RESEARCH ARTICLE

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Hitting moving objects: is target speed used in guiding the hand?

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Abstract We investigated what information subjects use when trying to hit moving targets. In particular, whether only visual information about the target's position is used to guide the hand to the place of interception or also information about its speed. Subjects hit targets that moved at different constant speeds and disappeared from view after varying amounts of time. This prevented the subjects from updating position information during the time that the target was invisible. Subjects hit further ahead of the disappearing point when the target moved faster, but not as much as they should have on the basis of the target's speed. This could be because more time is needed to perceive and use the correct speed than was available before the target disappeared. It could also be due to a speed-related misperception of the target's final position. The results of a second experiment were more consistent with the latter hypothesis. In a third experiment we moved the background to manipulate the perceived speed. This did not affect the hitting positions. We conclude that subjects respond only to the changing target position. Target speed influences the direction in which the hand moves indirectly, possibly via a speedrelated misperception of position.

Keywords Arm movement · Visuomotor control · Interception · Speed · Position

Introduction

In order to catch a ball, you have to take into account that the ball moves during your own movement. This means that you have to guide your hand to a future location of the ball and to arrive there in time. It is not known what visual information is used, and in what way, to guide the hand to the correct place at the correct time.

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A large number of previous studies and theories about the interception of moving objects emphasized the temporal aspect of the task. Examples are the studies about the optic variable tau (the ratio of image size to its expansion velocity) which (approximately) specifies time to contact between an approaching object and the potential catcher or hitter (Lee et al. 1983; Savelsbergh et al. 1991). In these studies it is proposed that subjects initiate their action when tau reaches a certain value. Michaels et al. (2001), Tresilian (1999), and van der Kamp et al. (1997) showed that it is not that simple, but they too concentrated on the timing. Something that certainly contributed to the emphasis on the temporal aspect of interception is the use of tasks in which subjects had to intercept targets in a more or less predestined area (Carnahan and McFayden 1996; Mason and Carnahan 1999; Port et al. 1997; Tresilian 1994). This makes temporal variables such as reaction time and movement time critical.

Other investigators did not specifically look at either temporal or spatial aspects, but viewed interception as a continuous coupling of action to the changing visual information about the target (Montagne et al. 1999; Peper et al. 1994; Smeets and Brenner 1995; Zaal et al. 1999). The disadvantage of models that are generated by this approach is that they are often very complex and therefore difficult to test. An exception is the proposed strategy of actively canceling the acceleration of the optical image of the ball in the vertical direction (Babler and Dannemiller 1993; Michaels and Oudejans 1992). Subjects reach the point of interception (with a ball that is approaching via a parabolic path) by running backward if the image accelerates and forward if it decelerates. However, this model probably cannot account for human performance (Brouwer et al. 2001; McBeath et al. 1995; Todd 1981) and only applies to a very specific task. It cannot be used to explain performance when intercepting targets that move perpendicularly to the movement of the hand.

As the spatial aspect of interception has received very little attention, we chose to investigate this in the present study. The timing was more or less fixed by instructing subjects to be as fast as possible. We examined where they intercept the target. We are particularly interested in whether, and if so how, subjects use the target's speed in guiding the hand to the place of interception.

An alternative to using the target's speed is to assume a certain target speed, and to continuously update the position toward which one is aiming on the basis of the target's constantly changing position (Smeets and Brenner 1995). According to this view, the only visual information about the current target that is used is its position. The assumed speed may be a (weighted) average of the speeds of previous targets (de Lussanet et al. 2001). We will refer to this as a default speed.

In the literature there are some indications that subjects use position and a default speed instead of the actual target speed to 'intercept' moving objects. One of these comes from a study about saccadic eye movements in response to step-ramp stimuli (Heywood and Churcher 1981). Subjects made a saccade toward a dot that jumped to the right and simultaneously moved rightward at a randomly chosen speed. To reach the target, subjects had to take the target's motion into account when planning the saccade. The results suggested that target speed was not used in doing this. Instead, in order to determine where to move with their eyes, subjects appeared to take the target position 100 ms before the saccade and to make a saccade to a position that was a fixed distance to the right of this.

There are also studies about manual interception in which the authors conclude that target speed is hardly used to guide the hand. Bairstow (1987) asked subjects to intercept moving targets that were presented on a monitor. He found that the starting direction of the hand hardly depended on target speed. In a similar task, Brenner and Smeets (1996) also found that subjects started to move as if they expected all targets to move at the same speed. However, van Donkelaar et al. (1992) suggest that if the reaction is delayed, the direction in which the hand starts to move does depend on the target's speed. Therefore, the starting direction may not be a suitable variable to investigate whether subjects use target speed in guiding their hand, since speed information may only manifest itself later in the movement. This might be because it takes relatively long to perceive the target's speed and transform this information into control of the muscles (Brenner et al. 1998).

It may seem a bit strange to distinguish between speed and changing position. Physically, speed is nothing more than the change of position over time. However, physiologically, the perception of position and speed seem to be separated. This can be demonstrated with the motion aftereffect (reviewed by Anstis et al. 1998). If you look at something stationary after having looked at a moving stimulus for some time, the static object appears to move. However, it does not appear to change its position accordingly. A similar dissociation is found when the background is moved. This changes the perceived speed but has no influence on the perceived position (Smeets and Brenner 1995).

In general, it is very difficult to disentangle the use of speed from that of position. In interception tasks, it is not enough to look at the direction in which the hand moves, because the changing position of a stimulus varies with its speed. If a subject moves his or her hand to a position further ahead of a fast target than of a slow one, this may be caused by the difference in speed, but it may as well be an effect of the difference in position. To investigate whether subjects use the actual speed of the present target to guide the hand to the interception point, or only use the target's position and a default target speed, we let subjects hit virtual spiders that moved at different speeds from the left to the right. After some time, the spiders disappeared from view. This prevents subjects from using information about the changing position of the target during the time it is invisible (Rosenbaum 1975). The position of the hit therefore reflects the speed subjects use to guide the hand to the target's position at the time of interception. We are interested in whether this is the actual or a default speed.

Experiment 1

We constructed two subsets of conditions. One subset tested the predictions of the hypothesis that, besides the target's position, the actual speed is used. The other tested the predictions of the hypothesis that only the position and a default speed are used. These two hypotheses are hereafter simply called hypothesis of actual and default speed, respectively. The first subset consisted of conditions in which spiders started at the same positions and moved at equal speeds but were visible for different times. If the actual speed of the target is used in guiding the hand to the interception point, the subjects should hit the same position in space, irrespective of the amount of time that the spiders were visible. The second subset of conditions was designed to examine the hypothesis that a default speed was used. In this subset, spiders that differed in speed disappeared at the same position after having been visible for the same amount of time. If subjects use a default target speed to guide the hand to the interception point, they should, on average, hit the same distance ahead of the point at which the spiders disappeared, irrespective of the speed at which the spiders ran before they disappeared. By testing the hypothesis in this way, we did not have to assume a particular value for the default speed. To be able to evaluate the hypotheses quantitatively, we transformed them into models that predict where the subjects will try to hit the targets. For this analysis we did have to specify the default speed; we assumed that it was the average target speed.

