

RESEARCH ARTICLE

Eli Brenner · Jeroen B.J. Smeets
Marc H.E. de Lussanet

Hitting moving targets

Continuous control of the acceleration of the hand on the basis of the target's velocity

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Abstract Previous studies on how we hit moving targets have revealed that the direction in which we move our hand is continuously adjusted on the basis of the target's perceived position, with a delay of about 110 ms. In the present study we show that the acceleration of the hand is also under such continuous control. Subjects were instructed to hit moving targets (running spiders) as quickly as possible with a rod. We found that changing the velocity of the target influenced the speed with which the rod was moved. The influence was noticeable about 200 ms after the target's velocity changed. The extent of the influence was consistent with a direct dependence of the acceleration of the hand on the target's velocity. We conclude that the acceleration of the hand is continuously adjusted on the basis of the speed of the target, with a delay of about 200 ms.

Key words Motor control · Velocity · Acceleration
Arm movement · Vision · Human

Introduction

Subjects have a tendency to move their hand more quickly towards fast targets than towards slow ones (Baird 1987; Bootsma and van Wieringen 1990; Carnahan and McFadyen 1996; van Donkelaar et al. 1992; van Donkelaar and Lee 1994; Li 1996; Savelsbergh et al. 1992; Wallace et al. 1992). In the only case we know of in which they failed to do so, this can be explained by the hand having moved less far to intercept the faster targets (Chieffi et al. 1992). Subjects even move their hand more quickly towards fast targets when explicitly instructed to hit the targets as quickly as possible (Smeets and Brenner 1995). Our explanation is that subjects do not use all the available visual information to predict when and where they will hit the target. Instead, they independently con-

trol the direction in which the hand moves and its acceleration (as suggested for direction and extent by Ghez et al. 1997). The direction in which subjects move their hand is based on the perceived position of the target. The hand's acceleration – and thereby the movement time – is based on the target's perceived velocity. This separation limits the subjects' options concerning the movement time, because their success in hitting the targets relies on the combination of the two influences (Brenner and Smeets 1996).

The suggestion that subjects do not use all the available visual information when dealing with moving targets is not new. For instance, information about the target's acceleration is either ignored altogether (Lee et al. 1983) or at least not fully utilised (Lee et al. 1997). Even the perceived velocity appears to be ignored when determining the *initial* direction in which the hand will move (Baird 1987; van Donkelaar et al. 1992; Smeets and Brenner 1995).

Subjects may occasionally respond before the visual information has been fully interpreted and modify their movements as the interpretation proceeds (van Donkelaar et al. 1992). However, information about target velocity must usually already have been interpreted by the time the hand starts to move, because the perceived target velocity influences the velocity of the hand from the start (Baird 1987; Smeets and Brenner 1995). It also influences the reaction time (van Donkelaar et al. 1992; Port et al. 1997; Smeets and Brenner 1995).

We have proposed that visual information about the target's position and velocity are not combined into a single prediction of when and where the target will be hit. Instead, the perceived position is used to determine the direction in which the hand will move and the perceived velocity to determine how fast it will move (Brenner and Smeets 1996). These two (simultaneous) mechanisms need not interact until the stage at which actual commands for the muscles are generated.

The advantage of separating the visual control of the hand in the proposed manner is that it simplifies the link between the visual information and the controlled aspect

E. Brenner (✉) · J.B.J. Smeets · M.H.E. de Lussanet
Vakgroep Fysiologie, Erasmus Universiteit Rotterdam,
Postbus 1738, 3000 DR Rotterdam, The Netherlands
e-mail: BRENNER@FYS1.FGG.EUR.NL, Fax: +31-10-4367594

of the movement. Simplicity is an advantage not only in terms of the required neuronal connectivity but also because computations that need fewer steps, or that involve fewer parameters, can presumably be done faster and more accurately. Speed of computation is important, because short visuo-motor delays can be beneficial when dealing with the unpredictable movements of everyday targets. An emphasis on quick processing of visual information, however, is only useful if the movement of the hand is under continuous visual control.

The direction in which the hand moves is known to be under the continuous control of the perceived position of the target, with a visuo-motor delay of about 110 ms (Brenner and Smeets 1997; Goodale et al. 1986; Prablanc and Martin 1992). This continuous control helps compensate for errors that arise when the target's displacement is not anticipated correctly (Baird 1987; Smeets and Brenner 1995). If variations in movement time – due to differences in hand acceleration – are also essential for hitting moving targets (Brenner and Smeets 1996), the acceleration of the hand should change when the target's velocity changes. In the present study we show that the acceleration of the hand is indeed under continuous visual control.

