and divided it by the 3.3 ms that separated them. The high spatial resolution allowed us to do without any additional filtering that could have influenced the time at which a response appeared to occur.

For statistical evaluation of the responses to the perturbations, we compared the lateral velocity of the rod at different times after corresponding leftward and rightward perturbations (for each subject), using one-tailed Mann-Whitney U tests. The direction of the response was determined from the difference between the lateral velocities 200 ms after the perturbation. We then searched backward from 200 ms until we reached a sample on which the difference in velocity was no longer significant at the 95% confidence level. That provided an upper limit of the time taken to respond to the perturbation. Using paired t tests, we compared those upper limits of the latencies for different conditions.

Results

Subjects took about 400 ms to react to the appearance of the target on the screen (reaction time) and another 250 ms for the rod to stop on the screen (movement time). Most subjects moved the rod toward the screen with an almost constant acceleration (see example in Figure 2). The reaction time obviously did not depend on the condition, because all conditions were the same until the subject reacted (and the order of presentation was unpredictable). The movement time was also very similar for all conditions. Most important, the perturbation did not delay the rod's movement toward the screen. Individual subjects were quite consistent in their reaction and movement times (with standard deviations of about 50 and 30 ms). However, there were considerable differences between subjects: Reaction times varied between 350 and 500 ms, and movement times between 170 and 430 ms. There was no clear relationship between a subject's reaction time and how fast he or she subsequently moved his or her hand.

The velocity with which subjects moved the rod toward the screen obviously influenced the trajectories. In Figure 3, the average trajectories, for each condition, for the subjects who moved the rod fastest and most slowly toward the screen are shown. The trajectories are shown from the instant that the perturbation occurred (or, when there was no perturbation, the instant that it would have occurred) until the rod reached the screen. For the subject who moved the rod slowest toward the screen, the trajectories were evidently influenced by the perturbations. That was not so for the subject who moved the rod fastest. The circles along the trajectories show how far the tip of the rod moved (on average) during the first 100 ms after the perturbation. It is evident that if it took longer than 100 ms to respond to the perturbation, the faster subject would have hit the screen before she could adjust her movement. The circles at the top of each figure show the targets' positions when the rod hit the screen. For the moving stimuli (Figure 3c, d), those positions obviously depended on the subjects' movement times.

The lateral velocity of the tip of the rod, as a function of the time since the perturbation (or absence thereof), for the same 2 subjects is shown in Figure 4. Both subjects moved