Materials and methods

Materials

The setup was designed to allow subjects to behave as freely and naturally as possible, while meeting the experimental requirements. A schematic view is shown in Fig. 1. Subjects used a



Fig. 1 A schematic view of the experimental setup. The subject sits in front of the monitor on which the stimuli are presented. Shutter spectacles make the stimuli appear on a protective screen. Infrared markers (IREDs) attached to the spectacles and the hitting rod allow the position of the head and the rod to be determined

22-cm long Perspex rod to hit simulated spiders that were running to the right over a background. A background was used to make the task more naturalistic and to facilitate the perception of the spider's motion and distance. By having the subjects wear liquid-crystal shutter spectacles and presenting different images to the two eyes, the spiders were made to appear three-dimensional, and the background to appear to be situated on a transparent Macrolon screen. The screen was placed in front of the monitor to protect the monitor from the impact of the rod, and it was tilted 30° backward to let the subjects hit more comfortably.

The radius of the hitting rod was 0.9 cm. It was held between the fingers and thumb like a pen. The rod was typically held in such a way that the tip was about 1 cm from the fingertips. The spider was yellow and had 1.5-cm legs, consisting of three segments. The legs moved as a real spider's would. The spider's body consisted of three segments with a total length of 0.85 cm. Including the legs its length was about 1.8 cm. The virtual height of the spider's body was 1.5 mm. The spider moved across a background of 4-cm red lines. The lines were placed at random within 15 cm of the center of the transparent screen, and their intensity faded at the edges. A new background was generated for each trial. Since subjects were free to move their head, the magnitude of the stimulus in terms of visual angles varied during the trials and between subjects. In general, 1 cm on the screen corresponds to about 1° of visual angle.

Three infrared markers (IREDs) on the hitting screen were used to calibrate the setup before the experiment began. Three more IREDs were attached to the shutter spectacles and two to the rod (one at the end furthest from the tip, and one 6.5 cm from the end). A movement analysis system (Optotrak 3010; Northern Digital) recorded the positions of the IREDs at 250 Hz. The recorded positions were not only necessary to answer the experimental questions, but were also used on-line during the experiment.

Information was needed about when and where the screen was hit, so that feedback could be given. As soon as the screen was hit, the spider appeared again. If it was a successful hit (if the center of the rod came within 1.8 cm of the center of the spider) the spider looked crushed, whereas if the subject missed the spider, the latter ran away from the rod. Note that this feedback was consistent with the use of the actual speed.

Information about the position of the rod was also necessary to help the subjects position the rod at the beginning of a trial. The rod had to be within 5 cm from a point 40 cm horizontally away from the center of the protective screen. Directions were given on the screen about where to hold the rod (for example, "further to the left"), and a green line that pointed out of the screen indicated the direction in which the rod had to be held. The next trial did not begin until the hand was in the required position. Otherwise, the subject was allowed to sit any way he or she wanted.

Information about the position and orientation of the spectacles was needed to determine the position of the subject's eyes in space (note that the orientation of the eyes with respect to the head was

Visible spider paths



Fig. 2 An overview of the design of experiment 1. The lines represent the paths of the spiders during the time that they are visible. Positions are relative to the projection on the screen of the hand's starting position. The time the spiders are visible (T_{vis} ; 150, 250, or 350 ms) is coded by the type of line, the spider speed (in cm/s) is indicated on the *right* of the paths. Conditions belonging to the subset of spiders that examines the use of actual speed are marked by a *square* at the starting point. Conditions belonging to the subset that examines the use of a default speed are marked by a *circle* at the disappearing point. Five conditions belong to both subsets

not measured). Eye positions were necessary to calculate appropriate images for the two eyes.

The delay in adjusting the stimuli to the subjects' movements was 21 ± 3 ms.

Design

The spiders ran at 6, 12, or 18 cm/s. The time for which the spiders were visible (T_{vis}) was 150, 250, or 350 ms. These times were chosen to be sure that the spider almost always disappeared before the subject hit the screen, but still to present the spiders long enough for subjects to judge their speeds.

As already mentioned, there were two (overlapping) subsets of conditions, each designed for examining one of the two hypotheses (see Fig. 2 for an overview). In the subset for examining the hypothesis of actual speed, there was one starting point for each spider speed. Each T_{vis} was used for each spider speed (ν). This resulted in $3(\nu)*3(T_{vis})=9$ conditions. In the subset for examining the hypothesis of default speed, there was one position at which the spiders disappeared for each T_{vis} . Spiders running at each speed were visible for each T_{vis} . The number of conditions in the second subset was therefore $3(T_{vis})=9$. The total number of conditions in the experiment could be restricted to 13, because 5 of the conditions belonged to both subsets. Each condition was repeated 15 times, which resulted in 195 trials per subject. The order of the trials was completely random.

Subjects and instruction

Ten volunteers, mostly from our department, participated in the experiment. They gave informed consent before participating. They were all right-handed and hit with their right hand. The subjects were instructed to hit the spiders as quickly as possible with the rod. We told them that the spiders would become invisible, but that they kept on running at the same speed and in the same direction, so it would still be possible to hit them. The feedback was



Fig. 3 Schematic overview of several used variables. T_{invis} is the time that the spider is invisible

also explained. Subjects could take a break whenever they liked by not returning their hand to the starting position.

Analysis and models

From a total of 1,950 trials, 43 were excluded from analysis for technical reasons (primarily because markers were hidden from view because the subject turned the rod). Another 11 trials were not analyzed because subjects arrived at the screen before the spider had disappeared. Seven more trials were discarded because the subject did not react within 600 ms or needed more than 1,000 ms to move the hand from the starting position to the screen.

A number of measures were defined (Fig. 3). The spider position is the (invisible) spider's lateral position at the time of the hit. The hitting position refers to the lateral position of the tip of the rod when it hits the screen. Both are measured relative to the starting point of the spider. If a subject hits the center of the spider, spider position and hitting position have the same value. The hitting error is the horizontal difference between the hitting position and the spider position. If the subject hits to the right of the spider's center, the hitting error has a positive value. If the subject hits to the left, its value is negative. The variable error is the standard deviation of the hitting error. It is determined separately for each T_{vis} , spider speed, and subject. The invisible displacement is the distance between the disappearing point and the spider position. The used invisible displacement is the distance between the disappearing point and the hitting position. This distance reflects the speed that the subject has used to guide his or her hand. According to one hypothesis this will be a default speed. According to the other it will be the actual speed.

We also measured reaction time (RT) and movement time (MT). Reaction time is defined as the time between target onset and the moment that the speed of the hand exceeds 0.1 m/s. Movement time is the time between movement initiation and arrival on the screen.

All statistical analyses concern both hits and misses. Differences between conditions were evaluated with repeated measures analyses of variance with target speed and T_{vis} as factors. The input for the analyses were averages for each subject, target speed, and T_{vis} . We took P<0.05 as the level of significance.