Materials and methods

The study consists of a single experiment in which the subjects' task was to hit moving targets with a rod (Fig. 1). They were explicitly instructed to do so as quickly as possible. The target always appeared on the left side of the screen and was always moving to the right. We manipulated the velocity of the target's rightward motion.

Targets and background

The targets and background were presented on a computer monitor (38×28 cm; 815×611 pixels) that was tilted backwards at an angle of 11°. Images were presented at a rate of 120 Hz. Liquid-crystal shutter spectacles were used to present alternate images to the left and right eyes, in order to make the visible background appear to coincide with a transparent, protective screen. The latter was tilted backwards at an angle of 28° to make the movement more comfortable. The distance between the centre of the monitor and the protective screen was about 8 cm. Predominantly red stimuli were used because the shutter spectacles work best at long wavelengths.

The target was a simulated spider. Its body consisted of three segments with a total length of 0.85 cm. Eight 1.5-cm legs "attached" to the middle segment moved in accordance with the spider's simulated velocity. The background was a plane consisting of 500 lines. The lines were distributed at random within 15 cm of the centre of the protective screen. Outside of the central 20 cm (diameter), their intensity faded gradually with their distance from the centre of the screen. The lines were 4 cm long and were oriented at random within the simulated plane.

The combination of presenting the target and background in front of the computer screen with the aid of shutter spectacles, and not restricting head movements, meant that structures' images had to change their positions on the computer monitor – if they were to appear to remain at the same position on the protective screen – when subjects moved their heads. The positions of the subjects' eyes were therefore taken into account when rendering the images (note that we account for the positions of the eyes in space, not their orientations).

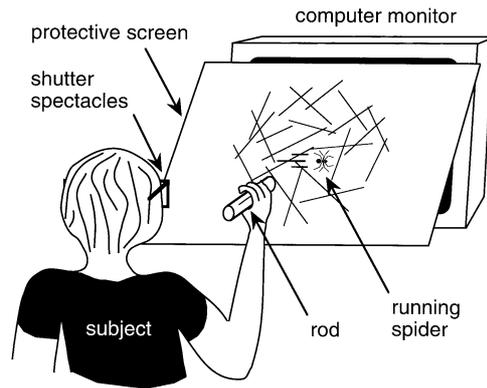


Fig. 1 Schematic view of a subject hitting a running spider with a rod. By presenting different images to the two eyes, with the aid of liquid-crystal shutter spectacles, we could make the spider appear to be running on a screen that protects the computer monitor from the impact of the rod

Measuring the subjects' movements

The positions of the subject's head and hand were recorded at 250 Hz by a movement-analysis system based on active infrared markers (Optotrak 3010; Northern Digital). The markers for measuring movements of the hand were attached to a Perspex rod (22 cm long, 0.9 cm radius) with which the subject was to hit the targets. Subjects held the rod between their fingers and thumb as they would hold a pen. The wires attached to the markers were long, thin and flexible so as not to restrain the subject's movements. We 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. This position was determined by extrapolation from the measured positions of two markers on the rod's central axis.

Four more markers were attached to the right ear-piece of the shutter spectacles for measuring movements of the head. We determined each eye's position from the positions of these markers and the distance between the subject's eyes. The delay in adapting the visual image to changes in the positions of the eyes was 21 ± 3 ms (mean and standard deviation).

Synchronisation

The "blue" component of the image generated by the computer was used to synchronise the information about the position of the rod (measured at 250 Hz) with the appearance and change in velocity of the target on the screen (presented at 120 Hz). This signal never reached the monitor, but was filtered (low-pass; 125 Hz) and fed to an analogue input channel of the movement-analysis system. In this 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) with the 4-ms resolution with which the positions of hand and head were determined (Brenner and Smeets 1997).

Procedure

The target only appeared if the tip of the rod was less than 5 cm from the "starting position": 40 cm away from a point 20 cm below the centre of the protective screen. Instructions on the screen helped subjects place the tip of the rod within the required region. Some time after this was accomplished, the target appeared. The target always appeared at the same position relative to the tip of the rod (20 cm above and 8 cm to the left of its orthogonal projection on the protective screen). Consequently, it did not always appear at the same position on the screen. We imposed no restrictions on how subjects should sit or move during the experiment, except that

they had to hold the rod at the starting position, without occluding the markers, to start each trial.

The initial velocity of the spider was either 4.5 cm/s or 7.5 cm/s. At some time within 400 ms of its appearing, this velocity changed. The change was either a 3 cm/s increase or a 3 cm/s decrease in velocity. Thus, there were four conditions: two initial target velocities, each combined with either an increase or a decrease in velocity. The condition and the moment at which the change occurred were determined at random for each trial. A few trials (less than 1%) were discarded because of errors in synchronisation, because the movement of the hand stopped before hitting the screen, because the subject missed the target by more than 10 cm, or because the subject did not react within 750 ms of the moment the target appeared.