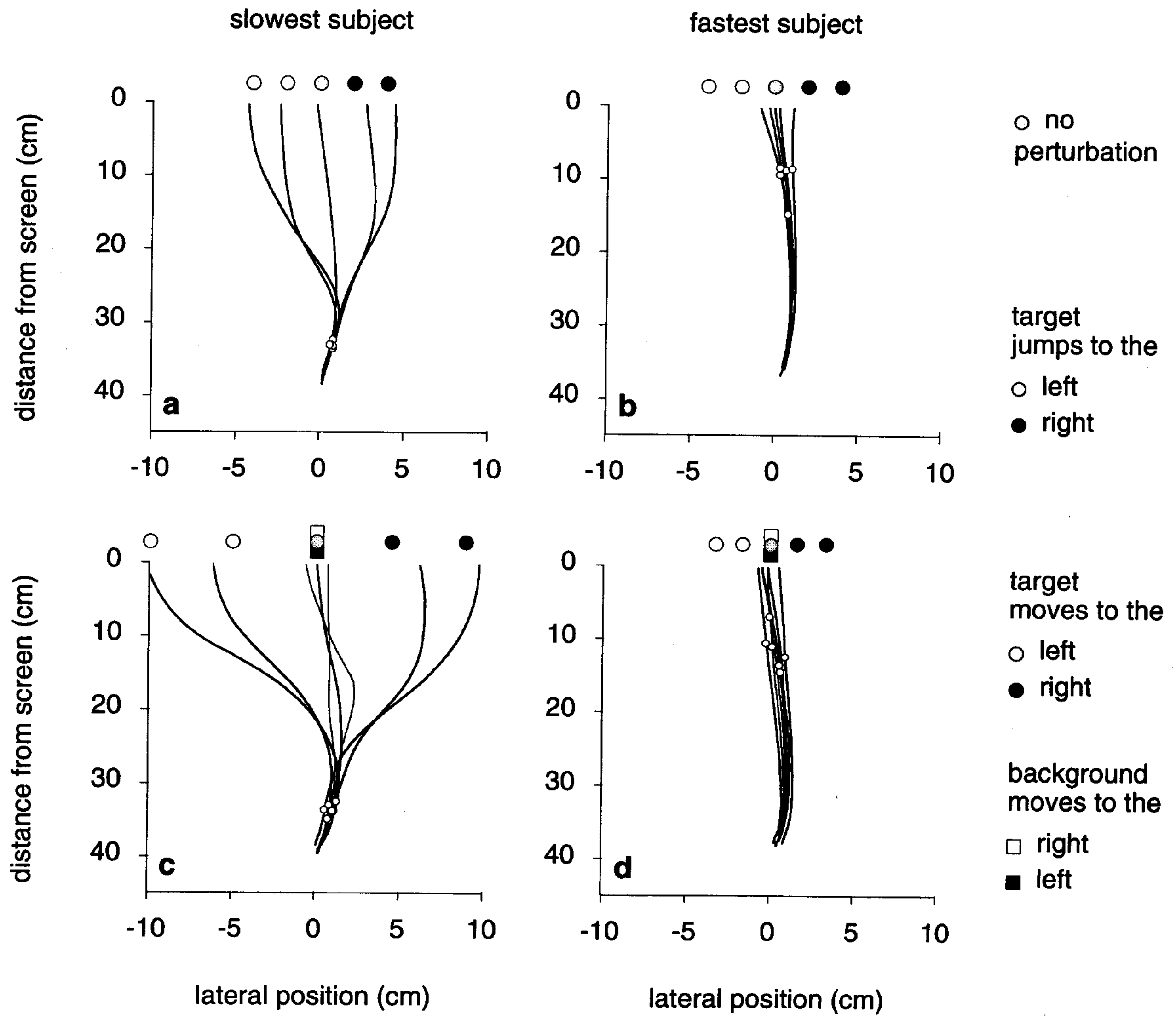

FIGURE 3. Average trajectories of our fastest (**b** and **d**) and slowest (**a** and **c**) subjects, for targets that either jumped (**a** and **b**, Experiment 1) or moved (**c** and **d**, Experiment 2) away as soon as the subject started hitting them. The position of the tip of the rod is shown from the moment at which the perturbation could occur (about 34 ms after the rod started to move) until the moment that the rod reached the screen (about 20 ms before it stopped moving). The circles on the trajectories show how far the tip of the rod moved during the first 100 ms after the perturbation. The symbols at the top of the figure indicate the average position of the target at the moment the rod reached the screen. For moving targets (**c** and **d**), the positions depended on the time it took the rod to reach the screen. The thin lines in **c** and **d** are for static targets on moving backgrounds. The slowest subject's hand initially moved in the same direction as the background (**c**).

the rod sideways in response to the perturbations. Most of the adjustment took place between 100 and 300 ms after the perturbation. The slower subject reached the screen after that time (transition to shaded area), so the adjustments are visible in her trajectories (Figure 3a, c). The faster subject hit the screen before her hand had time to move appreciably in response to the perturbation, so no adjustments are visible in her trajectories (Figure 3b, d). She responded as quickly (Figure 4b, d), but she had already hit the screen by the time she started doing so. When the background moved, both subjects initially moved the rod in the direction in which the background was moving rather than in the direction of the target's motion relative to the background.

The time it takes to respond to a perturbation is probably made most evident by the rod's lateral acceleration. Trajectories toward unperturbed targets were not straight (see Figure 3), so the rod's lateral velocity and acceleration were not zero. To estimate how long it took subjects to respond to the perturbations, we therefore isolated the additional acceleration in response to the perturbation by subtracting the acceleration on unperturbed trials from that on perturbed ones. Because there was no evident difference between the time it took to respond to the different directions and amplitudes of the perturbations, the additional accelerations (in the direction of the target's perturbation relative to the background) were averaged for each subject. Subjects took about 110 ms to respond to an abrupt displacement, about 120 ms to respond to target motion, and about 150 ms to respond to motion of the background (Figure 5). The large sudden changes in acceleration that are visible in the individual subjects' traces after 150–200 ms (Figure 5a, b) were caused by the rod's hitting the screen. That impact probably was also responsible for the somewhat less clear responses to background motion (Figure 5c).

Whenever the target was perturbed, we found a significant response in the direction of the perturbation. When the background moved, we always found a response in the direction in which the background moved, but the difference between the lateral velocities of the rod in response to leftward and rightward background motion was not significant (200 ms after the background started to move) for 1 of the 6 subjects. That subject's latency, therefore, could not be