We also transformed the two hypotheses into models that quantitatively predict the invisible displacements. The models are based on the assumption that the positions at which subjects hit the screen are where they want to arrive, and that systematic timing errors, which would introduce systematic spatial errors, are not made. For each trial and each model, we computed the predicted invisible displacement (*PID*). For the hypothesis that actual target speed (ν) is used, the predicted invisible displacement was computed as:

$$PID = T_{invis} \times v \tag{1}$$

where T_{invis} represents the time that the spider is invisible, i.e., the time between disappearance of the spider and the arrival of the hand on the screen. For the hypothesis that a default speed is used to guide the hand instead of the actual speed, we defined the default speed v_d as the average speed of all targets (i.e., 11 cm/s)¹. The predicted invisible displacement was computed as:

¹ We examined whether taking the speed of the previous spider instead of the average speed as the default speed improved the predictions of the default speed model. This was not the case.



Fig. 4A–C Reaction time, movement time, and variable error per T_{vis} and per spider speed. *Error bars* represent the standard error between subjects. A Reaction time is independent of T_{vis} and decreases significantly with target speed. **B** Movement time decreases es with T_{vis} and target speed. **C** Variable error becomes smaller when the spider is visible longer. Target speed does not significantly influence the variable error

$$PID = T_{invis} \times v_d \tag{2}$$

To evaluate the models, we determined the average used invisible displacement and compared it with the average predicted invisible displacement for each subject and each condition. To see whether the mean deviation of one model from the data was significantly different from that of the other, we performed a paired *t*-test on the average deviations (paired by subject and condition).

Results

General characteristics

The reaction time (Fig. 4A) does not depend on the time that the spider is visible [F(2,18)<1.0, P=0.92]. As found in previous studies (for example, Savelsbergh et al. 1992; Smeets and Brenner 1994), it decreases with increasing target speed [F(2,18)=6.33, P<0.01]. The movement time (Fig. 4B) decreases with increasing T_{vis} [F(2,18)=3.91, P=0.04] but the difference in average movement time between the longest and shortest T_{vis} is only 3 ms. The movement time is shorter when the spider moves faster [F(2,18)=3.4.67, P<0.01]. The variable error (Fig. 4C) decreases with increasing T_{vis} [F(2,18)=3.4.67, P<0.01]. The variable F(2,18)=3.4.67, P<0.01] and is independent of spider speed [F(2,18)=1.62, P=0.22].

Same starting point per spider speed



Fig. 5 Mean spider positions (*open circles*) and hitting positions (*solid circles*) for the subset of conditions that tests the use of actual speed. Positions are measured relative to the start of the spider's movement. The larger the value for position, the more to the right the spider had moved at the time of the hit (spider position), or the more to the right subjects hit (hitting position). In contrast to the predictions of the hypothesis of actual speed, hitting position depends on the time the spider was visible

Subjects could do the task remarkably well. The spiders were hit successfully in 79% of the trials. The number of hits depended on how long the spiders were visible; 70% of the spiders with a T_{vis} of 150 ms were hit, which increased to 79% and 84% when the spiders were visible for 250 and 350 ms, respectively. Fast spiders were more difficult to hit (73% successful hits) than slow and intermediate spiders (both 81%).

Our main interest is how the position of the hit depended on the experimental conditions. This will be discussed below.

Subset of conditions examining the use of actual speed

If subjects had used the actual speed, they would have hit spiders running at the same speed at the same position, irrespective of the time they were visible. In contrast, Fig. 5 shows that the hitting position was influenced by the time the spider was visible [F(2,18)=11.89, P<0.01]. Fast and intermediate spiders were hit further behind their centers when they were visible for 150 ms than when they were visible longer [significant interaction of T_{vis} and target speed on hitting position and on hitting error: F(4,36)=13.26 and F(4,36)=17.57, respectively, both P values <0.01]. The faster the spider, the more the hitting error (the difference between spider position and hitting position) depended on T_{vis} .

Subset of conditions examining the use of a default speed

If subjects had used the position and a default speed, they would have hit the same distance in front of the disappearing point for each T_{vis} , irrespective of the spider speed. This is clearly not the case (Fig. 6): they hit further ahead of the disappearing point for fast spiders than

Same disappearing point per Tvis



Fig. 6 Used invisible displacements (*solid circles*) and actual invisible displacements (*open circles*) from responses to the subset of conditions that tests the use of a default speed. In contrast to the predictions of the hypothesis of default speed, subjects hit further ahead of the disappearing point for fast spiders than for slow ones. Hitting error becomes less dependent on spider speed with increasing T_{vis}



Fig. 7A, B The used invisible displacement (*ordinates*) averaged for each subject and each condition plotted against the predicted invisible displacement (*PID*), as predicted by (**A**) the model that uses the actual spider speed and (**B**) the model that uses a default speed (*abscissas*). The *straight line* is the unity line. The mean deviation (*Md*) of the points from the unity line is given in the *lower right corner* of each figure

for slow ones [significant effect of spider speed on used invisible displacement: F(2,18)=1027.40, P<0.01]. Comparing the open and solid symbols shows that the hitting error was less dependent on spider speed when the spiders were visible longer [significant interaction of target speed and T_{vis} on hitting error; F(4,36)=22.73, P<0.01].

Models

We compared the used invisible displacements with the invisible displacements predicted by the two models (Fig. 7). The mean deviation of the used invisible displacements from the predicted invisible displacements is 0.40 cm for the actual speed model and 0.49 cm for the default speed model. The mean deviations were on the border of being significantly different [t(129)=1.95, P=0.05].

If actual target speed had been used correctly to guide the hand to the interception point, spiders starting at the same position and running at the same speed would have been hit at equal positions on the screen, irrespective of the time they were visible. This seems to be true for the slow spiders, but hitting positions are not equal for different values of T_{vis} for the spiders running at 12 and 18 cm/s (Fig. 5). This result suggests that a default speed of about 6 cm/s was used. However, if a default speed had been used to predict the interception point, the used invisible displacements would not have differed between spiders with equal disappearing points and an equal T_{vis} but different velocities. Figure 6 clearly shows that the used invisible displacements did differ. Thus, both hypotheses can be rejected on qualitative arguments. Analyzing the results quantitatively with the models failed to distinguish between the hypotheses of actual and default speed (Fig. 7).

The results presented in Fig. 6 suggest that actual and default speed are both used in hitting moving spiders, but both only partly. If subjects only used the actual speed, they would have hit the spiders correctly (maybe with a small bias). If subjects used a default speed, they would have hit the same distance ahead of spiders that were visible for the same time. Figure 6 shows that the result is something in between, though the longer the spiders are visible, the more the actual speed seems to be used.

In the following, we will examine two hypotheses which incorporate the notion that default speed and actual speed both play a role in guiding the hand to the interception point. They also both predict that the influence of actual target speed increases with T_{vis} . The first hypothesis is called the extrapolation hypothesis, and the second is the hypothesis of progressive use of speed. Like the hypothesis of default speed, the extrapolation hypothesis assumes that subjects guide their hand on the basis of target position and not speed. The effect of target speed arises from a speed-related misperception of target position. The hypothesis of progressive use of speed refines the hypothesis of the actual speed. It assumes that speed itself is used, but considers that time is needed to perceive and use speed information.