Subjects received feedback on their performance. The spider was “squashed” if we considered it to have been hit. This was so if the centre of the rod was within 1.8 cm of the “centre” of the spider. If subjects hit to the left of the spider, the latter ran away to the right. If they hit to the right, it ran away to the left. If they hit above it, it ran downwards. If they hit below it, it ran upwards. Subjects could vaguely see their hand’s contour occluding part of the image when the hand was close to the screen.

Subjects and instructions

Seven subjects took part in the experiments, including the authors. The only special instructions subjects received was that they should hit the targets as fast as they could. Each subject tried to hit between 800 and 1200 spiders, during two or three sessions. Two (non-author) subjects’ data were excluded after preliminary analysis, because the final velocity of their hand did not increase systematically with target speed (on the trials in which the target velocity changed within 25 ms of the target appearing: 3–15 trials per velocity; see section Comparing the model with the data). We observed systematic shifts in these subjects’ movement time during the sessions, which may have masked the expected influence of target velocity. Alternatively, they may have used a different strategy that does not involve changes in movement time. In either case their data cannot be used to determine whether the acceleration of the hand is under continuous control on the basis of target velocity.

Analysis

Figure 2 shows the velocity of one subject’s hand on an arbitrary trial. The velocity is shown from the moment the target appeared and was computed by dividing the distance between two consecutive positions of the tip of the rod by the 4-ms interval that separates the measurements. To obtain the velocity at the moment that the position of the tip of the rod was determined, we used the mean of the velocities during the intervals before and after that moment.

As in our previous studies (Smeets and Brenner 1995; Brenner and Smeets 1997), the rod moved towards the screen with an almost constant acceleration. The final velocity of the hand was rather arbitrarily defined as the velocity 40 ms before the hand stopped on the screen. The graphical representation in Fig. 2 is not quite correct, because the figure only shows the component of the velocity of the hand that is orthogonal to the screen. This was used to determine the moment the hand stopped on the screen and the reaction time (threshold of 0.2 m/s), but the values that were used for the further analysis were the final *tangential* velocity of the hand and the hand’s *tangential* acceleration.

To determine the delay with which changes in target velocity influence the acceleration of the hand, the rod’s acceleration was computed by dividing the difference between the velocities during the intervals before and after a given moment by the 4-ms interval that separates them. The resulting acceleration traces were synchronised with respect to the moment at which the target velocity changed, and then averaged (first within and then across subjects). In order to detect a change in the acceleration of the hand, the hand must be moving when the change occurs. If it takes 200 ms for a change in target velocity to result in a change in the acceleration of the hand (our ini-

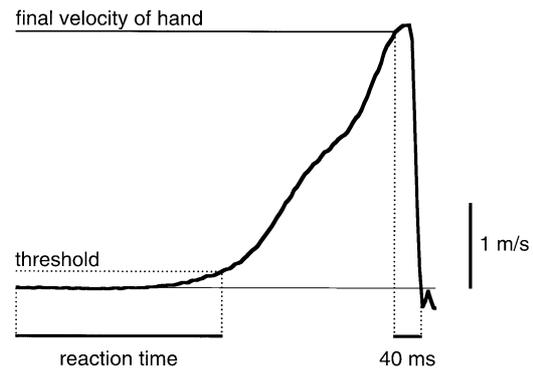


Fig. 2 Velocity of the tip of the rod during a single trial. The velocity is shown from the moment the target appeared (*left*) until just after the rod hit the screen (*right*). The final velocity of the hand is defined as the velocity 40 ms before the rod changed its direction with respect to the screen. Subject J.B.

tial estimate based on Fig. 6; see Results), a change in the acceleration of the hand can only be detected if the hand is moving 200 ms after the target’s velocity changes. Trials were therefore selected in which the change in target velocity occurred between 200 and 50 ms before the reaction time. This ensured that the rod will have started moving but will not yet have reached the screen by the time the response was expected. The high spatial resolution and large number of trials allowed us to do without any additional filtering, which could influence the time at which a response appears to occur. To examine the mean pattern of the acceleration during a hit, we also averaged the same acceleration traces after synchronising them with respect to the reaction time.

A simple model

A very simple model for the control of the acceleration of the hand was formulated to help interpret the measured final hand velocities. To keep the model simple, all variability was ignored. The only parameters involved are the distance to the screen, the mean reaction time, the visuo-motor delay, and the mean measured value of the final velocity of the hand for each target velocity on its own (based on trials in which the change occurred within 25 ms of the target appearing). The model is based on the assumption that the acceleration of the hand is constant from the moment the hand starts to move, and that the acceleration is directly controlled by the velocity of the target (with the visuo-motor delay that we determined in the manner described in the preceding paragraph).