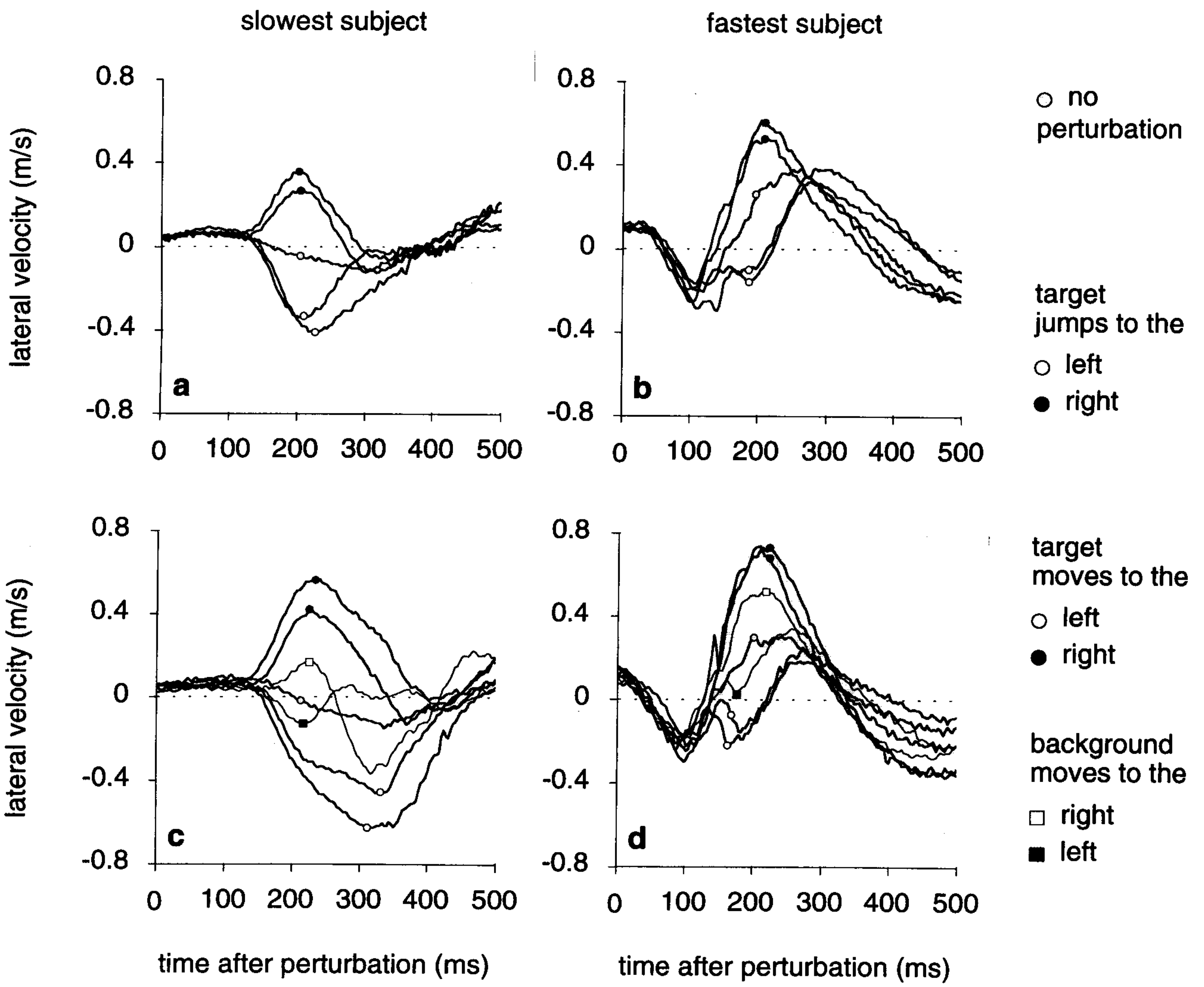

FIGURE 4. Average lateral velocity of the tip of the rod for the same subjects and conditions as in Figure 3. Positive values indicate movement to the right; negative values, movement to the left. Time was measured from the first frame in which the target could be at a new position. The transition to a shaded background indicates the average moment that the subject hit the screen. Note that the fastest subject's response continued after she had hit the screen. The symbols indicate the conditions represented by individual traces; their positions on the traces are arbitrary. White symbols indicate that the target had moved to the left, and black symbols indicate that it had moved to the right, relative to the background.

determined according to the protocol described in the Method section.

The upper limits of the latencies are shown in Figure 6. Altogether, the statistical analysis supported the latencies we estimated from Figure 5. The upper limits for abrupt displacements were about 10 ms longer than the latencies we estimated from the acceleration plots. Those for motion onset were about 20 ms longer. The larger difference for moving targets could have been caused, at least partly, by the smaller number of trials in each condition in the second experiment (a smaller number of trials will increase the estimate of the upper limit because it reduces the likelihood