Extrapolation hypothesis

It has long been known that the position of a dot which is flashed while the eyes are moving is misperceived in the direction of the eye movement (Mita et al. 1950; Mitrani et al. 1979). This does not only happen in the dark (Brenner and Cornelissen 2000). Brenner et al. (2001) proposed that this misperception arises because the perceived position of a target is determined by combining incoming retinal information with outgoing oculomotor commands, without any consideration of neuro-



Fig. 8A–D Schematic representation of the changing predicted invisible displacement (*PID*) as a function of time according to the extrapolation model (**A**, **B**) and the model of progressive use of speed (**C**, **D**). A situation is depicted in which the spider speed is higher (*steep line segments*) than the default speed (*flatter line segments*). Dashed line segments indicate the visible spider movement, continuous line segments the extrapolation. **A** and **C** represent the case in which the spider is visible briefly. In **B** and **D** the spider is visible longer. T_{ext} is the extrapolation time, T_{change} is the time after the start of the trial, at which the use of default speed changed into the use of actual speed

nal or muscular delays². This means that during pursuit the moving target is perceived at a position which the eye will look at, and the target will occupy, a fixed time (the extrapolation time) later. When dealing with targets that disappear while they are being pursued, the influence of the mislocalization is equivalent to using the actual speed during an extrapolation time, and a default speed during the remaining T_{invis} . This hypothesis predicts that spiders with a long T_{vis} will be hit better, not because they are visible for a long time, but because of the brief time they are invisible, so that the advantage of the predictive value of the misperception is relatively large.

To evaluate the extrapolation hypothesis, we transformed it into a model that quantitatively predicts the invisible displacement for each trial (visualized in Fig. 8A, B). We assumed that subjects were pursuing the target with a gain of 1 by the time it disappeared. In order to find an exact value for the extrapolation time (T_{ext}) we fitted the model to the data. This also provided us with an additional test for the validity of the hypothesis, because we expected the fit to result in a value that corresponds to values of mislocalizations during pursuit eye movements. However, this additional test is not very

 $^{^2}$ The hypothesis of Brenner et al. (2001) predicts that the mislocalization starts at the time that the first oculomotor command is given to pursue the target, before the actual eye movement has started.

critical because mislocalizations of 100 ms (Brenner et al. 2001), 153 ms (Mitrani and Dimitrov 1982), and 207 ms (Mitrani et al. 1979) have been found.

For each trial, we checked whether the extrapolation time exceeded the time between disappearance of the spider and arrival at the screen. If so, only the actual speed is used in guiding the hand (Eq. 3a). If not, the prediction is based on a mixture of actual and default speed (Eq. 3b). If $T_{invic} < T_{avi}$:

$$PID = T_{invis} \times v \tag{3a}$$

Otherwise:

$$PID = T_{ext} \times v + (T_{invis} - T_{ext}) \times v_d \tag{3b}$$

A range of extrapolation times from 0 ms to the maximal T_{invis} were evaluated with the help of a program written in Matlab 5.0. The best fit of the model to the data was defined as that giving the lowest mean deviation of the used invisible displacements from the predicted invisible displacements (see Materials and methods). To estimate the reliability of the resulting parameter value, we calculated its standard error using the bootstrap method (Press et al. 1992) with 50 bootstrap trials. The analysis resulted in an extrapolation time of 156 ± 10 ms, which is a plausible value. The mean deviation of the data from the prediction was 0.32 cm (Fig. 9A). This mean deviation is lower than the deviations found previously, but one should keep in mind that this value is the result of fitting one parameter.

Hypothesis of progressive use of speed

As already mentioned in the Introduction, findings of van Donkelaar et al. (1992) suggest that if the reaction is delayed, so that subjects receive relatively long exposure to the target's speed before the hand starts to move, the direction in which the hand starts to move does depend on the target's speed. The hypothesis of progressive use of speed builds upon this finding. According to this hypothesis, the used target speed changes from a default speed to the actual one. If moving targets are visible too briefly, subjects do not have the opportunity to perceive the speed correctly, and therefore the final position of the hand will depend on a speed that lies between the default and the actual speed, depending on the exact T_{vis} .

Like the extrapolation hypothesis, this hypothesis combines default and actual target speed. However, the hypothesis of progressive use of speed predicts that subjects hit the long-visible spiders more successfully because they had more time to correctly perceive the speed of the target. Thus, according to this hypothesis, the T_{vis} and not the T_{invis} is the important factor.

To test the hypothesis of progressive use of speed, we again created a model which quantitatively predicts the invisible displacements (visualized in Fig. 8C, D). We implemented one fixed time after the start of the trial, at which the use of default speed abruptly changed into the



Fig. 9A, B The used invisible displacement for each subject and each condition plotted against the invisible displacement predicted by (A) the extrapolation model and (B) the model of progressive use of speed

use of actual speed. To determine a value for this time (T_{change}) we used the same analysis as described in the section about the extrapolation hypothesis. A range from 0 ms to the maximal summed reaction and movement time was examined. Again, the average speed (11 cm/s) was taken to be the default speed. We used three different formulas depending on the timing.

If $T_{vis} > T_{change}$:

$$PID = T_{invis} \times v \tag{4a}$$

(4b)

 $PID = T_{invis} \times v_d$ Otherwise:

 $PID = (T_{change} - T_{vis}) \times v_d + (RT + MT - T_{change}) \times v \quad (4c)$

Equation 4a was used for all trials in which the spider was still visible at T_{change} . In this case, the predicted invisible displacement reflects the actual speed. Equation 4b was used for trials in which the movement ended before T_{change} . In these cases, subjects did not have enough time to use speed information in their movement. Thus, only the default speed will manifest itself in the predicted invisible displacement. Equation 4c was applied to the remaining trials. In these trials, both the default and the actual speed play a role. The default speed determines the guidance of the hand in the time between disappearance and T_{change} , and after T_{change} , the actual speed is used in guiding the hand. This means that if the spider is visible for a brief time, default speed determines the hitting position to a greater extent than if the T_{vic} is long.

The fit yielded a T_{change} of 307±8 ms and a mean deviation from the data of 0.33 cm (Fig. 9B). This model describes the data as well as the extrapolation model does [t(129)=1.80, P=0.07], again with one fit parameter.

We rejected the original hypotheses and proposed two new ones. Both the extrapolation hypothesis and the hypothesis of progressive use can better explain the present data than the hypotheses which only take the actual or the default speed into account (though that is not surprising since we added a free parameter). However, on the basis of this experiment we cannot decide for one of the two new hypotheses. We will evaluate them further in experiment 2.

Experiment 2

We already mentioned a major difference between the extrapolation hypothesis and the hypothesis of progressive use. Both hypotheses predict that spiders with a long T_{vis} , i.e., spiders which are hit with a short T_{invis} , will be hit best, but for different reasons. We will use this difference in the following experiment.

