Perception and Action Are Based on the Same Visual Information: Distinction Between Position and Velocity

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Ss were presented with spiders running from left to right at various velocities over a structured background. Motion of the background influenced the perceived velocity of the spider: Motion of the background in the opposite direction than the spider increased the perceived velocity. The perceived position of the spider was not influenced by background motion. Ss were asked to hit the spiders as quickly as possible. Fast spiders were hit with a higher velocity than slow spiders. The same effect was found if the spiders only differed in apparent velocity, induced by motion of the background. The trajectory of the hit was not influenced by motion of the background. The authors concluded that although velocity is nothing but the change of position in time, velocity and position are processed independently. Furthermore, these two separately processed sources of information are used in both perception and action.

To make a goal-directed movement, our nervous system has to specify the position of the goal in one way or another. How this specification takes place is the subject of many studies. According to the cognitive approach (e.g., Paillard, 1991), an internal representation of the environment is built, and this representation is used by the motor system. According to the ecological approach (e.g., Lee & Young, 1986), no intermediate representation is assumed. In the latter view, an invariant is extracted from sensory signals for direct use in motor action. Both approaches leave open for debate which invariant or what kind of representation is used for which task.

Many authors (e.g., Bridgeman, Kirch, & Sperling, 1981; Goodale & Milner, 1992; Goodale, Milner, Jakobson, & Carey, 1991; Loomis, Da Silva, Fujita, & Fukusima, 1992; Pélisson, Prablanc, Goodale, & Jeannerod, 1986) argue that sensory signals are transformed differently for perceptual and motor tasks. In the cognitive view, this distinction is interpreted as two different internal representations: an egocentric (motor) one and an allocentric (cognitive) one (Paillard, 1991). An alternative hypothesis is that the same transformation (or representation) is used for perception and action, but that the specific requirements of the task determine which source of information is used. Spatial information consists of several aspects, such as position, distance, direction, and velocity. In reality, an object with a velocity changes position. However, as velocity and position are derived from different visual cues, motion and position can be processed independently in the human brain (e.g., Paillard & Amblard, 1985). This is not only the case in the

visual system, but also in the motor system. It is for instance possible (by muscle tendon vibration) to elicit the sensation of a continuous motion of the arm combined with the sensation of a stationary arm position (Sittig, Denier van der Gon, & Gielen, 1985).

According to this second hypothesis, the distinction between *perception* and *action* originates from comparing perceptual and motor tasks that require different kinds of information. In the experiment of Bridgeman et al. (1981), for instance, the perception of an object's *velocity* was compared with a motor response to a *position*. Support for this view can be found in recent literature on other aspects of spatial vision. Abrams and Landgraf (1990) asked subjects to reproduce either the final location or the displacement of an object. Illusory motion affected the tasks differently, indicating independent processing of location and displacement. By asking subjects to move their hand slowly toward a target and to adjust a pointer to match the direction of the target, de Graaf, Sittig, and Denier van der Gon (1991) showed that direction and position are also processed separately, with the same systematical errors in both perception and action.

In this article, we examine whether the different perceptual and motor responses to induced motion are caused by processing the same sources of information differently (Bridgeman et al., 1981; Paillard, 1991), or by processing different sources of information. To resolve this issue, we need perceptual and motor tasks that make use of information about both position and velocity. Targets moving on a structured background give an observer information about both position and velocity. As the perceived target velocity depends on the target's motion relative to the background (e.g., Brenner, 1991), concomitant movement of the background will perturb velocity information. Such background motion should not influence the information on position at any instant. We determine the perceived position and velocity of the target by asking subjects to match the position and velocity of two subsequently presented targets. We

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show how information about position and velocity is used in motor control by asking the subjects to hit the target.

The reason we asked subjects to hit the target is that we needed a task that requires information not only on position but also on velocity. Studies on the control of arm movements (Sittig et al., 1985; Smeets, Erkelens, & Denier van der Gon, 1990; Wadman, Boerhout, & Denier van der Gon, 1980) have shown that velocity is an important control parameter in fast goal-directed arm movements. If motion perception is used in motor control, it is therefore quite likely that fast goal-directed arm movements toward a moving target are influenced. Different target velocities obviously result in different positions at which the target is hit. To discriminate between the effects of target motion and the target's position when hit, the arm movements can be compared to movements toward stationary targets.

In the views of Bridgeman et al. (1981) and Paillard (1991), a change in perceived motion induced by movement of the background will only influence the allocentric representation of space, and thus cognitive perception. As motor control uses an egocentric representation (for which the background and its motion are irrelevant), arm movements will not be affected by the perceived induced motion. An alternative hypothesis (probably favored by many ecologists) is that both (veridical) position information and (perturbed) velocity information will be used together to determine the timing and position of the hit.

After describing the general experimental setup, we describe three experiments. The third (motor) experiment is the main experiment of the article; the first two (perception) experiments were designed to quantify the perceptual effects of the stimulus used in the third experiment. The first two experiments were performed after the third experiment in order to be able to use parameters (e.g., the average reaction time [RT]) from the motor experiment in the design of the perception experiments. For the clarity of the argumentation, however, we reversed the order, and described the perceptual effects of the stimulus before concentrating on the motor responses. The article concludes with a model, which shows that the experimental trajectories can be explained without the use of the velocity of the target. A preliminary report on the experimental results has been published (Brenner & Smeets, 1994).

General Experimental Setup

The apparatus used in the experiments had to perform two tasks quickly and synchronously: to generate images and to measure the subject's movements. Both tasks were taken care of by dedicated machines, controlled and synchronized by an additional personal computer (control-PC). An overview of the experimental setup is given in Figure 1.

Images were generated on a Unix-based graphical workstation (Silicon Graphics Iris 4D 210GTX). The monitor of the system was protected by a transparent screen, oriented at 30° with the vertical. Three-dimensional images were created by presenting different images to both eyes, separated using LCD shutter spectacles (Neucom Electronic GmbH).
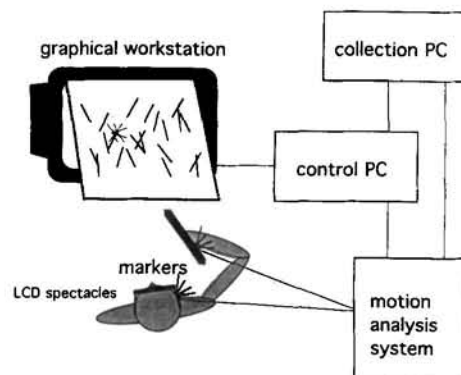

Figure 1. Overview of the experimental setup.