Figure 3 shows a schematic representation of this model. Two trials are shown; during one trial the target moves at a constant velocity (dashed line), during the other it increases its velocity some time before the reaction time (solid line). In the former case, the acceleration of the hand is constant from the moment it starts to move. In the latter it increases abruptly some time after the change in target velocity. We will henceforth substitute a value of 200 ms for this visuo-motor delay, in anticipation of the results. An increased acceleration obviously results in a steeper slope of the velocity and in a faster change of position. As the distance to the screen is constant, a larger acceleration therefore results in a shorter movement time and a higher final velocity.

For each target velocity (v_i), the value of the acceleration of the hand (a_i) was determined from the mean final velocity of the hand (v_f) on trials during which the target only moved at that velocity, and the distance to the screen (d). Assuming that the velocity increases linearly with time (i.e. constant acceleration),

$$v_i = a_i \times MT \quad \text{and} \quad d = \frac{1}{2} a_i \times MT^2$$

where MT is the movement time, so that

$$a_i = v_i^2 / 2d$$

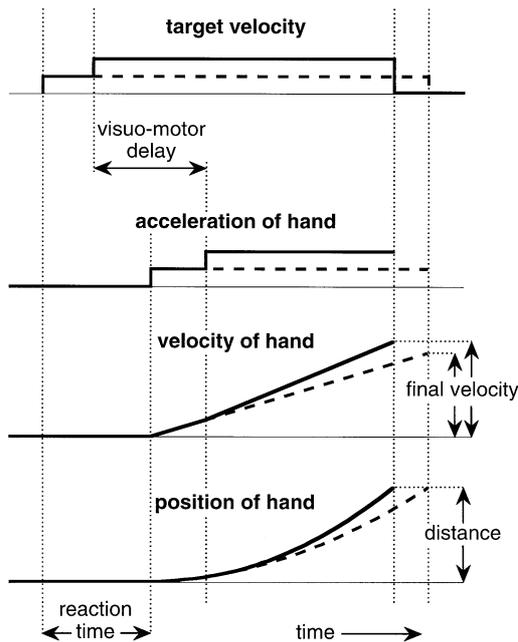


Fig. 3 Schematic representation of the model. Time is from left to right, starting just before the target appears. The *dashed lines* are for a target moving at a constant velocity. The *solid lines* are for a target that increases in velocity some time before the reaction time. The different parts show (from top to bottom) the velocity of the target; and the predicted acceleration, velocity and position of the hand. The *vertical dotted lines* indicate the moments at which (from left to right): the target appears; its velocity changes; the hand starts to move; the hand responds to the increase in target velocity; and the hand reaches the screen (two lines because this occurs sooner if target velocity increases)

Having determined the acceleration for each target velocity, and the delay between a change in target velocity and the change in the acceleration of the hand, we can predict the final velocity of the hand for any interval between the moment the target appears and the moment its velocity changes.

If the change in target velocity occurs more than 200 ms before the reaction time, the final velocity of the hand will be the same as it would have been if the target had immediately been moving at the second velocity. If the change occurs later, then the acceleration of the hand may change during the movement (as shown by the solid lines in Fig. 3). This will be so unless the hand reaches the target before its acceleration can change, i.e. unless the change in target velocity takes place less than 200 ms before the hand hits the screen. If the acceleration of the hand does change, the final velocity of the hand will depend on how long the hand undergoes each magnitude of acceleration. These durations are determined by the moment of the change (plus the 200-ms delay) and by the distance that the hand has to move to reach the screen (which determines when the movement ends; see the hand velocity and position traces in Fig. 3).

Comparing the model with the data

In order to determine whether the measured data are consistent with this simple model for the control of the acceleration of the hand, we first averaged the five subjects' data. We did not want more weight to be given to subjects with a larger final velocity of the hand or to subjects who responded more vigorously to the differences in target velocity. Each measured final velocity of the hand was therefore first transposed to a normalised value (Smeets and Brenner 1995). This value, the *equivalent target velocity*, was determined as follows: First, the mean final velocity of each subject's hand was deter-