According to the extrapolation hypothesis, the T_{vis} of a moving spider has no direct influence on performance. Spiders that have been visible for a long time and spiders that are visible briefly will in principle be hit equally well. However, the time between disappearance of the spider and the hand's arrival on the screen does make a difference. Subjects only benefit from the predictive value of the misperception for the duration of the extrapolation time. During the remaining time until the hand's arrival on the screen, the hand is guided by the default speed. Hence, increasing the T_{invis} beyond the extrapolation time will result in increasingly stronger dependency on the default speed and thus in increasingly worse performance.

In contrast, according to the hypothesis of progressive use of target speed, the time that the moving target is visible is the important variable. The shorter the T_{vis} , the more a subject has to rely on the default speed, because there was not enough time to perceive the real target speed. If a moving target is visible long enough to perceive the actual target speed, the time between the target's disappearance and the hand's arrival is not important. In this case, a long T_{invis} may result in more noise, but the same average results are predicted.

In experiment 1, a longer T_{vis} automatically imposed a shorter T_{invis} . Therefore we do not know whether spiders which were visible for 350 ms were hit best because they had the longest T_{vis} , or because there was little time left after their disappearance. In the following experiment we tried to separate these issues. Subjects were asked to hit disappearing and non-disappearing spiders. The disappearing spiders were visible for either 150 or 442 ms, and disappeared at equal positions. In order to get the same T_{invis} for both values of T_{vis} , subjects had to wait for a tone before they were allowed to start moving their hand. The non-disappearing spiders were at the same position as those visible for 442 ms when the tone sounded.

The extrapolation hypothesis predicts that the two types of disappearing spiders will be hit at equal positions, with equal hitting errors, as these are invisible for the same time. Further, it predicts that hitting errors resulting from hitting non-disappearing spiders will be lower and independent of spider speed. The hypothesis of progressive use of speed predicts that hitting longvisible and non-disappearing spiders will result in equal hitting positions and hitting errors as they are both Visible spider paths



Fig. 10 An overview of the design of experiment 2. The *lines* represent the paths of the spiders relative to the hand's starting position during the time that they are visible. The T_{vis} (150, 442 ms, or continuous) is coded by the *type of line*, the spider speed (in cm/s) is indicated on the *right* of the paths. The *notes* indicate the position of the spider when the tone sounded

visible long enough to be able to use the correct speed. Additionally, it predicts that the errors resulting from hitting briefly visible spiders will be the highest and the most dependent on spider speed.

Materials and methods

Materials and design

The materials are the same as in experiment 1. The design is summarized in Fig. 10. The spiders ran at 6, 12, or 18 cm/s. They did not disappear from view or were visible for 442 or 150 ms. If the spiders disappeared, they always disappeared 2 cm to the left of the starting position of the subject's hand. Subjects had to wait for a tone before they were allowed to react. In a pilot study, we found that if the tone sounded an equal amount of time before disappearance, subjects reacted about 100 ms later when the T_{vis} was short than when it was long. As we wanted to get the same T_{invis} for each T_{vis} , we tried to cancel this effect by presenting the tone 142 ms before the briefly visible spider disappeared, and 42 ms before the disappearance of the longer visible spider. The tone presented with the non-disappearing spiders sounded after an equal amount of time as with the long-visible spiders, i.e., 400 ms after presentation onset. We also presented catch trials: spiders without a tone which were not to be hit. The results of these trials were not analyzed. These trials were included to train the subjects to only react after they heard the tone. During the whole experiment, if the subject started too soon (before the tone sounded or within 80 ms after the tone) or started moving in a catch trial, a message appeared on the screen that he or she had done so. Those trials were repeated later in the experiment.

The total number of trials was 180, of which 45 were eatch trials (3 spider speeds * 15 trials) and 135 were experimental trials (3 T_{vis} * 3 spider speeds * 15 trials). The order was randomized.

Subjects and instruction

Ten volunteers from our department participated in the experiment. Seven of them had participated in the previous experiment. All subjects gave informed consent before participating in the experiment. Except for one, they were all right-handed. All subjects hit with their preferred hand. The instruction was the same as in experiment 1, with the addition that they had to start the movement as soon as possible after they heard the tone. We also told the subjects about the trials in which there would be no tone and in which they were thus not allowed to hit the spider.

Analysis

From a total of 1,350 experimental trials, 3 were excluded from analysis for technical reasons. One additional trial was not analyzed because a subject needed more than 900 ms to move the hand from the starting position to the screen, and another was discarded because the subject missed the spider by more than 7 cm.

The reaction time is measured from the onset of the tone (instead of from the onset of the trial). As the spiders were (approximately) at the same position relative to the hand at the reaction time, we now measured the spider position and hitting position relative to the projection on the screen of the starting position of the hand instead of relative to the starting position of the spider. For the analysis of the models, we assumed again that the default velocity equaled the average speed, now 12 cm/s.

The statistical tests we used are the same as in experiment 1.

Results

General characteristics

As we anticipated in our design, the reaction time (Fig. 11A) depended on T_{vis} [F(2,18)=217.84, P<0.01]. It also depended on spider speed [F(2,18)=9.68, P<0.01]. The movement time (Fig. 11B) was independent of the time that the spider was visible [F(2,18)=2.86, P=0.08] and depended on spider speed [F(2,18)=18.33, P<0.01]. The variable error (Fig. 11C) decreased with increasing T_{vis} [F(2,18)=19.53, P<0.01] and became larger when the spiders ran faster [F(2,18)=4.86, P=0.02].

In all, 75% of the spiders were hit successfully. As in experiment 1, the number of hits depended on T_{vis} : 62% of the spiders with a T_{vis} of 150 ms were hit, 77% of the spiders which were visible for 442 ms were hit, and 86% of the non-disappearing spiders were hit. Spiders running at 12 cm/s were hit best (81%). The percentages of successful hits toward fast and slow spiders were 68% and 76%, respectively.

Results regarding the extrapolation hypothesis

Though we tried to prevent it, the T_{vis} was still negatively correlated with T_{invis} ; the T_{invis} was on average 410 ms when spiders were visible for 150 ms and 376 ms when spiders were visible for 442 ms. However, if trials with a T_{invis} of 480 ms and longer are discarded, the average T_{invis} is about the same when briefly visible spiders are hit (368 ms) as when long-visible spiders are hit (367 ms). We decided to use only this selection of trials to compare the two types of disappearing spiders. As a result, the conditions with a T_{vis} of 150 ms are represented by 351 instead of 447 trials, and the conditions in which spiders were visible for 442 ms are represented by 422 instead of 450 trials.