Each eye received newly calculated images at 60 Hz. The images were constructed to give the appropriate three-dimensional impression for the actual positions[1] of the subjects' eyes. Images consisted of a background of about 40 yellow lines on the transparent screen (line length = 4 cm, random orientation between ±60° around vertical in a 18 × 16 cm area on the screen, about 0.5 m from the subject) and a red or green spider (length of body and head = 0.8 cm; length including legs = about 2 cm). Both background and spider could move horizontally (left–right). The spider's legs moved as a real spider's would, in accordance with its motion relative to the background. To mask the appearance and disappearance of lines at the borders of the background, the intensity of the lines faded in a 4-cm area on the left and right sides. The effective luminance of the spider was 0.8 cd/m².

Movements of the subject's head and hand were recorded by a motion analysis system that was based on active infrared markers (Optotrak 3010, Northern Digital, Inc.). The markers for measuring movements of the hand were attached to a perspex rod (22 cm long, 1 cm radius) held by the subject. Markers for measuring movements of the head were attached to the LCD shutter spectacles. The resolution of the position measurement was better than 0.1 mm in all three dimensions. Position data were collected by another PC (collection-PC) at 300 Hz for 1.5 s per trial using the Optotrak Collect computer program (Northern Digital, 1991).

The control-PC regulated the generation of the images and the collection of the data by the collection-PC. It calculated the actual position of the subject's eyes and of the tip of the rod (a position referred to as "position of the hand") from the markers' positions, and sent these data to the graphical workstation. The software on the graphical workstation and the control-PC was home built. Due to the nature of the Unix operating system on the workstation, the timing between the systems was slightly variable. The total delay of the feedback from position to image was 35 ± 10 ms.

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[1] Here, *eye position* means the three-dimensional position of the eye in space, and not the orientation of the eye.

Experiment 1: Perception of Velocity

It is known that a moving background changes the perceived velocity of a moving object (Brenner, 1991; Duncker, 1929). The magnitude of this effect depends on the exact experimental conditions. The aim of this experiment was to study how motion of the background influences subjects' perception of spider velocity in our experimental setup. This was done by asking subjects to match the velocities of two spiders.

Method

Subjects. Six volunteers (including the authors) from our department participated in the experiment. Except for the authors, the subjects were naive with respect to the exact purpose of the experiment.

Experimental procedure. Subjects sat on an adjustable chair in front of the graphical workstation. They were allowed to position the chair so that they could comfortably view the background on the screen while holding a computer mouse with their hand. The only light in the room was that produced by the image on the screen. Thus, subjects could not see their hand, nor had they any other visual points of reference. Spiders appeared 8 cm to the left of the center of the screen and moved to the right. After 250–500 ms (randomly chosen) of running, the spider was removed from the screen. During the next 500 ms, only the background was visible. After that, the next spider appeared (see Figure 2).

Two kinds of spiders appeared in alternation: test spiders (colored red) and reference spiders (colored green). The velocity of the test spider and its background remained constant during a trial. The velocity of the reference spider (running on a static background) was controlled by the position of the mouse. Subjects were instructed to change the velocity of the green spiders by repositioning the mouse, until it matched the velocity of the red spider. When
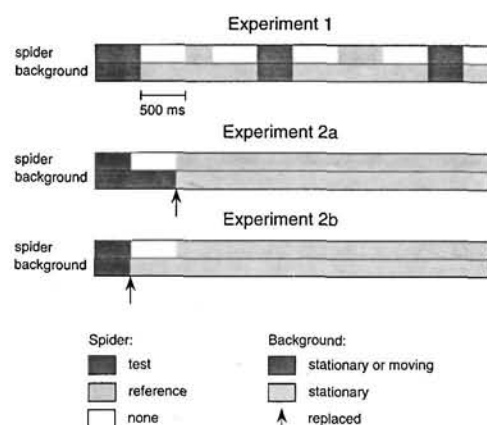
they were satisfied, they pushed the mouse button, and the next trial started. To examine the effect of background motion, the background could move during the presentation of the test spider.

The experiment consisted of 45 trials. The combinations of velocity of the test spider and the background are listed in Table 1. The trials were presented in random order.

Data analysis. The question we want to answer in this and the subsequent experiment is how much effect motion of the background has on the apparent motion of the spider. To answer this question, we devised a method for analyzing individual subjects' responses that could be used for all the experiments (Figure 3). We first fitted a regression line to a subject's responses in the trials with a moving spider and a static background. Using the parameters of this fit, we then deduced the apparent spider velocity from the responses for each trial. From these, we calculated an average apparent spider velocity for each condition. In Experiment 1, the regression will yield a slope of 1.0 and zero intercept, so that the computed apparent velocities will be equal to the velocities reported by the subjects. The advantage of this method is that it yields comparable results (apparent spider velocities) for all experiments and measured variables.

Values for different conditions were compared with two-tailed paired t tests, with a confidence level of $p = .95$. All statistics and bar charts were generated by the Statview 4.0 computer program (Abacus Concepts, 1992). The intersubject variability is indicated by the standard error of the mean.

Results

None of the subjects reported any difficulty with the task of matching the velocities of the spiders. The velocities of the red and green spiders were matched quite accurately when the background was stationary: The slope (calculated for each subject individually) was .97 ± .08, with a correlation coefficient of .93 ± .03. The effects of background motion in Experiment 1 are summarized in Figure 4. Motion of the background gave rise to large perceptual errors: Background motion at 6 cm/s in the opposite direction than the spider increased the perceived velocity by about 4 cm/s; a similar decrease was found if the background moved in the same direction.

Discussion

In our experimental setup, motion of the background indeed led subjects to misjudge the spider's velocity. The effect is not complete: The perceived velocity is between the absolute velocity of the spider and its velocity relative to the background. This is probably due either to additional references, such as the borders of the background, or to a conflict between the perceived velocity and the perceived change of position.

Experiment 2: Perception of Position

In Experiment 2, we investigated whether the perceived position of the spider is also influenced by motion of the background. In analogy to the task in Experiment 1, we tested perception by asking subjects to match the positions of two spiders. To investigate whether motion of the back-

Figure 2. Time course of Experiments 1 and 2. When the test spider was present, the background could be moving or stationary, depending on the stimulus (see Table 1). In Experiment 2a (position perception), the background was replaced by a new one when the reference spider appeared; this prevented subjects from using elements of the background as a reference. In Experiment 2b, the background was replaced by a new one when the test spider disappeared, thereby eliminating possible effects of background motion during the absence of the spider.

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Table 1

Summary of the Stimuli Used in the Nine Conditions of the Perception Experiments

Background	Spider velocity (cm/s)	Background velocity (cm/s)
Static	6	0
	9	0
	12	0
	15	0
	18	0
Moving	6	−6
	12	6
	12	−6
	18	6

Note. Negative numbers indicate that the background and the spider moved in opposite directions. In all cases, number of trials = 5.

ground in the absence of the spider had any effect, two versions of the experiment were performed (Experiment 2a and 2b).

Method

Subjects. The same 6 people who participated in Experiment 1 served as subjects in Experiment 2a; 4 of them also participated in Experiment 2b.