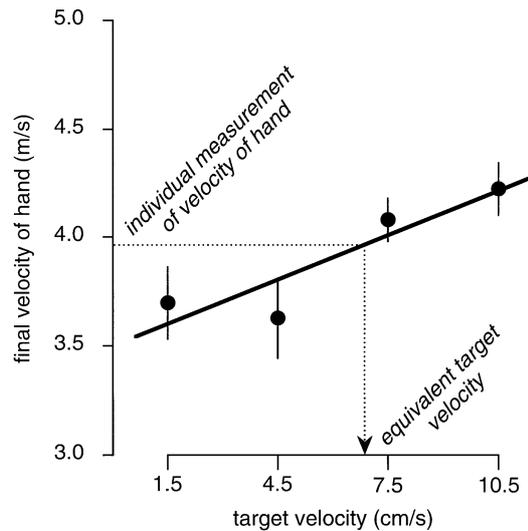


Fig. 4 Determining the equivalent target velocity. The *circles* show the mean final velocity of the subject's hand (and standard errors) when the target moved at a single velocity. The *thick line* is a fit to these four points. The relationship between target velocity and final velocity of the hand – as defined by this line – is used to translate the measured final velocity of the hand on each individual trial into an equivalent target velocity (*dotted lines*). Data for subject J.B.

mined for each target velocity in isolation. This was achieved by selecting the trials in which the change in target velocity occurred less than 25 ms after the target appeared. One subject's mean values are shown as circles in Fig. 4. Next, a line was fit to these four points. This line is an estimate of the relationship between the target's velocity and the final velocity of the subject's hand. Such an estimate can be used to find the target velocity for which any given final velocity of the hand would be expected, as shown by the dotted line in Fig. 4. We call this target velocity the *equivalent target velocity*, because it is the single velocity for which we would expect the subject in question to have the same final velocity of the hand as for the presented combination of two target velocities.

Each measured final velocity of the hand was "translated" into an equivalent target velocity. The equivalent target velocities for each condition, and each delay between the target appearing and its velocity changing, were then averaged across all five subjects. The delays between the target appearing and its velocity changing were random multiples of about 8 ms (due to the 120-Hz frame rate of the screen), but have been grouped into 50-ms bins for clarity of presentation. Each bin includes all values lying between 25 ms before and 25 ms after the indicated value.

Statistics

The systematic influence of target velocity on movement time is small in comparison with the variability due to other causes. We therefore confirmed the effects by subjecting the calculated equivalent target velocities to an analysis of variance with the factors Subject, Initial target velocity (4.5 cm/s or 7.5 cm/s), Change in velocity (increase or decrease) and Time of change in velocity (the 9 bins). To evaluate whether our model can help understand the data, we also calculated the difference between each equivalent target velocity and the value predicted by the model. These "residuals" were subjected to an analysis of variance with the same factors.

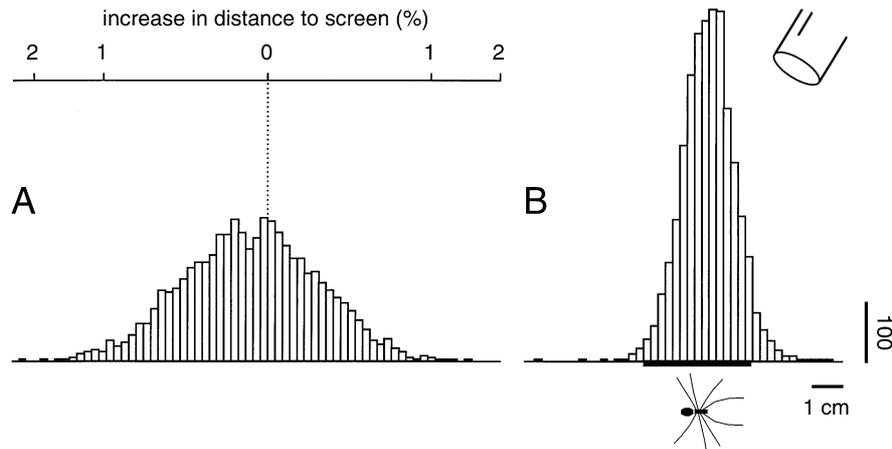


Fig. 5A, B Distribution of horizontal positions at which the screen was hit. The positions are determined either relative to the rod's initial horizontal position on that trial (**A**) or relative to the spider's position when the rod hit the screen (**B**). The height of the bars indicates the number of occurrences. The axis at the top in **A** indicates about how much further the rod had to move when it hit the screen to the left or right of its initial position, rather than moving straight to the screen. The *horizontal black bar* in **B** shows which spiders were considered to have been hit. The spider and the tip of the rod are shown (approximately to scale) for comparison