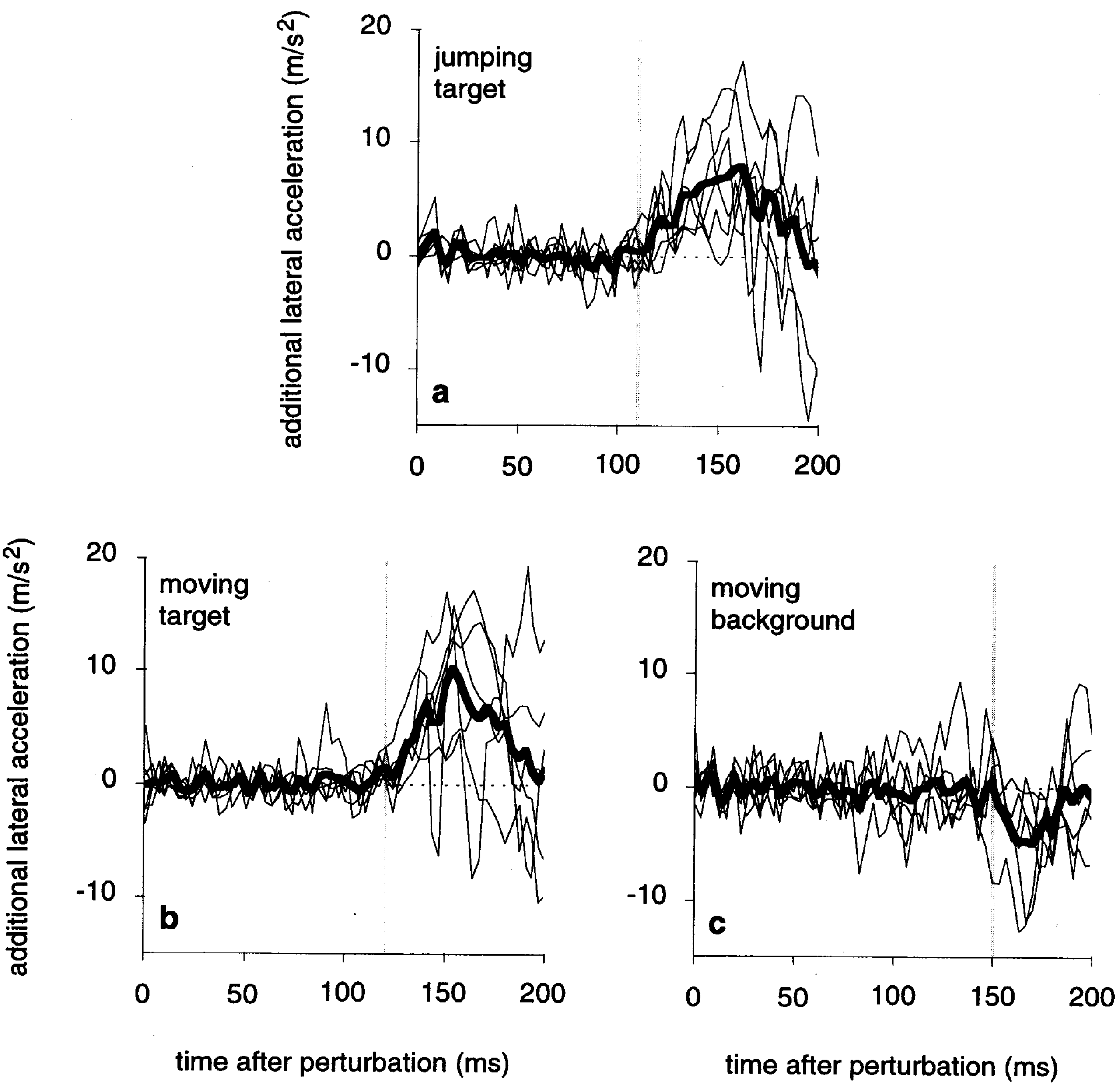

FIGURE 5. Difference between the average lateral acceleration of the tip of the rod on trials in which the target was displaced and on ones in which it was not. Positive values indicate an acceleration in the direction of the perceived displacement (**a**, Experiment 1) or motion (**b** and **c**, Experiment 2). For the moving background (**c**), that was in the opposite direction to the one in which the background was moving. In that case, the rod moved in the direction in which the background was moving, rather than in the direction in which the target appeared to move. The thin lines show the average acceleration (for both amplitudes and directions of the displacement) for individual subjects. The thick line shows the average of all 6 subjects. The shaded, vertical line shows our estimate (by eye) of the time it took for the hand to react to the (changed) visual information.

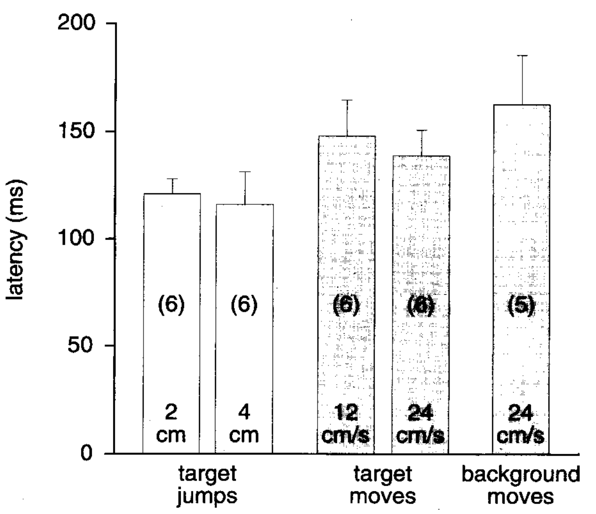

FIGURE 6. Upper limits of the latencies: last samples for which the lateral velocity of the rod was not significantly different after leftward and rightward perturbations. Means and standard deviations (between subjects) are given, with the number of subjects in brackets. The shading divides the latencies into two categories (equivalent to the two experiments). Paired *t* tests revealed no significant differences between conditions within each category (95% confidence level) but significant differences for all comparisons between conditions in different categories. Only 5 subjects' data were averaged for the background motion condition, because the 6th subject showed no significant difference in lateral velocity of the rod 200 ms after the perturbation, which made it impossible to determine the upper limit of the latency according to our protocol.

that a difference in velocity will be statistically significant). The smaller number of trials probably also contributed to the fact that the upper limits were significantly shorter when the target jumped than when it moved ($p < .02$ for all four comparisons; note that the variability may also have differed between the two experiments, because variability is known to depend on both experience with the task and uncertainty about the position of the target; Georgopoulos et al., 1981). There was a tendency for larger jumps and faster motion to have shorter latencies, but those differences were not significant (respectively, $p = .38$ and $p = .06$). Likewise, the longer average latency of the response to background motion was not significant ($p = .10$ and $p = .06$, for comparison with the slower and faster target motion, respectively).