Experimental procedure. Subjects sat in the same setup as in Experiment 1. A red test spider appeared 2–4 cm (randomly chosen) to the left of the center of the screen and moved to the right. After running for 367 ms (2.2–6.6 cm), the spider disappeared from the screen. During the next 500 ms, only the background was visible. In Experiment 2a, if the background had moved while the spider was visible, it kept doing so during these 500 ms (see Figure 2). Subsequently a new (static) background was presented. In Experiment 2b, the background was replaced at the moment the spider disappeared from the screen.

After the 500 ms, a static green reference spider appeared. The position of the spider was coupled to the position of the mouse. Subjects were instructed to change the position of the green spider until it matched the position at which the red spider disappeared. When they were satisfied, they pushed the mouse button, and the next trial started.

The experiment consisted of 45 trials. The velocities of spider and background are listed in Table 1. The combinations of test spider velocity and background velocity were presented in random order.

Data analysis. For each subject, the relationship between spider velocity and reported position was determined from the trials with a static background (as sketched in Figure 3). Correct responses will yield a slope of 0.367 s (the duration of the presentation). Using this relationship, we computed the apparent spider velocity from the set position on each trial. This yields results in the same format as those of Experiment 1.

Results

Within-subject variability (correlation coefficient of the regression was $r = .90 \pm .01$) was larger for matching the final position of a moving spider (Experiment 2a) than for matching its velocity (Experiment 1). Subjects made sys-

tematic errors in Experiment 2a: The slope was $.42 \pm .04$ s, with an intercept of -0.4 cm. Thus, subjects reported a position 0.4 cm to the left of the position that the spider would have reached 50 ms after it disappeared. The effect of background motion in Experiment 2a is summarized in Figure 5A. Motion of the background had no effect on the perceived position of the spider. Experiment 2b (Figure 5B) showed that there was no effect of the continuation of the background motion during the 500 ms between the disappearance of the test spider and the appearance of the reference spider.

Discussion

Whereas motion of the background had a clear effect on the perceived velocity (Experiment 1), it did not affect the perceived position (Experiment 2). It is interesting to note that subjects did extrapolate the trajectory of the spider. This extrapolation was independent of the motion of the background and corresponded to the position at which the spider would have been 50 ms after it disappeared.

Several mechanisms can contribute to this phenomenon. For the first mechanism, we assume that efferent information about the orientation of the eyes (which pursue the spider) is the source of position information. Due to delays in the neural pathways involved in making eye movements and to delays due to the mechanical characteristics of the eye and eye muscles, the actual eye position will always lag behind the commanded eye position. If the nervous system uses the commanded eye position ("efference copy") at the moment of disappearance, this will be a position that the eye will reach some time later. Thus, the spider will be perceived to have been further than it actually was. A second
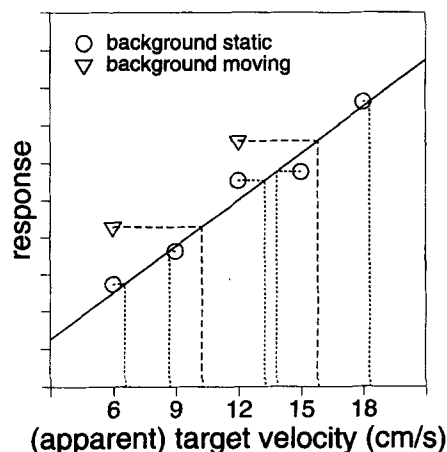

Figure 3. The transformation from measured response (arbitrary units) to apparent velocity. A relation between a measured response and the velocity of the spider was determined for the trials with a static background, using linear regression. With this regression, we derived for each response value the corresponding apparent target velocity (dotted lines). The apparent velocities for trials with a moving background were obtained using the same fit (dashed lines).
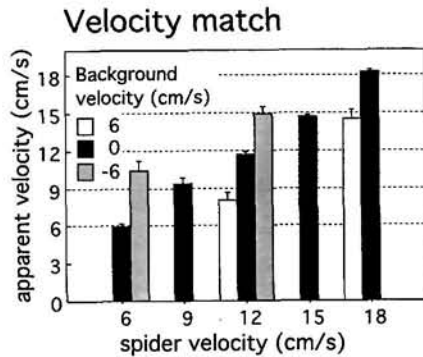
Figure 4. Experiment 1: the effect of background motion on the perceived velocity. The apparent velocity of the test spider for the five velocities of the reference spider, and three background velocities, as revealed by matching its velocity. Solid bars indicate a static background, white bars a background that moves in the same direction as the spider, and gray bars a background that moves in the opposite direction than the spider is moving. See Figure 3 for the method of calculating the apparent velocity. Means are calculated over all trials of all subjects; error bars indicate the intersubject standard error of the mean. For all moving background conditions, the apparent spider velocity was significantly different from the apparent velocity in the corresponding static background condition.

mechanism is that subjects perceive the disappearance of the spider always some (short) time after the actual disappearance and determine the eye position at that instant. Both effects can lead to a misjudgment of position corresponding to a fixed amount of time, and can therefore explain the phenomenon.

In this experiment, each trial consisted of only one test spider, whereas in Experiment 1, the subjects could see as many test spiders as they liked. We are therefore not surprised that the within-subject variability in Experiment 2 is higher than in Experiment 1. For comparison with Experiment 2, it would have been better if only one test spider had been presented in Experiment 1. However, it proved to be almost impossible for subjects to match the velocity in this way.

Now that we have characterized the perceptual effects of our stimulus, we can describe the main experiment.

Experiment 3: Hitting a Running Spider

The two previous experiments showed that motion of the background had a clear effect on the perceived spider velocity, whereas the perceived position of the spider remained unaffected. In Experiment 3, we wanted to study which information is used to guide the hand to moving spiders.

Method

Subjects. Twelve right-handed volunteers from our department participated in the experiment, including the participants of Experiments 1 and 2. Except for the authors, all subjects were naive

with respect to the exact purpose of the experiment. Subjects were rewarded for their cooperation in this experiment with a small box of Smarties (Nestlé S.A.). The experiment was carried out on three different days. On each day, the best performing subject (for method of rating see next section) received a Mars Bar (Mars B.V.).

Experimental procedure. Subjects sat on an adjustable chair in front of the graphical workstation, holding the perspex rod with their right hand. They viewed the background, which only disappeared from view when it was replaced by messages about the experiment. These messages guided the hand to within 5 cm of a point at 40 cm from the center of the screen. The exact starting position of the hand varied between trials. Subjects had no visual references other than the stimulus on the screen.