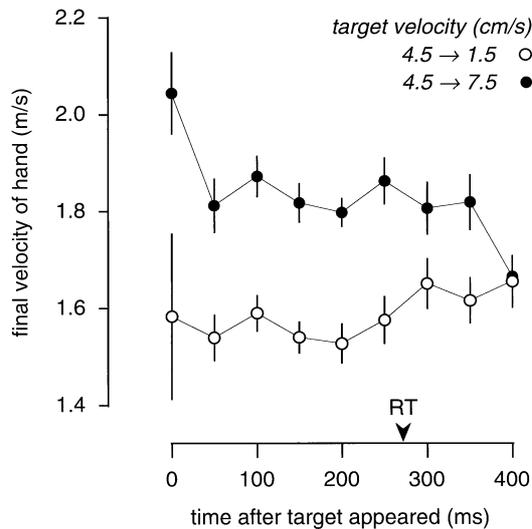


Fig. 6 Mean final velocity of subject J.S.'s hand for various intervals between the target appearing and its velocity changing. The *arrow marked RT* indicates the mean reaction time during these trials. The *bars* show the standard errors. Data for the slower initial target velocity. Note that this subject's values for the final velocity of the hand are much smaller than those of subject J.B. (Fig. 4)

Results

Figure 5 shows the distribution of the horizontal positions at which the rod hit the screen. The position is shown both relative to the horizontal position of the rod when the target appeared (Fig. 5A) and relative to the spider's position when the rod hit the screen (Fig. 5B). It is evident from Fig. 5A that the spiders were hit long before they reached

the edge of the screen and that the distance to the screen hardly depended on where the target was hit. It is evident from **B** that subjects hit most of the spiders: the thick black line below the histogram indicates the range for which the spider is considered to have been hit.

Figure 6 shows the final velocity of one subject's hand for the targets that initially moved at 4.5 cm/s. The horizontal axis shows the time at which the change in target velocity took place. At this time the target either decreased its velocity to 1.5 cm/s (open symbols) or increased its velocity to 7.5 cm/s (solid symbols). The data in the first bins are for targets that were moving at the new velocity (1.5 cm/s or 7.5 cm/s) within 25 ms of their appearing on the screen. They can therefore be considered to represent targets moving at 1.5 cm/s and 7.5 cm/s. The difference between the open and solid symbols confirms that this subject hit slower targets more gently.

If the change in target velocity occurs just before the end of the trial, the subject is unable to modify the velocity of his hand, so that the direction of the change is irrelevant. This appears to be the case in the last bin (at 400 ms). In that case both symbols presumably represent the response for 4.5 cm/s targets. As was to be expected, this value lies between that for the 1.5 cm/s and 7.5 cm/s targets. The arrow (RT) indicates the mean reaction time during these trials. It is evident that the change in target velocity influenced the speed of this subject's hand even if it occurred when the hand was already moving.

If the acceleration of the hand is influenced during the movement, it is important to know how long it takes for visual information to influence this acceleration. The data in Fig. 6 suggest that the visuo-motor delay is about 200 ms, because the mean time it took this subject to hit the targets was 564 ms, whereas the last moment at which a change in target velocity had an influence on the final velocity of his hand was between 350 and 400 ms.

Constant acceleration

In order to examine how constant the acceleration is during the movements, we averaged the acceleration traces of

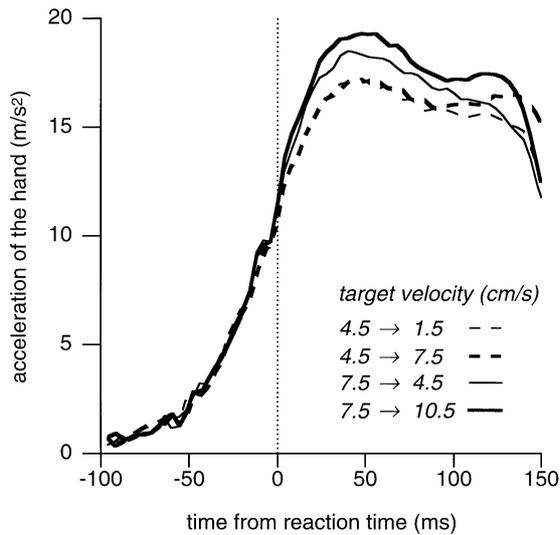


Fig. 7 Mean acceleration of the tip of the rod. The acceleration is shown for 100 ms before and 150 ms after the moment the hand reached a velocity of 0.2 m/s. It is evident that the movement actually started at least 50 ms before the velocity exceeded this threshold. Mean of selected trials (ones in which the change in target velocity occurred between 200 and 50 ms before the hand reached the velocity threshold; 546–560 trials per condition) from all five subjects

the selected trials (about 40% of all trials) after synchronising them with respect to the reaction time. Separate averages for the four conditions are shown in Fig. 7. Of course, the acceleration is not really constant. However, after an initial increase, the mean acceleration did remain at approximately the same level until just before the hand reached the screen.