EXPERIMENT 3. PERCEIVED MOTION

Method

We assumed, on the basis of previous findings, that when the background is moving, the target will appear to move in the opposite direction. That assumption was confirmed in a separate experiment. Because we were interested in the initial response to the moving background rather than in a rational interpretation of the stimulus, we used a choice reaction time task to assess the influence of moving the background.

In the third experiment, we used the same stimuli as in the second experiment, except for stimuli that remained static. We presented target motion at 12 or 24 cm/s to the left or to the right (four conditions; 10 presentations each) and background motion at 24 cm/s to the left or to the right (two conditions; 5 presentations each). The target appeared at a random position within the central 3 × 3 cm of the background. After a random interval of 2–4 s, either the target or the background started moving. Subjects were asked to respond to such motion as quickly as possible. They were instructed to press the left button of the computer mouse if the target moved to the left and the right button if the target moved to the right. The 50 trials were presented in random order.

Six subjects took part in the experiment (3 of whom, including the authors, had taken part in Experiments 1 and 2). They sat with their chins on a chin rest, about 55 cm from the protective screen, so we did not need to account for movements of their heads. The subjects were instructed to respond as quickly as possible so that we would be certain to get the first reaction to the illusory target motion.

Results

The main results of the choice reaction time task are shown in Figure 7. The general tendency is evident: All subjects most often responded to background motion by pressing the button corresponding to the direction of motion opposite to the one in which the background was moving. Thus, the perceived motion was indeed as predicted. Presumably because of the emphasis on speed, subjects sometimes pressed the right button when the target moved to the left, and vice versa. They appeared to make slightly more mistakes when the background moved than when the target did. The finding that all 6 subjects responded to the moving background, in the second experiment, by moving the rod in the direction in which the background was moving, implies that the subjects did not use the illusory motion to anticipate where they would hit the target.

EXPERIMENT 4. PERCEIVED POSITION

Method

We also examined how moving the background influences the target's perceived position. In the fourth experiment, again with the same stimuli as in the second experiment, subjects were asked to indicate the position at which they saw the target disappear.

The target appeared at a random position within the central 3 × 3 cm of the background. After a random interval of 300–400 ms, the target disappeared or either the target or the background started to move. If the target had not disappeared, it did so (and the background stopped moving) 33, 67, or 100 ms later (after two, four, or six frames had been

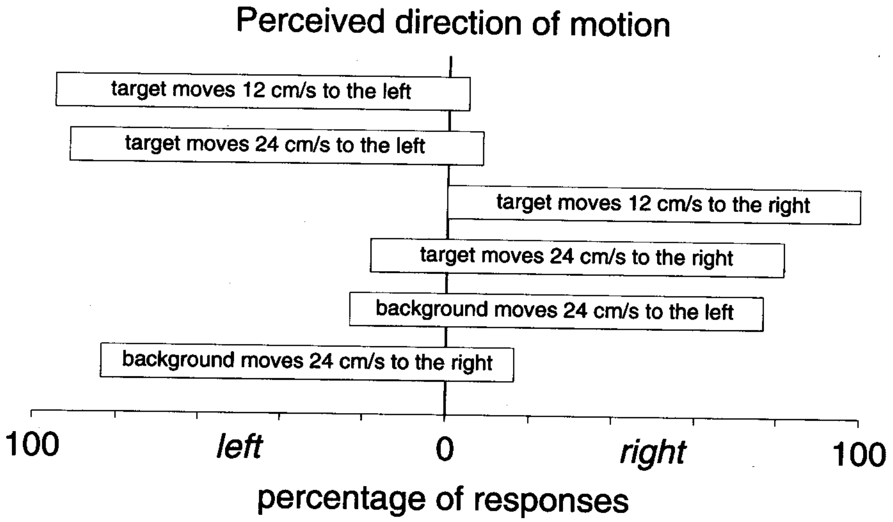

FIGURE 7. Summary of the responses in the choice reaction time task (Experiment 3). When the target moved to the left, subjects almost always responded by pressing the left button. Similarly, when the target moved to the right, they almost always pressed the button on the right. When the background moved to the left, subjects usually pressed the right button, and vice versa. Thus, they responded to the induced motion.

presented to each eye). After 1 s with only the stationary background visible, a new disk appeared (at a random position within a 5-cm × 5-cm square centered on the position at which the target disappeared; note that the background remained visible throughout the experiment). The subjects could move that new disk around by moving the computer mouse. They were asked to place the new disk at the position at which the target disk had disappeared. They were explicitly warned in advance that the target may move at the end of its short presentation and that they should indicate the final position before it disappeared. They could take as long as they liked. Subjects indicated that they were satisfied with their match by pressing a button of the computer mouse. One second later, the next target appeared.