Subjects positioned the chair so that they could start the movement with an almost fully flexed elbow and both upper and lower arm more or less parallel to their trunk. They could not see the hand, although they could deduce its approximate position from the occlusion of the background once the hand was near the screen. Spiders could appear on the left side of the screen moving to the right, or at rest on positions around the center of the screen. The position at which the spider appeared was constant with respect to the actual position of the hand and was thus variable on the screen. For the moving spiders, this position was independent of the spiders' velocity. Data collection started at the moment the spider appeared.
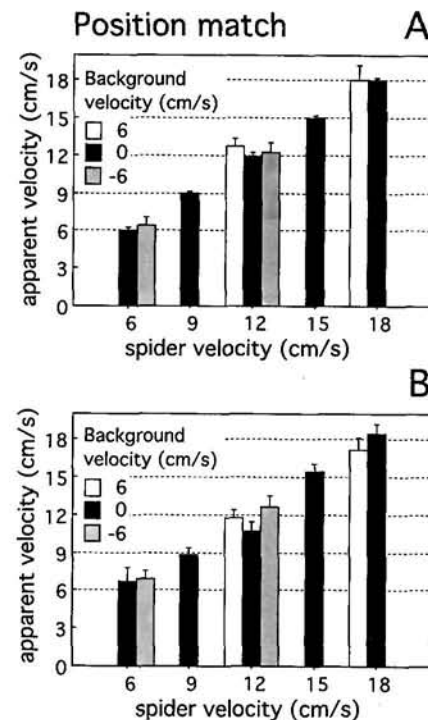

Figure 5. Experiment 2: the effect of background motion on the perceived position. The apparent velocity of the test spider for the five spider velocities, as revealed by matching the final position. See Figure 4 for further details. None of the moving backgrounds had a significant effect on the perceived position of the spider. Panel A: Experiment 2a, in which the background was replaced by a new one when the reference spider appeared. Panel B: Experiment 2b, in which the background was replaced by a new one when the test spider disappeared. No significant difference was found between the results of Experiments 2a and 2b.

Subjects were instructed to hit the spider with the perspex rod as fast as possible once it appeared on the screen. If the center of the rod was within 1.8 cm of the center of the spider when the screen was hit, the spider stopped running and was "squashed." If the subject hit behind the spider, it kept running in the same direction; if the hit was in front of the spider, it ran away in another direction. Subjects were given as many trials as they liked (about 20) to get used to the experimental setup. They were instructed to move both accurately (to hit the spider) and fast: The sum of RT and movement time (MT) was to be minimized. The experimenter occasionally gave the subjects feedback on their speed. The subjects' performance was rated according to the following formula:

$$Points = \sum_{spider \, = \, hit} \frac{100}{RT + MT},$$

in which RT and MT are expressed in ms. This rating was only used to motivate the subjects to move fast and accurately. The subjects gained between 12.8 and 23.0 points.

The experiment consisted of 192 trials. The spider and background velocities that we used are listed in Table 2. Apart from the same combinations of spider and background velocity as in the perception experiments, we also presented stationary spiders. This enabled us to study the effect of target position alone on the movement of the hand. The combinations of spider velocity and background velocity were presented at random. Subjects could rest as often as they liked by simply not moving the rod back to the starting area. All subjects completed the experiment (including instruction and practice trials) within 1 hr.

Data analysis. The velocity component perpendicular to the screen was calculated by numerical differentiation of the position data, without any filtering or smoothing. The onset and end of the movement were determined by a threshold of 0.1 m/s for this velocity. Trials were excluded from further analysis if the movement did not end on the screen, if infrared markers were not visible for more than 30 ms, or if either the RT or the MT was more than

Table 2
Summary of the Stimuli Used in the 12 Conditions of Experiment 3

Type	Start position (cm)	Spider velocity (cm/s)	Background velocity (cm/s)
Moving spider, static background	−8	6	0
	−8	9	0
	−8	12	0
	−8	15	0
	−8	18	0
Moving spider, moving background	−8	6	−6
	−8	12	6
	−8	12	−6
	−8	18	6
Static spider, static background	−3	0	0
	0	0	0
	3	0	0

Note. Negative values for the velocity of the background indicate it moved in the opposite direction than the spider was moving. In each of the static spider conditions, number of trials = 10; in each of the other conditions, number of trials = 18.
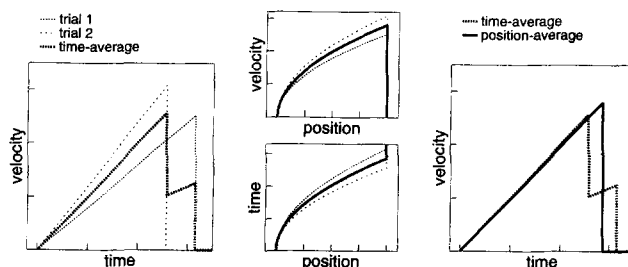
Figure 6. Method for calculating average velocity profiles. Left panel: If the average velocity is calculated directly from the velocity as a function of time, the averaged velocity profile will not resemble the individual velocity profiles. This is due to the dispersion caused by the different durations of the movements. Center: As the distance moved was almost identical on all trials, we can average both time and velocity as functions of position. Right panel: By plotting the obtained position-averaged velocity as a function of the position-averaged time, a velocity profile is obtained that does resemble the profiles of the individual trials.

700 ms. For all subjects, at least 90% of the trials could pass all these criteria.

To calculate an average velocity profile, we devised the following procedure (see Figure 6). As MT varied between trials, calculating the average velocity as a function of time would always yield a large dispersion. As the distance was almost the same for all trials, the average of velocity as function of distance to the screen was not disturbed by dispersion. We therefore calculated (by linear interpolation) the average velocity and the average time it would take to hit the screen for each position and plotted this velocity as a function of this time. In this way, the shape of the velocity profiles was preserved.

To be able to average the trajectories, we calculated (by linear interpolation) for each trial the displacement in the lateral (left–right) direction as a function of the distance to the screen. This was done after low-pass filtering the position data with a second-order digital Butterworth filter (Ackroyd, 1973). The filter was applied in both forward and reverse direction to prevent phase shift. The effective cutoff frequency was 25 Hz.

To characterize the arm movements, we used two values. For the velocity of the movement, we determined the maximum velocity in the direction of the screen on each trial. These velocities were then averaged for each condition. To characterize the shape of the trajectory, we determined the direction in which the hand was moving when it was at 30 cm from the screen on each trial. This point was reached 100–150 ms after the onset of movement.

These two characteristic values were analyzed in the same way as the perceptual judgments in Experiments 1 and 2 (Figure 6). Because there is no particular correct velocity or trajectory, we cannot give an expected slope for the fit.