The differences between the conditions are also as expected. Immediately after the reaction time, the acceleration traces are grouped by initial target velocity. Later in the movement, the traces for increases and decreases in velocity gradually diverge. The gradual shift is presumably caused by the change in target velocity influencing the acceleration of the hand at different times – between 0 and 150 ms after the reaction time – on different trials.

Visuo-motor delay

In order to determine the visuo-motor delay, we averaged the acceleration of the hand after synchronising the acceleration traces with respect to the moment at which the change in target velocity occurred. Figure 8 shows the mean acceleration of the hand for each of the four conditions. In accordance with our initial estimate, the traces for targets that changed to a higher velocity (thick lines) and those for targets that changed to a lower velocity (thin lines) diverge about 200 ms after the change in target velocity.

Because we selected trials on which the hand was not yet moving when the change occurred (see Materials and methods), the acceleration at the moment of the change is

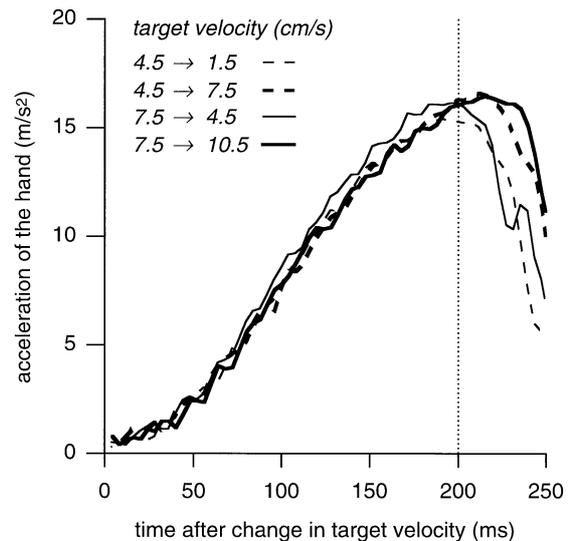


Fig. 8 Mean acceleration of the tip of the rod. The acceleration is shown for 250 ms from the moment the target velocity changed. Mean of selected trials (see Fig. 7) from all five subjects

almost zero. As the time from the change progresses, the hand is moving on ever more trials, so that averaging these trials gives rise to a more gradual increase in the mean acceleration of the hand than in Fig. 7 (and masks the dependence of acceleration on the initial target velocity).

Comparison with the model

The mean equivalent target velocities are shown in Fig. 9. The mean data show the same general pattern as the data shown in Fig. 6. The analysis of variance revealed significant influences of Initial target velocity ($P < 0.0001$) and Change in velocity ($P < 0.0001$), and a significant interaction between Change in velocity and Time of change in velocity ($P < 0.0001$). There were also significant differences between subjects (both main effects and interactions) and a significant interaction between Initial target velocity and Time of change in velocity ($P = 0.04$).

In order to determine whether this pattern of results could be due to direct, continuous control of the acceleration of the hand (on the basis of the velocity of the target), we compared the data to the prediction of our simple model. The predicted final velocity of the hand, as a function of when the change in velocity took place, is shown by the thick lines. The model predictions have been transformed to equivalent target velocities in the same manner as the experimental data. Although the variability in the experimental data is large, the model captures the general pattern quite well: There was a difference between the conditions if the change in target velocity took place early during the trial, and this difference gradually disappeared as the moment that the change in target velocity took place shifted from 100 to 300 ms after the target appeared. The difference was absent if the change took place later during the trial.