Each of the 19 conditions (2 × 3 × 3 + 1; respectively, leftward or rightward motion, three durations of motion, target moving at 12 or 24 cm/s or the background moving at 24 cm/s, and presentation with no motion) was presented six times, all in random order. There were 6 subjects, who sat with their chins on a chin rest, about 55 cm from the protective screen. Three of these subjects, including the authors, had taken part in the third experiment. The other 3 had not performed any of the previous experiments.

Results

The main results of the position-matching task are shown in Figure 8. In that figure, the average set lateral position of the matching disk (relative to the position at which the target first appeared) is shown for each condition. When the target moved during the last few frames, subjects correctly identified the position at which it disappeared. They did so reasonably accurately (circles close to lines). When the background moved, subjects made systematic errors (the lateral position of the squares should obviously have always been zero). They tended to indicate a position that was shifted in the direction in which the background was moving. That is, the shift in position was opposite in direction to the one in which the target appeared to be moving (Experiment 3).

The subjects were inclined to indicate the target's original position on the background. However, they could not simply have misunderstood the task, because the previously occupied position on the background did not influence the settings when the target moved and the background was static. We propose that subjects attribute the uniform motion of the retinal image of the background (or most distant surface; Brenner, 1991) to their own self-movement, in which case the (static) target "should" have moved with the background. Interpreting uniform motion of the retinal image of the background as ego-motion normally may help to guide the hand to a fixed position in the stationary environment when we move, much as it has been proposed to help stabilize our gaze on items in the stationary environment when we do so (short latency ocular-following responses; Gellman, Carl, & Miles, 1990).

DISCUSSION

We found that it takes subjects about 110 ms to respond to unpredictable perturbations of a target's position. That value is very close to Prablanc and Martin's (1992) and

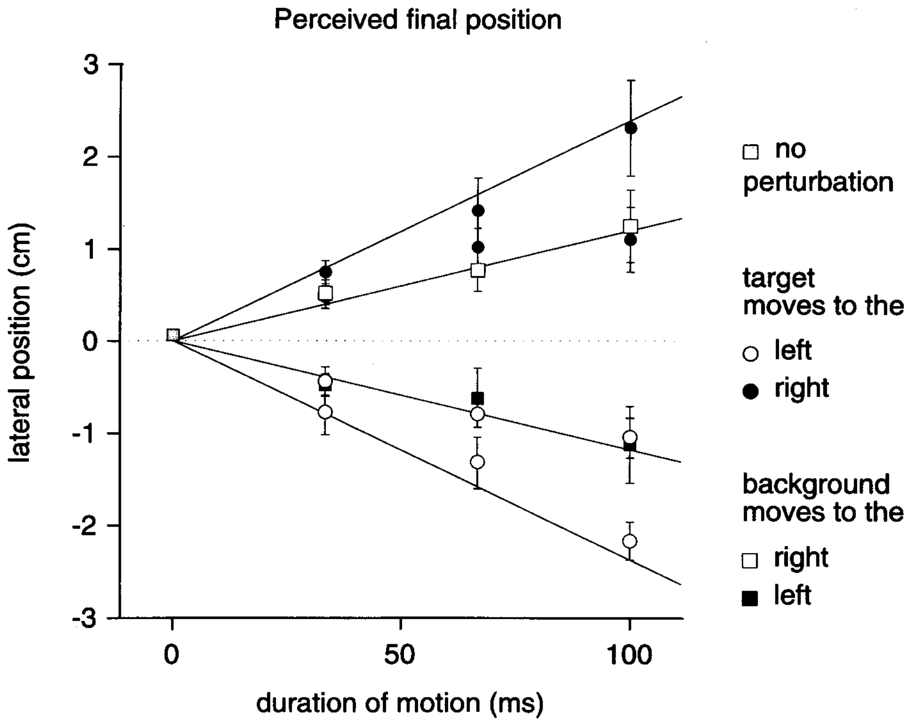

FIGURE 8. Summary of the responses in the position-matching task (Experiment 4). Average set lateral position of the matching disk (to the right of the initial position of the target disk, with standard errors between subjects). The symbols show matches for static targets on a static background (shaded square), static targets on a background that moved during the last few frames of the presentation (other squares), and targets that moved across a static background during the last few frames (circles). Open symbols represent conditions in which the perceived motion was to the left. Filled symbols represent conditions in which the perceived motion was to the right. The lines indicate the actual position of the moving targets (as a function of the duration of motion). Moving the background during the last few frames influenced the perceived final position of static targets (squares not on dotted line). Moreover, that displacement was in the direction of background motion rather than in the direction of perceived target motion.

Soechting and Lacquaniti's (1983) estimates and confirms that some corrections can be made during most movements.