Results

The movements had an average RT of 377 ± 12 ms. The velocity of the spider had a clear effect on this basic parameter (see Figure 7). The RT was shorter (<370 ms) for fast spiders than for the slowest and static spiders (>390 ms). For the slow spiders, the RT also depended on the background motion: The RT was shorter if the background moved in the opposite direction than the spider, and longer
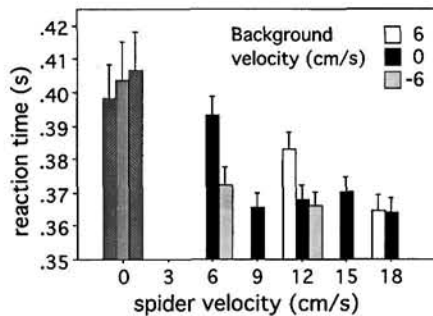
Figure 7. An overview of the reaction times (RTs) in Experiment 3. For the running spiders, solid bars indicate a static background, white bars a background that moves in the same direction, and gray bars a background that moves in the opposite direction than the spider. For the static spiders, the three bars on the left (at Point 0) indicate the three positions at which they appeared. These positions corresponded more or less to the positions at which (from left to right) slow, average, and fast moving spiders were hit. Error bars indicate the intersubject standard error of the mean. The RT did not differ significantly between static spider positions. For the moving spiders, background motion had a significant effect on the RT when the velocity of the spider relative to the background was less than 12 cm/s.

if both background and spider moved in the same direction. Both the effect of spider velocity and of background motion were only present for the lowest velocities tested. The RT was not different for static spiders at different positions.

The MT was on average 320 ms ± 20 ms (see Figure 8). It varied from more than 340 ms for the static and slow spiders to less than 290 ms for the fastest spiders. This effect was not due to the fact that slow and fast spiders were hit at different positions, because the MT did not differ systematically between static spiders at different positions. The movement time was shorter not only when the spider was really moving faster, but also when motion of the background gave the impression that it moved faster.

To give an idea of the variability within and between subjects, we plotted examples of trajectories of two subjects (Figure 9). The movements toward the moving spiders are more variable than those toward the static spiders. This is due to differences in RTs and MTs that result in different spider positions when the spider is moving. The variability with respect to the position of the spider is equal for both conditions.

For a better look at the movements, we plotted averages of the trajectories and of the velocity profiles of the tip of the perspex rod in Figures 10 (background stationary) and 11 (moving spiders).

The lower part of Figure 10 shows the velocity profiles (component perpendicular to the screen) of the movements of the hand for static and moving spiders on a stationary background. As the movements ended on the screen, subjects did not need to decelerate their arms themselves. This led to the asymmetric velocity profiles seen in Figure 10: The subject's arm accelerated during almost the whole trajectory. The plot reveals a clear effect of spider velocity on MT and maximum velocity: The faster the spider runs,

the faster the hand moves. This relationship is present right from the onset of the movement. It helps the subjects hit the spider, because the time it takes for the spider to reach the position that the hand is aiming at decreases with its velocity. This effect is not due to the fact that faster spiders were hit further to the right: All static spiders were hit with similar maximum velocities. That maximum hand velocity depends on the spider's velocity makes it a good candidate for effects of background motion.

The upper part of Figure 10 shows that the trajectories of movements toward moving spiders are somewhat different from those of movements toward stationary spiders at corresponding positions. For instance, the spiders moving at 18 cm/s are hit somewhat to the right of the static spiders at 3 cm. The trajectories to these moving spiders, however, start off further to the left than those toward the static spiders. It seems that the beginning of the trajectories toward the moving spiders is not directed at their final position; to hit the spider, the movements are corrected "on the way."

To compare the trajectories of movements toward spiders with and without motion of the background, we plotted them in Figure 11. In the upper part of this figure, we see only very small effects of background motion. Most of these small differences can be explained by differences in the timing of the movement: If the RT (or MT) is longer, the spider is at different positions during the motion. This results in a slight shift of the trajectories. Note that the shape of the trajectories is not affected by motion of the background.

The effects of the background motion on MT and on maximum hand velocity are clearly visible in the lower part of Figure 11. For instance, the trace of the hand's velocity for the trials in which spider and background moved in opposite directions at 6 cm/s is quite different from the one in which the spiders moved at the same velocity on a static background.

The direction in which the hand was moving at 30 cm from the screen varied more or less linearly with the velocity of the spider; the slope of this relationship was $1.14 \pm 0.50°/m$, with a correlation coefficient of .68 ± .12. To examine the effect of induced motion on the trajectory of
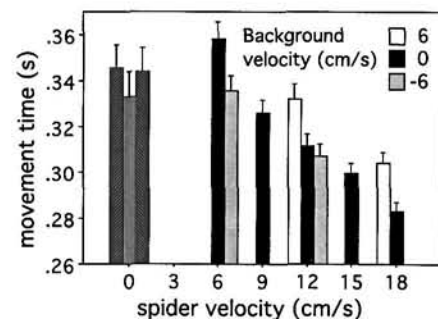

Figure 8. An overview of the movement times in Experiment 3. The movement time was shorter for (apparently) faster spiders than it was for (apparently) slower spiders; it did not depend on the position at which static spiders were hit. (See Figure 7 for further details.)
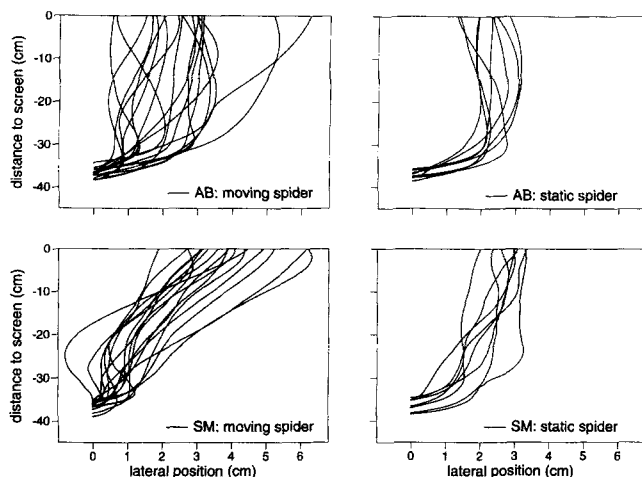
Figure 9. Examples of trajectories of the hand toward the screen. All trials (which could pass the criteria mentioned in the Data Analysis section) of two subjects toward two targets are plotted. The targets are the spider moving at 18 cm/s and the static spider at 3 cm. The average movement time of Subject S.M. was 355 ms; for A.B. it was 255 ms. Their average reaction times were 374 ms and 440 ms, respectively. On average, Subject A.B. hit 0.8 cm to the left of the spider in all conditions.

the hand, we used this relationship to calculate the apparent spider velocity from the direction at 30 cm from the screen, for all spiders and background velocities (Figure 12). Motion of the background has no systematic effect on these apparent velocities, and thus on the direction in which the hand is moving.

The maximum velocity in the direction of the screen also varied with the velocity of the spider; the slope of this relation was 3.8 ± 1.9, with a correlation coefficient of 0.48 ± 0.15. To examine the effect of induced motion on the velocity of the hand, we calculated the apparent spider velocity from the maximum hand velocity, for each combination of spider and background velocity (Figure 13). Motion of the background in the opposite direction than the spider caused an increase in the apparent spider velocity, and thus in the maximum velocity of the hand. Similarly, motion of the background in the same direction as the spider caused a decrease in the maximum velocity.