Figure 12A shows the spider position and hitting position per T_{vis} and spider speed. There is a trend toward



Fig. 11A–C Reaction time (from the onset of the tone), movement time, and variable error per T_{vis} and per spider speed. *Error* bars represent the standard error between subjects. A Reaction time decreases with spider speed and T_{vis} . B Movement time decreases with spider speed and is shortest when the spiders are visible for 442 ms. C Variable error increases with spider speed and decreases with T_{vis}



Fig. 12A, B Spider positions (*open circles*) and hitting positions (*solid circles*) for each T_{vis} and each spider speed. Positions are measured relative to the projection of the hand's starting position. **A** A selection of the data is presented to achieve the same T_{invis} for spiders that are visible for 150 and 442 ms. The effect of spider speed on hitting position and hitting error was not significantly different for the different times that the spiders were visible. This is consistent with the predictions of the extrapolation hypothesis. **B** All responses to trials in which the spiders were either visible for 442 ms or did not disappear at all. Contrary to the predictions of the hypothesis of progressive use of speed, spiders that did not disappear were hit with a smaller hitting error which was less dependent on spider speed

hitting longer visible spiders better. However, in accordance with the extrapolation hypothesis, the hitting positions and hitting errors were not significantly different for the different times that the spiders were visible [interaction T_{vis} and spider speed on hitting position F(4,36)=1.45, P=0.26 and on hitting error F(4,36)=2.72, P=0.09]. Thus, the extrapolation hypothesis is not contradicted.

Results regarding the hypothesis of progressive use of speed

As there was no need to select the data to test the hypothesis of progressive use of speed, the values for a T_{vis} of 442 ms in Fig. 12B are not identical to those in Fig. 12A. Figure 12B shows that long-visible spiders are not hit at the same positions as the non-disappearing spiders [interaction of spider speed and T_{vis} on hitting position: F(4,36)=12.21, P<0.01]. The hitting errors when hitting non-disappearing spiders are smaller and less dependent on target speed than when the spiders are visible for 442 ms [interaction spider speed and T_{vis} : F(4,36)=15.16, P<0.01]. These findings contradict the hypothesis of progressive use of speed.

Models

To compare the hypotheses quantitatively, we applied the models described for experiment 1 to the data of experiment 2. Only the trials with disappearing spiders were considered. The same computations and value for the parameter were used as in the first experiment. Figure 13 shows that the mean deviation is the same for both models [t(59)=0.13, P=0.90].

We also repeated the fitting procedure on the data of the disappearing spiders in experiment 2 to see whether we would get the same parameter values for the models as in experiment 1, and whether this would decrease the mean deviations. Instead of an extrapolation time of 156±10 ms, we found that $T_{ext}=243\pm11$ ms described these data best (mean deviation of 0.40 cm). However, the mean deviation was not significantly smaller than with $T_{ext}=156$ ms [mean deviation=0.44, t(59)=1.14, P=0.26]. Fitting the data to the model of progressive use of speed resulted in T_{change} =334±40 ms (mean deviation=0.44 cm), which is close to the previously found T_{change} of 307±8 ms. The mean deviation was not significantly lower than with T_{change} =307 [mean deviation= 0.44 cm as well, t(59)=0.53, P=0.60]. The mean deviations from the models using the parameter values from the fit to the data of experiment 2 were also not significantly different [*t*(59)=1.17, *P*=0.25].

The mean deviations between the used invisible displacements and the predicted ones in this experiment are higher for both models than in the first experiment. Still, the extrapolation model and the progressive use model perform much better than the simple models. For the



Fig. 13A, B The used invisible displacement (*ordinates*) averaged for each subject and each condition plotted against the invisible displacement predicted by (**A**) the extrapolation model and (**B**) the model of progressive use of speed (*abscissas*), using the parameter values found in experiment 1. The mean deviation of the points from the unity line is 0.44 cm for both models

data of experiment 2, the actual speed model yields a mean deviation of 0.58 and the default speed model yields a mean deviation of 0.77.

Discussion

According to the hypothesis of progressive use of speed, subjects should be able to make optimal use of speed both when a non-disappearing spider is presented and when a spider is presented that is visible for a long time. However, these two types of spiders were hit at different positions. Hitting errors were lower and depended less on spider speed when spiders did not disappear than when they disappeared after being long visible. A second prediction of the hypothesis of progressive use of speed was that the subjects' use of speed would be better when the spider was visible long than when it was visible shortly, so that the hitting errors would become smaller and less dependent on spider speed. In contrast, we found that when T_{invis} was kept constant, an increase of T_{vis} from 150 to 442 ms did not change the hitting positions and hitting errors significantly. We thus reject this hypothesis.

The extrapolation hypothesis correctly predicted that T_{invis} would make a difference, so that hitting errors resulting from hitting non-disappearing spiders would be the lowest and the least dependent on spider speed. It also correctly predicted that the effect of speed on hitting positions and hitting errors would not depend on T_{vis} as long as the spiders were invisible for the same time. We conclude that the extent to which target speed has an effect on hitting position and error depends more on the time between the target's disappearance and the hit than on the time that the target is visible. This is in accordance with the extrapolation hypothesis.

Still, there is reason for caution before concluding that this hypothesis is a valid explanation. Firstly, though it is not significant, there is a trend for smaller hitting errors when spiders are visible for 442 ms than when they are visible for 150 ms, despite the equal T_{invis} . Secondly, the quantitative models did not favor the extrapolation hypothesis above the hypothesis of progressive use of speed. It is possible that this is due to the assumptions we made. Concerning the extrapolation hypothesis, it would be interesting to measure eye movements during the interception of moving objects. The relation between the quality of the pursuit and the position of the hit could be explored. In the present study, we assumed that subjects always pursued the targets with a gain of 1, and that the first command to do so was given within the shortest T_{vis} (i.e., within 150 ms). However, Carl and Gellman (1987) found that targets moving at 10°/s are only pursued smoothly after approximately 250 ms.

One could argue that both mechanisms play a role in guiding the hand to the point of interception. Together they will predict that a long T_{vis} as well as a short T_{invis} increase the chances of a successful hit. We constructed a hybrid model in which not only a time was implemented at which the used speed changed from the default into the actual speed, but also an extrapolation time that defines how long the actual speed continues to guide the hand after the target has disappeared. Whereas the T_{change} is defined as a fixed time after the start of the presentation, the T_{ext} is a fixed time after the disappearance of the spider. The used invisible displacements of experiment 1 appeared to be described best by T_{change} =167 ms and T_{ext} =166 ms. The *PID*s computed by the hybrid model are almost equal to the ones computed by the extrapolation model. This is because the value of T_{change} is only slightly higher than the T_{vis} of 150 ms, and lower than the other times that the spiders were visible, while the T_{ext} approximates the 156 ms extrapolation time we found earlier. Though the hybrid model has two fitted parameters instead of one, the mean deviation was 0.32 cm which is the same as the mean deviation of the extrapolation model. Thus, adding one parameter did not improve the fit to the data of experiment 1. We therefore reject this model.

Although target speed is not used completely or correctly in guiding the hand to the interception point of a moving target, experiment 1 shows that it does play a role. In experiment 2 we tested two more specific hypotheses that differed in the nature of the influence of target speed. According to the extrapolation hypothesis, speed has an indirect effect through affecting the perceived position of the target. According to the hypothesis of progressive use of speed, subjects take target speed itself into account while guiding their hand. The extrapolation hypothesis explains better how the hitting position is determined than the hypothesis of progressive use of speed, but it was not supported unequivocally. In a third experiment we use a different approach to see whether we can find additional support for the idea that the measured effect of speed is caused by a speed-related misperception of the target rather than a direct use of speed in guiding the hand.