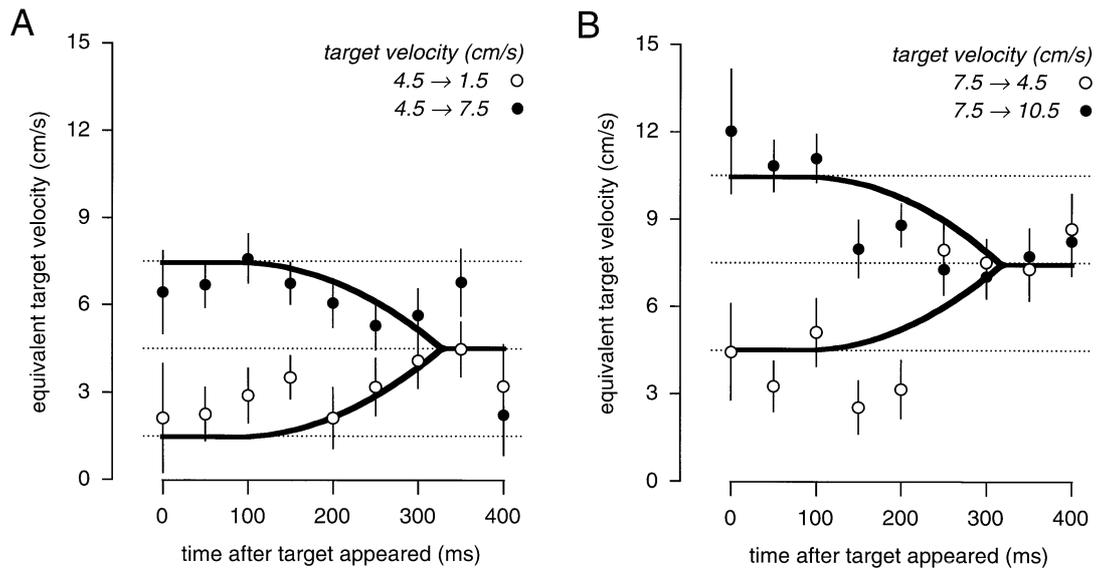


Fig. 9A, B Mean normalised velocity of the hand (equivalent target velocity; see Fig. 4) for various moments at which the target velocity changed. The *dotted lines* show the three target velocities involved. The *points* are means of all the data for all five subjects (and overall standard errors). The *thick curves* show the prediction of the simple model. **A** Initial target velocity of 4.5 cm/s. **B** Initial target velocity of 7.5 cm/s

That this model could account for much of the general pattern is demonstrated by an analysis of the residual variability (the differences between the equivalent target velocities and the values predicted by the model). An analysis of variance on the residual variability no longer showed significant influences of Initial target velocity ($P=0.19$) or Change in velocity ($P=0.23$) and – most importantly – no longer showed a significant interaction between Change in velocity and Time of change in velocity ($P=0.61$). The significant differences between subjects and the significant interaction between Initial target velocity and Time of change in velocity were of course still present, because the model does not predict these effects.

Discussion

From these results we conclude that the acceleration of the hand is under continuous control. Our data are consistent with a direct dependence of the instantaneous acceleration of the hand on the velocity of the target 200 ms earlier. The visuo-motor delay of 200 ms is considerably longer than the 110 ms that has been found for adjustments to the direction of the hand (Brenner and Smeets 1997; Prablanc and Martin 1992). A possible reason for the longer visuo-motor delay is that determining the target's velocity takes more time than detecting its position. The minimal time needed for detecting motion is between about 30 and 70 ms for the velocities at which our spiders moved (van Doorn and Koenderink 1982). However, the

time it takes to perceive a change in velocity is longer – presumably because velocity signals are smoothed over time (McKee and Welch 1985; Snowden and Braddick 1991) – and increases with the initial speed (Dzhafarov et al. 1993). The longer visuo-motor delay may therefore be inevitable.

In the Introduction we mentioned that separating the visual control of the direction and velocity of the movement of the hand could result in faster responses to unexpected changes in a target's movement. The results of the present study support this suggestion, by showing that it takes almost twice as long for the velocity of the hand to react to a change in target velocity than it does for the direction of the hand to react to a change in target position. Waiting for new velocity information before adjusting to a change in position would therefore delay one's responses. However, if the longer delay is indeed caused by the time it takes to acquire new velocity information, then a combined control on the basis of the latest measures of position and velocity, despite them relating to different moments in time, need not increase the visuo-motor delay.

There are clear discrepancies between the model and the data in Fig. 9. However, these discrepancies are not systematic. Despite averaging across five subjects, with a total of well over 5000 trials, the experimental data do not show the smooth pattern we expected. The reason for this is that the influence of target velocity on the final velocity of the hand is modest in relation to the variability due to other causes. This is not surprising considering the large number of trials that were needed to obtain enough different values for the time at which the change occurred. Factors such as fatigue and responding to feedback (e.g. intentionally reducing the speed of the hit after repeatedly missing the target) certainly contributed to the variability in the final velocity of the hand.

Beside deviations from the model due to variability in the data, the model itself is clearly based on several oversimplifications. For instance, the acceleration of the sub-

jects' hands is not really constant from the reaction time until 40 ms before the hand stops on the screen (Fig. 7). Moreover, if velocity signals are smoothed, as suggested above, the transition in the perceived target velocity must be gradual rather than abrupt. Furthermore, individual subjects' strategies appear to differ. Nevertheless this simple model catches the general trends in the data quite well, without any parameter being explicitly fit for this purpose. Thus we consider the agreement between the model and the data sufficiently good to act as support for the hypothesis that the control of the acceleration of the hand by the (perceived) velocity of the target could be very simple.

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