On average, the subjects hit the screen near the center of the spider, with a standard deviation of 1.4 cm. The average final error in hitting the spider was slightly influenced by motion of the background. This effect was only significant for the extreme velocities of the spider: Subjects hit 0.5 cm behind the fast spider when it seemed to move more slowly, and 0.4 cm in front of the slow spider when it seemed to move faster.

Discussion

From the results of this experiment, it is clear that the velocity of the hand movement is based on (relative) velocity information, whereas the trajectory of the movement is

based on position information. Other aspects of the results deserve some discussion.

On average, the effect of background motion on the velocity of the hand movement resembles the effect on the perceived velocity. However, some minor differences exist. The effect of background motion on the maximum velocity of the hand is larger for the extreme spider velocities (6 and 18 cm/s) than for the intermediate velocity (12 cm/s). This effect was not visible in Experiment 1. An explanation could be that in Experiment 1, subjects could observe several spiders of the same velocity before they had to report their percept. In Experiment 3, they had to react at once, so that their responses could be influenced by expectations. The latter will lead to responses that tend toward the average response: a contraction bias (Poulton, 1979).

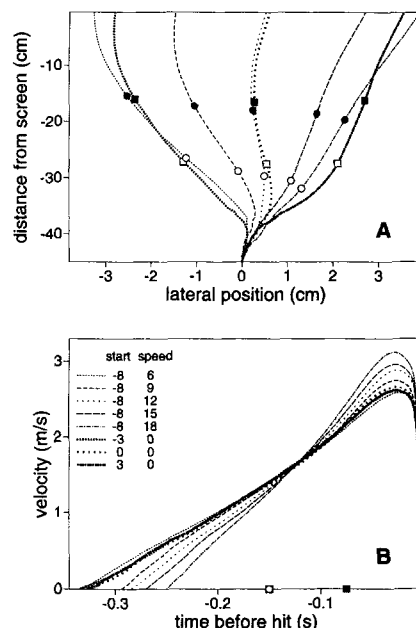The RTs were quite long, about 150 ms longer than those

Figure 10. Panel A: The average trajectories of the hand movements toward the spiders (both moving and stationary) on a stationary background. The horizontal axis denotes the lateral position of the hand relative to its position at the start of the trial. The vertical axis denotes its distance from the screen. The moving spiders start at (−8, 0), thus to the left of the top of the figure. The hand movements started at a position between (0, −45) and (0, −35). The symbols indicate the position of the hand 75 ms (filled) and 150 ms (open) before the hit. Different line styles represent different stimulus conditions (moving/static spider, static background). The starting position (cm) and the velocity of the spider (cm/s) represented by each line style are indicated in the figure (thin lines and circles for moving spiders; thick lines and squares for stationary spiders). The trajectories are averages of all trials of all subjects. Note the different scales for the two axes. Panel B: The component of the velocity perpendicular to the screen as a function of the time before the rod reached the screen. This plot is made indirectly: The average velocity at a certain distance is plotted as a function of the average time before the hit at that position (see Figure 6).
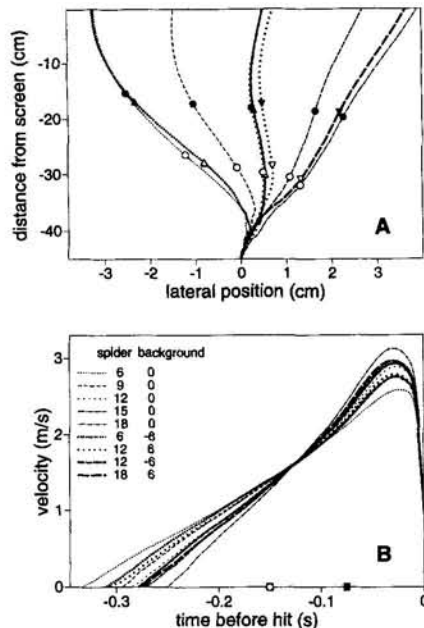
Figure 11. Panel A: The trajectories of the hand movements toward the moving spiders on stationary and moving backgrounds. The symbols indicate the position of the hand 75 ms (filled) and 150 ms (open) before the hit. Different line styles represent different stimulus conditions (moving spider, static/moving background). The velocity (cm/s) of the spider and of the background represented by each line style are indicated in the figure (thin lines and circles for a stationary background; thick lines and upward pointing triangles for a background moving in the opposite direction than the spider; thick lines and downward pointing triangles for a background moving in the same direction as the spider). All spiders start at (−8, 0), thus to the left of the top of the figure. The trajectories are averages of all trials of all subjects. Note the different scales for the two axes. Panel B: The component of the velocity perpendicular to the screen as a function of the time before the rod reached the screen. This plot is made indirectly: The average velocity at a certain distance is plotted as a function of the average time before the hit at that position (see Figure 6).

stow (1987) for an intercepting task. In that experiment, subjects were free to choose their movement velocity. In our experiment, the task was to hit the spider as soon as possible. One would therefore expect subjects always to move with the highest possible velocity. However, the experiment showed that this is not the case.

This finding, together with the differences between the trajectories to moving and stationary targets, reveals the strategy used by the subjects. For the stationary targets, subjects know the position of the goal from the start. For the moving spiders, the arm starts to move toward an expected target position. Determining this position is not simple, because it depends on the velocities and positions of both the hand and the target. Two mechanisms compensate for errors made in the initial estimate of the target position. The velocity at which the hand moves is adjusted (from the start) to the velocity of the target, and the expected target position is adjusted during the movement (Pélisson et al., 1986; van Sonderen, Gielen, & Denier van der Gon, 1989). Although the effect of the use of velocity control is small (about 10%), it is a remarkable new finding. How the trajectories are adjusted is discussed in the next section.

Model of Trajectory Formation

Two questions remained to be answered: Why are the trajectories of the hand to stationary targets different from those to moving targets, and how are the hand movements to the moving targets made without using perceived target velocity to extrapolate target motion? We used a simple (linear) model to create a phenomenological description of the trajectories of the hand. We ignored the biomechanics of the human arm and replaced these by a description of the effective mechanical behavior of the hand. Our goal was to give a simple mechanistic description of the trajectory of the hand in terms of spider positions. In the model, spider velocity is not used for predicting positions, because the experiments showed that perceived velocity had no effect on the trajectories. With the model, we aimed to show that
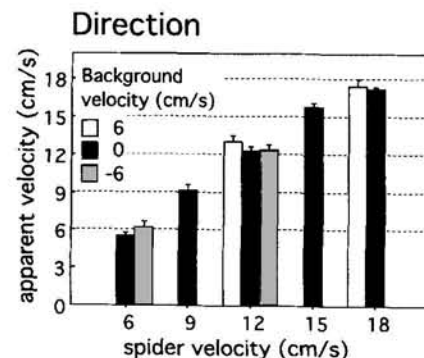
in comparable tasks, such as the interception task in the experiment of van Donkelaar, Lee, and Gellman (1992). In their experiment, the starting direction was independent of the target velocity. When van Donkelaar et al. delayed the response by a separate go signal, both the RT and the hand trajectories became comparable to those in our experiment.