Experiment 3

Again subjects hit briefly visible spiders running from the left to the right, but this time we sometimes moved the background to manipulate the perceived speed of the spiders. If the background moves to the left, the perceived motion of the spider is faster than if it moves to the right (Smeets and Brenner 1995). Thus, if subjects use perceived speed itself to guide their hand, they should hit more to the right (ahead of the invisible spider) if the background moves to the left than if the background moves to the right.

Materials and methods

Materials and design

The materials are the same as in experiment 1. We used a short T_{vis} of 200 ms so that possible differences in hitting positions between the conditions would become more obvious. We knew from experiment 1 that 200 ms is long enough to ensure that target speed has an effect. Both the spiders and the background disappeared, because we wanted to manipulate the perceived speed of the spider and to reduce possible effects of a moving background after the spider had disappeared. When the rod arrived at the screen, the background and the spider appeared again to give the subject feedback as in the other experiments. During the feedback, the background was static.

The starting point of all spiders was 8 cm to the left of the starting position of the subject's hand. The spiders ran at 6, 12, 18, or 24 cm/s. Spiders running at 12 or 18 cm/s always ran across a background that was moving at 6 cm/s, either to the left or to the right. The background started to move at the same time as the running spider appeared. The background was static when the spiders ran at 6 or 24 cm/s. This yielded six conditions. We presented 15 trials per condition, which results in a total of 90 trials for each subject. The order was randomized.

Subjects and instruction

Ten volunteers from our department participated in the experiment, after giving informed consent. Six of them had participated in both previous experiments and one had only participated in experiment 2. One subject was left-handed, the rest were right-handed. They all hit with their preferred hand. The instruction was the same as before. We told the subjects that the background could move (though this was not necessary because the background's motion was clearly visible).

Analysis

From the total of 900 trials, 2 were excluded from analysis for technical reasons. We did not define any new measures to describe the results of this experiment.

We performed repeated measures analyses of variance for the factor spider speed on averages from the complete dataset for each subject and spider speed. Separate repeated measures analyses of variance were performed on the subset of data in which the background moved. These had target speed and background direction as factors.

Results

General characteristics

Reaction time (Fig. 14A) and movement time (Fig. 14B) decreased with increasing spider speed, as they had in the previous experiments [F(3,27)=6.32 and F(3,27)=



Fig. 14A–C Reaction time, movement time, and variable error for each spider speed and background motion in experiment 3. *Error bars* represent the standard error between subjects. **A**, **B** Reaction time and movement time both decrease with spider speed and are independent of background motion. **C** Variable error did not systematically depend on spider speed. Variable error was higher when the background moved in the opposite direction than the spider (*against*) than when it moved in the same direction (*with*)

6.54, respectively, both P<0.01]. Direction of background motion did not affect reaction time and movement time [F(1,9)<1.0, P=0.95 and F(1,9)=1.46, P=0.26, respectively]. There was a significant effect of spider speed on variable hitting error [F(3,27)=3.40, P=0.03] but this was not systematic (Fig. 14C). Direction of background motion significantly affected the variable hitting error as well [F(1,9)=7.00, P=0.03].

Of all spiders, 65% were hit successfully. In contrast to the previous experiments it appeared that fast spiders, in terms of absolute and apparent speed, were easiest to hit. From the highest to the lowest spider speed, the percentages of hits were 76%, 69%, 61%, and 54%. Of the apparently faster spiders (i.e., with a background moving in the opposite direction), 67% were hit successfully. Of the apparently slower spiders, 63% were hit. Spiders running over a static background were hit in 65% of the trials. Note that the average hitting percentage was the same when the background moved as when it was static.

Hitting positions

Figure 15 shows the hitting position and spider position for each spider speed and for each background motion.



Fig. 15 Spider position and hitting position (relative to the start of the spider's movement) for each speed and background motion. Subjects do not hit further behind spiders when the background moved in the same direction as the target (with) than when it moved in the opposite direction (against). This contradicts the idea that subjects use perceived speed, because the spider appears to be slower if the background moves in the same direction

Spider speed had a significant effect on hitting position and hitting error [F(1,9)=65.53 and F(1,9)=39.87, respectively, *P* values <0.01]. Direction of background motion did not significantly influence hitting position or hitting error [F(1,9)=2.92, P=0.12 and F(1,9)=2.69, P=0.14].

Discussion

If subjects had used perceived speed in hitting moving spiders, they would have hit further in front of the disappearing point when the spider appeared to move faster than when it appeared to move more slowly. In contrast, we found no effect of the direction of background motion on hitting position and hitting error. The trend was even the opposite; subjects tended to hit further to the left (i.e., behind the spider) when the background moved to the left (and the spider appeared to move faster) than when it moved to the right. This trend might be explained by the finding that for brief presentations (tested for 100 ms or less) the perceived position shifts in the direction of the moving background (Brenner and Smeets 1997), possibly because the egocentric reference system is affected by a moving background (Mohrmann-Lendla and Fleischer 1991). Consequently, if only target position is used, subjects may hit a bit more to the left if the background moves to the left and more to the right if the background moves to the right.

In conclusion, the results of experiment 3 support the suggestion that target speed is not used in guiding the hand when hitting moving objects. They are consistent with the idea that only target position and a default speed are used.

In the previous experiments, subjects made the smallest systematic errors when hitting spiders running at the average speed (Figs. 6, 12), suggesting that the average spider speed is not a bad estimate for a hypothetical default speed. In the present experiment, subjects hit spiders running at 18 cm/s best (Fig. 15). We have no explanation for this.

Summary and general discussion

In experiment 1 we tested whether subjects use target speed or whether they only use target position and a default speed in guiding their hand to intercept moving targets. We observed that there was a partial effect of target speed on the hitting position. The magnitude of the effect depended on the time that the target was visible (or the time between the target's disappearance and the hit). In experiment 2 we tested specific, refined versions of the hypotheses that either target position and a default speed or the actual speed is used. According to the extrapolation hypothesis subjects use the perceived position and a default speed, and the effect of the target's actual speed occurs via misperception of the target position. It predicts that the effect of target speed will become weaker with a longer T_{invis} . According to the hypothesis of progressive use of speed, it takes longer to use the actual speed, so that the longer the T_{vis} , the better subjects are able to use speed. We found that only the T_{invis} significantly influenced the effect of target speed. Thus, the extrapolation hypothesis was favored above the hypothesis of progressive use of speed. However, as the evidence was not overwhelming we performed a third experiment in which the general question whether subjects use only position and a default speed or the actual (perceived) speed was tested in another way. The perceived speed was manipulated by moving the background. The results indicated that the hitting positions were not affected by illusory target speed.

At first sight, our conclusion that target speed is not used in guiding the hand to the place of interception seems to be in conflict with the results of experiments 1 and 2 in which an effect of target speed on hitting positions was found. However, the extrapolation model (that we tested in experiment 2) is an example of how target speed can have an indirect effect on the hitting position. Target speed influences the perceived position of the moving target so that if that misperceived target position is used, you will find an effect of target speed. This influence is fundamentally different from directly using target speed because it cannot be used to make predictions for arbitrary moments. In experiment 3 we moved the background so that the target speed was misperceived. This did not affect the hitting positions, as would be expected on the basis of the hypothesis that you do not use target speed but target position.