When the background moved (in the second experiment), subjects diverted their hands in the direction opposite to the one predicted by the perceived motion (third experiment). They moved the rod in the direction in which the background was moving, as they would if they were responding to the change in the target's perceived position (fourth experiment). That finding provides compelling evidence for the notion that we adjust our movements only in response to changes in the target's perceived position. In the following section, we show that that notion is in accordance with the rest of our subjects' performance, although that may not immediately be evident from the results.

Guiding the Hand to the Target

We found that it took about 110 ms to respond to a sudden change in target position (Figure 5a). It took about 10 ms longer to respond to motion onset (Figure 5b). The moving target was displaced by steps of either 1 or 2 mm (as simulated on the protective screen) every 8 ms (120-Hz frame rate), with consecutive positions presented, in turn, to the left and right eyes. A target that is seen with both eyes has to move 0.15° (about 1.2 mm at a viewing distance of 45 cm) for the change in position to be detected (Smeets & Brenner, 1994). A slightly higher threshold when the displacement is initially seen by only one eye could easily give rise to a 10-ms-longer response latency for moving targets.

In the introductory comments, we proposed that comparing responses to targets that suddenly started moving with responses to targets that jumped to their new positions would reveal whether subjects use the targets' motion to anticipate the position at which the targets will be hit. Our reasoning was that if subjects respond only to the moving target's position, the initial response—for a barely detectable change in position—will be extremely small. Thus, the response to motion onset should be more gradual than to a sudden jump. A comparison of the average additional lateral accelerations in Figure 5a and b does not suggest that that difference in response occurs, but the shapes of the responses in those figures tells us little about the shape of individual responses. In Figure 5, the responses were averaged with respect to the moment of the perturbation. Consequently, variability in the latency of the response caused different parts of individual responses to be averaged, resulting in flatter average traces. We therefore recalculated average responses for each type of perturbation. This time, however, we synchronized the individual responses with respect to the first instant at which the additional lateral acceleration reached a threshold value (an average of 5 m/s^2 during the next 67 ms).

Figure 9 shows the data for the 2 subjects for whom the moving targets were closest to 2 or 4 cm to the left or right of the initial position (the distance the other targets had jumped) when the rod hit the screen. We have already argued that if those subjects used information on the target's motion to anticipate where they would hit the target, the lateral acceleration in response to the targets that suddenly started to move should have been the same as that in response to the targets that suddenly jumped away. It is evident that the responses were indeed very similar for both kinds of perturbations. However, the lateral acceleration was also almost identical for the targets that were to be hit at 2 cm and at 4 cm. That finding suggests that the subjects may have ignored the amplitude of the perturbations altogether, responding only to their direction.

Both humans and monkeys have been shown to apply an excessive amount of force to modify the trajectory of their hand when a target is displaced (Georgopoulos et al., 1981; Massey, Schwartz, & Georgopoulos, 1986). Georgopoulos (1990) has suggested that subjects increase the force to compensate for the reduced use of sensory information. In the present study, several subjects may even have had to respond maximally to the perturbations if they wanted to stand any chance of hitting the targets. Indeed, the rate of change in lateral acceleration (and, thus, in force) was quite constant, and probably close to the maximal change in acceleration that one can achieve for that kind of movement (Wadman, Denier van der Gon, & Derksen, 1980). That subjects always responded with the same (possibly maximal) lateral force would account for the fact that the