That RT depends on stimulus velocity has been reported by many researchers (e.g., Collewijn, 1972; Tynan & Sekuler, 1982; van Donkelaar et al., 1992). There are several models that could explain this phenomenon (e.g., Collewijn, 1972; van den Berg & van de Grind, 1989). These models are all based on absolute target velocity. Our results question these models, in that relative motion seems to be the basis of the phenomenon. A complete description of the contribution of absolute and relative motion to RTs is given elsewhere (Smeets & Brenner, 1994).

The finding that the velocity of the hand movement depends on the target velocity has been reported by Bair-

Figure 12. The apparent velocity of the spider as revealed by the direction in which the hand was moving when it was 30 cm from the screen in Experiment 3. None of the moving backgrounds introduced a significant change in direction. (See text for further details.)
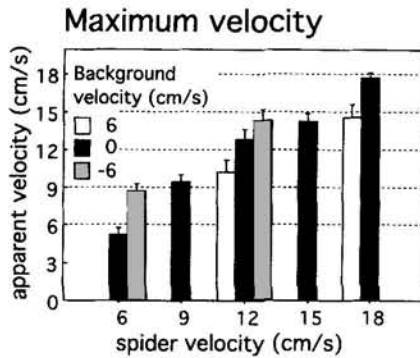
Maximum velocity

Figure 13. The apparent velocity of the spider as revealed by the maximum velocity of the hand during the movement toward the spider in Experiment 3. Motion of the background had a significant effect on the maximum velocity for three of the four moving background conditions; it did not reach significance for spiders at 12 cm/s with the background moving in the opposite direction. (See text for further details.)

it was possible to create trajectories similar to those we found in the experiment without the use of velocity to predict future target positions. For this goal, a very simple model with few parameters (which is a caricature of human physiology) was the best approach.

An adequate type of model for this approach is the mass-spring (or equilibrium-point) model, as introduced in the study of motor control by Feldman (1966; see Bizzi, Hogan, Mussa-Ivaldi, & Giszter, 1992, for a recent discussion). Although these models were developed for analysis at the level of muscles and joints, they can also be used at a more abstract level of description. Flash (1987) has shown that a mass-spring model can be very useful to investigate the trajectory formation in goal-directed movements. As the motion in the direction of the screen was independent of target position in our experiment, we only needed a model for the lateral hand motion. This yields an important simplification of the calculations.

Method

The motion perpendicular to the screen was modeled by a constant acceleration (3.2 m/s²). In this way, a velocity profile similar to those of Figure 10 was reproduced. By neglecting the effect of different spider velocities on the hand velocity, we could also assume that the stiffness (k) and viscosity (b) of the arm are equal for all trials. Explicit modeling of different velocity profiles would require variations of the stiffness and viscosity, as these depend on muscle activation (Cannon & Zahalak, 1982). The modest aim of our model did not justify the introduction of these extra parameters.

The lateral position ($x[t]$) of the hand was modeled as a damped oscillator,

$$m\ddot{x} + b\dot{x} + k(x - x_e) = 0, \quad (1)$$

in which x_e denotes the equilibrium position (which corresponds to the estimated target position) and a dot the derivative with respect to time. We could choose any one of the three parameters freely

without any effect on the equation. We chose the mass m to be one: This value was in the same order of magnitude as the effective mass of the hand and simplified the calculations. The other two parameters (the stiffness k and viscosity b) were determined by fitting the solution to this equation (see Appendix) to the data of the static experiment (with x_e being the actual spider position).

For hand movements to moving spiders, we assumed that the estimated target position was an expected spider position. This position changed during the movement as new information becomes available about the actual spider position. As we did not want to predict spider position on the basis of a perceived velocity, we used an expected spider velocity v_e, which was equal for all moving spiders. The predicted spider position is the sum of the actual spider position $x_s + v_s(RT + t)$ and the expected displacement of the spider in the remaining time $v_e(MT - t)$. In these equations, x_s is the position at which the spider appears, v_s is the spider's velocity, and $t = 0$ is the moment the hand starts to move. The spiders thus started moving at $t = -RT = -365$ ms. MT is the duration of the movement to the screen: 340 ms. The estimated target position thus varied as a function of time t:

$$x_e = x_s + v_s(RT + t) + v_e(MT - t). \quad (2)$$

We assumed that subjects can distinguish between static and moving spiders, probably on the basis of the position at which they appeared. The estimated spider velocity v_e was therefore given one of two values. It was zero for the static spiders. The value of the estimated velocity v_e for the moving spiders was the only parameter that was varied.

experimental trajectories
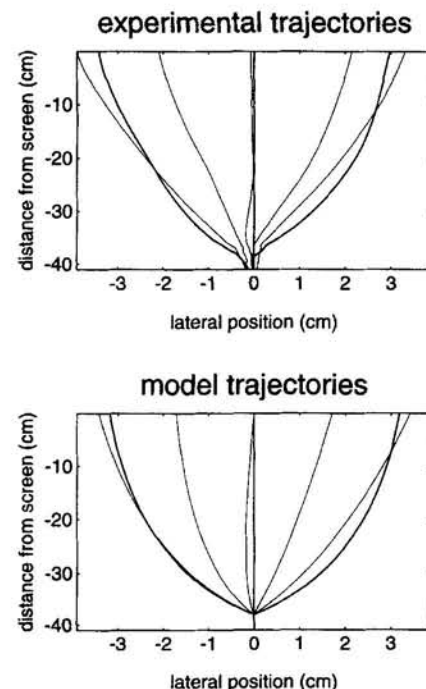

model trajectories

Figure 14. Top panel: The measured trajectories of the hand, corrected for biomechanical effects. The hand started at positions between (0, −45) and (0, −35); on average at (0, −38). Bottom panel: The trajectories of the hand as calculated by the model. The model hand started at (0, −38). (Thick lines = trajectories toward static spiders; thin lines = trajectories toward moving spiders.)

Results

Using Equation 2 with v_e = 9 cm/s to calculate the expected spider position x_e, we solved Equation 1 (see Appendix) to obtain the trajectories of the lower panel of Figure 14. The corresponding experimental trajectories in Figure 10 were affected by the biomechanics of the arm. We assumed that the deviations from a straight line in the trajectory to the static target that lies straight ahead were due to the biomechanical properties of the arm, and that these properties had comparable effects on the other trajectories. In the upper panel of Figure 14, we accounted for such biomechanical effects by subtracting these deviations from all the trajectories of Figure 10. In this way, the trajectory toward the central stationary target became a straight line.