Our results indicate that perceived target speed is not used in guiding the hand to the position of interception. Previous research indicates that it is used in guiding the timing of the hand. More specifically, subjects move faster to fast targets than to slow ones (see, for example, Bootsma and van Wieringen 1990; Brouwer et al. 2000; Wallace et al. 1992; influence of target speed on movement time in the present study). This is also observed when subjects are asked to always move as quickly as possible and when the perceived speed is manipulated by moving the background (Smeets and Brenner 1995). This suggests that the information used to guide the hand's timing differs from the information used to determine the hand's spatial trajectory. It may therefore be impossible to understand interception as a continuous coupling between action and the changing visual information, without distinguishing between spatial and temporal aspects, as these may in fact be controlled separately to a certain extent.

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References

- Anstis S, Verstraten FAJ, Mather G (1998) The motion aftereffect. Trends Cogn Sci 2:111–117
- Babler TG, Dannemiller JL (1993) Role of image acceleration in judging landing location of free-falling projectiles. J Exp Psychol Hum Percept Perform 19:15–31
- Bairstow PJ (1987) Analysis of hand movement to moving targets. Hum Mov Sci 6:205–231
- Bootsma RJ, Wieringen PCW van (1990) Timing an attacking fore-hand drive in table tennis. J Exp Psychol Hum Percept Perform 16:21–29
- Brenner E, Cornelissen FW (2000) Separate simultaneous processing of egocentric and relative positions. Vision Res 40:2557– 2563
- Brenner E, Smeets JBJ (1996) Hitting moving targets: co-operative control of 'when' and 'where'. Hum Mov Sci 15:39–53
- Brenner E, Smeets JBJ (1997) Fast responses of the human hand to changes in target position. J Mot Behav 29:297–310
- Brenner E, Smeets JBJ, Lussanet MHE de (1998) Hitting moving targets: continuous control of the acceleration of the hand on the basis of the target's velocity. Exp Brain Res 122:467–474
- Brenner E, Smeets JBJ, Berg AV van den (2001) Smooth eye movements and spatial localisation. Vision Res (in press)
- Brouwer A, Brenner E, Smeets JBJ (2000) Hitting moving objects: the dependency of hand velocity on the speed of the target. Exp Brain Res 133:242–248
- Brouwer A, Brenner E, Smeets JBJ (2001) Perception of acceleration with short presentation times: can acceleration be used in interception? Perception 30(suppl):36
- Carl JR, Gellman RS (1987) Human smooth pursuit: stimulusdependent responses. J Neurophysiol 57:1446–1463
- Carnahan H, McFadyen BJ (1996) Visuomotor control when reaching toward and grasping moving targets. Acta Psychol 92:17–32
- Donkelaar P van, Lee RG, Gellman RS (1992) Control strategies in directing the hand to moving targets. Exp Brain Res 91:151–161
- Heywood S, Churcher J (1981) Saccades to step-ramp stimuli. Vision Res 21:479–490
- Kamp J van der, Savelsbergh G, Smeets J (1997) Multiple information sources in interceptive timing. Hum Mov Sci 16:787– 821
- Lee DN, Young DS, Reddish PE, Lough S, Clayton TMH (1983) Visual timing in hitting an accelerating ball. Q J Exp Psychol A 35:333–346
- Lussanet MHE de, Smeets JBJ, Brenner E (2001) The effect of expectations on hitting moving targets: influence of the preceding target's speed. Exp Brain Res 137:246–248
- Mason AH, Carnahan H (1999) Target viewing time and velocity effects on prehension. Exp Brain Res 127:83–94
- McBeath MK, Shaffer DM, Kaiser MK (1995) How baseball outfielders determine where to run to catch fly balls. Science 268:569–573
- Michaels CF, Oudejans RRD (1992) The optics and actions of catching fly balls: zeroing out optical acceleration. Ecol Psychol 4:199–222

- Michaels CF, Zeinstra EB, Oudejans RRD (2001) Information and action in punching a falling ball. Q J Exp Psychol A 54:69–93
- Mita T, Hironaka K, Koike I (1950) The influence of retinal adaptation and location on the "Empfindungszeit". Tohoku J Exp Med 52:397–405
- Mitrani L, Dimitrov G (1982) Retinal location and visual localization during pursuit eye movement. Vision Res 22:1047–1051
- Mitrani L, Dimitrov G, Yakimoff N, Mateeff S (1979) Oculomotor and perceptual localization during smooth eye movements. Vision Res 19:609–612
- Mohrmann-Lendla H, Fleischer AG (1991) The effect of a moving background on aimed hand movements. Ergonomics 34:353–364
- Montagne G, Laurent M, Durey A, Bootsma R (1999) Movement reversals in ball catching. Exp Brain Res 129:87–92
- Peper L, Bootsma RJ, Mestre DR, Bakker FC (1994) Catching balls: how to get the hand at the right place at the right time. J Exp Psychol Hum Percept Perform 20:591–612
- Port NL, Lee D, Dassonville P, Georgopoulos AP (1997) Manual interception of moving targets. I. Performance and movement initiation. Exp Brain Res 116:406–420
- Press WH, Teukolsky SA, Vetterling WT, Flannery BP (1992) Numerical recipes. Cambridge University Press, Cambridge, pp 691–699
- Rosenbaum DA (1975) Perception and extrapolation of speed and acceleration. J Exp Psychol Hum Percept Perform 1:395–403

- Savelsbergh GJP, Whiting HTA, Bootsma RJ (1991) Grasping tau. J Exp Psychol Hum Percept Perform 17:315–322
- Savelsbergh GJP, Whiting HTA, Burden AM, Bartlett RM (1992) The role of predictive visual temporal information in the coordination of muscle activity in catching. Exp Brain Res 89:223–228
- Smeets JBJ, Brenner E (1994) The difference between the perception of absolute and relative motion: a reaction time study. Vision Res 34:191–195
- Smeets JBJ, Brenner E (1995) Perception and action based on the same visual information: distinction between position and speed. J Exp Psychol Hum Percept Perform 21:19–31
- Todd J (1981) Visual information about moving objects. J Exp Psychol Hum Percept Perform 7:795–810
- Tresilian JR (1994) Approximate information sources and perceptual variables in interceptive timing. J Exp Psychol Hum Percept Perform 20:154–173
- Tresilian JR (1999) Visually timed action: time-out for 'tau'? Trends Cogn Sci 3:301–110
- Wallace SA, Stevenson E, Weeks DL, Kelso JAS (1992) The perceptual guidance of grasping a moving object. Hum Mov Sci 11:691–715
- Zaal FTJM, Bootsma RJ, Wieringen PCW van (1999) Dynamics of reaching for stationary and moving objects: data and model. J Exp Psychol Hum Percept Perform 25:149–161