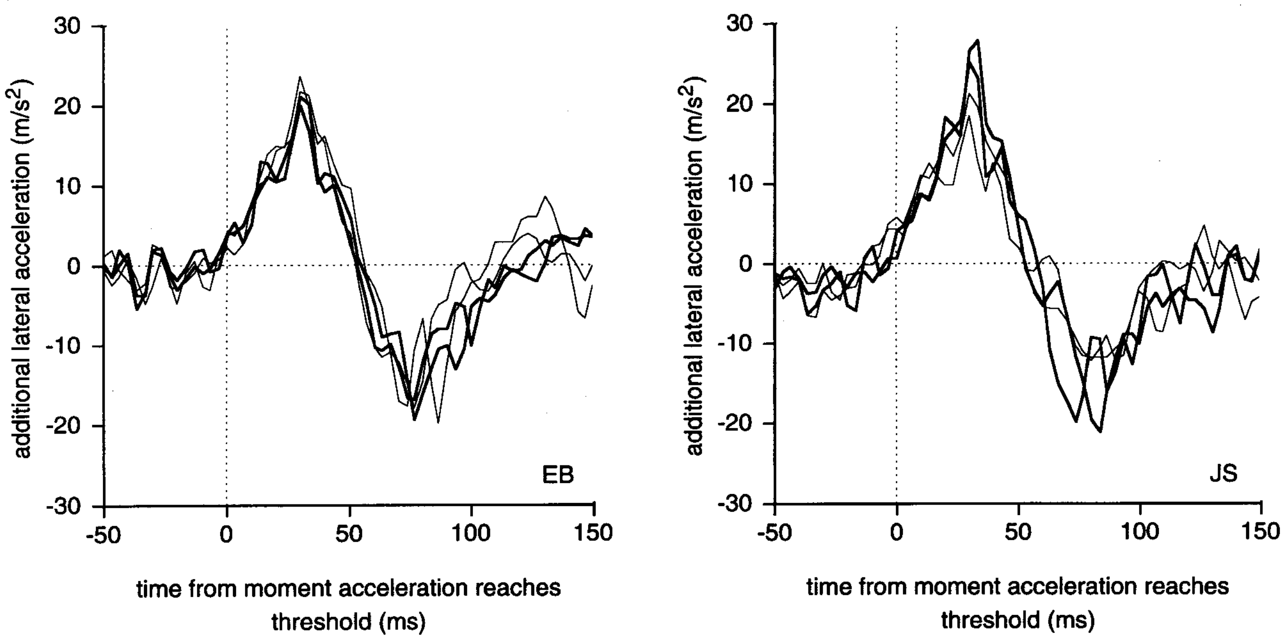

FIGURE 9. Average additional lateral acceleration in the direction of the target's displacement. Two subjects' responses for each velocity of target motion (12 or 24 cm/s; thin lines; Experiment 2) and jump size (2 or 4 cm; thick lines; Experiment 1). The lateral acceleration traces were synchronized with respect to the moment they reached a threshold (an average of 5m/s^2 during 67 ms) before being averaged. Note that the response to the two kinds of perturbations, and to the two values of each perturbation, were extremely similar.

response to motion onset was not more gradual than the response to sudden displacements, and for the fact that the reponse was similar for the two amplitudes of perturbation. Those findings also explain why the response often continued long after the screen had been hit (see Figure 4).

The direction of the response must depend on visual information. It has long been known that our visual system processes information on a target's motion independently of information on its changing position (e.g., Exner, 1888). However, motion and changing position are normally so closely related that one cannot tell which source of information is being used. Moving the background helps us distinguish between the two. Although the target actually remained static, subjects responded to the moving background. They moved the rod in the direction of the illusory change in position, rather than in the direction of the illusory motion. Thus, we can conclude that adjustments during goal-directed movements are driven by (illusory) changes in the position of the target. Note that we are not proposing that the conscious percept drives the adjustments but simply that the same information on the target's position forms the basis for the percept and the adjustments.

Vision of the Hand

In our experiments, part of the image on the screen was occluded when the hand was close to the screen. Except for that, however, subjects had no visual information on the position of their hands. The reason for our not allowing subjects to see their hands is related to the illusory target motion when the background moves. Illumination that allows subjects to see their hands also illuminates other structures in the background. Illumination of background structure reduces the illusion of target motion because those structures obviously do not move. Thus, our study examined only how we use visual information on the position of the target to guide the hand toward it. We assumed that kinesthesis provides us with the information that is needed to bring the hand to that position (i.e., that the retinal image of the target is related to the position of the tip of the rod on the basis of kinesthetic information on the orientation of the eyes, head, shoulder, arm, and hand).

Normally, we can see our hand, so that we also could use visual information on the target's position relative to our hand to guide the hand toward the target (Carlton, 1981; Elliott & Allard, 1985; Keele & Posner, 1968; Smith & Bowen, 1980; Zelaznik, Hawkins, & Kisselburgh, 1983). However, we cannot judge visual information about our hand's position relative to the target accurately enough to adjust the hand's trajectory until it is close to the target (Carlton, 1981). That makes it unlikely that subjects would have reacted differently if they had been allowed to see their hands, because the fact that subjects were instructed to reach the targets as quickly as possible (and the resulting constant acceleration of the hand) implies that the hand is close to the target only during the very last moments of the movement.

Link With Our Previous Work

In our previous work on hitting moving targets, the target was moving as soon as it appeared. The direction of motion (Smeets & Brenner, 1995b) and the velocity (Brenner & Smeets, 1994, 1996; Smeets & Brenner, 1995a) of a target that was moving from the start clearly influenced performance, although it was evident that subjects did not determine in advance where they would hit the target. Subjects clearly were also responding to new information during the movement. We have previously shown that all that is required during the movement is information about the target's changing position (Brenner & Smeets, 1996; Smeets & Brenner, 1995a), and the present results provide confirmation that, indeed, that information is probably the only information that is used.

A response latency of 110 ms is much faster than the time it takes to initiate even a very simple movement in response to a visual stimulus (e.g., Smeets & Brenner, 1994). That suggests that we are dealing with adjustments to ongoing movements, rather than to newly planned movements that replace (e.g., Georgopoulos et al., 1981) or are added to (e.g., Flash & Henis, 1991) the original movement. The visual information that can influence the adjustments appears to be quite limited. Presumably, some information, if considered before movement onset (i.e., during the reaction time), can lead to better performance, but that information takes too long to process to be of any use for adjusting ongoing action.

NOTE

1. Failing to respond to such an illusion—pointing at the veridical final target position—has been taken as evidence that the illusion influences only perception (Bridgeman et al., 1981), but recent research shows that background motion does influence motor responses if the responses themselves require information on motion (Brenner & Smeets 1994; Masson, Proteau, & Mestre, 1995; Smeets & Brenner 1995a, 1995b).

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Submitted January 22, 1996
Revised October 20, 1996