Taking the limitations of the model into account, the model trajectories resemble the measured trajectories very well, both for moving and static spiders.

Discussion

The model shows that the trajectories of the movements can be explained by a very naive model. Apart from assuming that subjects have information about the spider's position and on the duration of their own movement, we assumed that subjects have two expected spider velocities: 0 cm/s for the static spiders, and 9 cm/s for the moving spiders. As these two types of spiders appear at very distinct positions, this last assumption is not unreasonable.

Subjects could obtain the expected velocity v_e of the spider in several ways. If we assume that they average all spider velocities, they will get 9 cm/s as the expected velocity. If the expected velocity for each movement is the velocity of the spider in the previous trial, the average trajectories will seem to be based on the average spider velocity. Subjects could also use a "default velocity," that is not based on previous experience, as was shown for the onset of ocular pursuit of invisible targets with unpredictable velocity (Becker & Fuchs, 1985). Furthermore, the calculation of v_e(MT − t) does not have to be made explicitly; the same equation describes aiming at a gradually diminishing position in front of the actual spider.

The model shows that the movements of the hand toward the moving spiders can be understood without the use of the spider's velocity. As velocity information is not used for the formation of the trajectory, induced motion will not affect the trajectories. This was one of our experimental results. A prediction from the model is that the starting direction will depend on the RT. For short RTs, the actual spider positions x_s + v_s(RT + t) will almost coincide at t = 0, so that the movements will start in the same direction. This conforms to the experimental results of van Donkelaar et al. (1992).

In conclusion, our model reproduces the experimental data quite well, while fulfilling the requirements that the trajectories of movements to static spiders are different from those to moving targets, and that motion of the background has no effect on the trajectories.

General Discussion

The research presented in this article differs from the research of other authors by the combined approach: We used one stimulus to test both perception and action and one motor task to study both position and velocity. We can hereby discriminate between the two hypotheses mentioned in the introduction. In one motor task we saw the results of processing both position and velocity information (as revealed by the perception experiments). This is incompatible with the hypothesis that there are distinct egocentric (motor) and allocentric (perception) representations of external space; it supports the hypothesis that both tasks use the same representation of (separately processed) position and velocity of the target.

This hypothesis is not in conflict with other experimental results. For instance, neurological data have been used to support the two-representations hypothesis (Goodale et al., 1991). A deficit in cognitive processing, while motor performance is undamaged, is described by Goodale et al. as a damage in the allocentric representation. The same phenomenon can also be described as a damage to one of the output paths of a single representation, thus to the ability to use a representation for certain purposes, rather than damage to the representation itself.

The notion that position and velocity are processed independently (for use in both perception and action) is similar to Abrams and Landgraf's (1990) hypothesis that position and displacement are processed independently (for perception). In their experiment, subjects were asked to reproduce either the final location or the displacement of an object. Illusionary motion affected the tasks differently. According to them, this result supported the hypothesis of separate processing of position and displacement. However, their results could be interpreted in another way, as was done by Honda (1990) in a more or less similar paradigm. According to Honda, judging displacement is a cognitive task, while indicating a position is a motor task. A similar disagreement exists concerning the experiment of Farber (1979). In Farber's experiment it was shown that manual tracking of a target moving on a background was influenced by motion of that background. Bridgeman fits this result into his theory by arguing that the cognitive system overrules the motor system in this task (Bridgeman et al., 1981).

These different interpretations are possible because different tasks were used to show the separate processes. The conclusion then depends on whether you label a task "cognitive" or "motor." In our experiment, we demonstrated the separate processing of position and velocity in one and the same task: a fast goal-directed arm movement.

The results of our experiment are somewhat difficult to interpret using an ecological approach. An important aspect of this approach is the assumption that all the degrees of freedom of a movement are coordinated to achieve the goal of the movement (Bernstein, 1967). When we started the experiment, we expected to find an effect of the induced motion in the initial part of the movement, where one could expect signs of extrapolation of the spider's position. In the last part of the movement, we expected a reduced effect of

the induced motion percept, as the actual position of the spider would be sufficient information. What we found was quite different: The trajectory and the speed of the movement seem to be determined independently. The trajectory was adjusted on the basis of the changing spider position, whereas the velocity profiles of the hand showed an effect of the induced motion percept over the whole movement. This leads to the conclusion that the timing and the trajectory of a movement are not coordinated on the basis of a single perceptual variable.

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Appendix

Solution of the Mass-Spring Equation

For the model, we want to find solutions to differential equations of the form

$$\ddot{x} + b\dot{x} + kx = kx_e(t) \tag{A1}$$

For a fixed estimated target position x_e, the solution of this problem can be found in any textbook on classical mechanics. We expect solutions in the underdamped range ($k > b^2/4$), for which case the general solution of Equation A1 is

$$x = x_e - Ae^{-b/2t}\cos(\omega t + \phi), \tag{A2}$$

in which $\omega = \sqrt{k - b^2/4}$. The integration constants A and ϕ can be determined by applying appropriate boundary conditions: $x(0) = \dot{x}(0) = 0$ (hand starts at $x = 0$ with zero velocity). After some algebra, the solution becomes

$$x = x_e - x_e e^{-bt/2}\left(\cos(\omega t) + \frac{b}{2\omega}\sin(\omega t)\right). \tag{A3}$$

By fitting the data of the movements to the static spiders to this solution (Levenberg-Marquardt method, Press, Flannery, Teukolsky, & Vetterling, 1987), we obtained as estimates for the stiffness $k = 30$ N/m and viscosity $b = 3.6$ Ns/m. These values are in the range of values measured for the effective stiffness and viscosity of the human arm (Flash, 1987).

If the estimated target moves with a constant velocity v, Equation A1 is nonhomogeneous:

$$\ddot{x} + b\dot{x} + kx = k(x_0 + vt). \tag{A4}$$

The way to solve this kind of equation can be found in many textbooks on mathematics. The solution of a nonhomogeneous differential equation is the sum of one particular solution and the general solution to the homogeneous equation (Equation A1 with $x_e[t] = 0$). A particular solution is easily found: Substitute $x = Bt + C$ in Equation A4, which yields

$$x = vt + x_0 - bv/k. \tag{A5}$$

The general solution to Equation A4 is the sum of the general and particular solution; with the substitution $x_0 - bv/k = x_1$, this yields

$$x = vt + x_1 + Ae^{-b/2t}\cos(\omega t + \phi). \tag{A6}$$

After applying the boundary conditions ($x[0] = \dot{x}[0] = 0$) and some algebra, the solution becomes

$$x = vt + x_1 - x_1 e^{-bt/2}\left(\cos(\omega t) + \left(\frac{b}{2\omega} + \frac{v}{x_1\omega}\right)\sin(\omega t)\right). \tag{A7}$$

A short check is the substitution $v = 0$ in Equation A7, which reduces again to Equation A3, as (of course) is expected.