THE VISUAL GUIDANCE OF BALLISTIC ARM MOVEMENTS

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INTRODUCTION

To hit a moving object, you must reach some position at the same time as the object. The position at which you will hit the object depends on the object's speed and direction of motion, as well as on the timing of your own movement. We investigated the information used to extrapolate the position of a moving object during both the planning and the execution of fast (ballistic) arm movements.

To make goal-directed movements, the nervous system has to transform sensory information into activations of various muscles. If a target is moving, or if one is moving oneself, the sensory information is continuously changing. The best way to control ones action is to take these changes into account to predict the future position of the target. How does the nervous system use information about target motion in the control of goal-directed action?

Spatial information is only meaningful when it is defined with respect to a frame of reference. Two frames of reference are important when considering visuo-motor co-ordination. Arm movements are defined with respect to an egocentric frame of reference (Paillard, 1991), which is also used to perceive positions. For the perception of motion, however, an allocentric frame of reference is also used: the (stable) visual surrounding (Brenner and Smeets, 1994a; Smeets and Brenner, 1994). This dissociation between the perception of position and motion is the basis for our first question: does the nervous system use (allocentrically perceived) motion to predict a future target position for goal-directed arm movements? To answer this question we studied goal-directed movements to targets which were moving over a structured background. We separated the contributions of position and motion by moving the background on some of the trials.

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Multisensory Control of Posture, Edited by T. Mergner and F. Hlavačka
Plenum Press, New York, 1995

Spatial information is not only used to plan fast goal-directed arm movements. It is also used to adjust the movements (Prablanc, Pélisson and Goodale, 1986). To study the control of ongoing movements, we studied arm movements towards targets which started moving when the hand started moving. The duration of the arm-movements was about the same as the reaction time. Assuming that correcting ongoing movements is based on the same spatial information processing as the planning of these movements, it would take longer than the duration of these movements to react to changes in the environment. For this reason, such fast movements are in general named 'ballistic'. It is possible, however, that more limited spatial information is used for faster feedback. By studying 'ballistic' movements, we ensure that we are dealing with on-line control of the movements, rather than with corrective (sub)movements superimposed on the ongoing movements.

METHODS

We used a graphical workstation to present the stimuli, and active infrared markers to measure the subjects' movements (see Fig. 1). Targets moved at five different velocities or in five different directions. Allocentric information was selectively manipulated by moving the background in some conditions. In all experiments, trials with and without background motion, and with various directions and speeds, were randomly intermixed. In all experiments, subjects were completely free to move their eyes and heads. An extensive description of the set-up and experimental procedure is given elsewhere (Smeets and Brenner, 1995).

To examine which spatial information is used for planning arm movements, two experiments were carried out: one to compare the use of position and speed, the other to compare the use of position and direction of motion. Each experiment consisted of two parts. In the first part, we investigated how subjects perceived the targets' motion. In the second part, we studied how subjects used this perceived information to control their goal-directed action. It has been argued that visual information is treated separately for perception and action (Bridgeman et al, 1981; Goodale and Milner, 1992). However, we have shown that both egocentric and allocentric information is used in both perception and action (Brenner

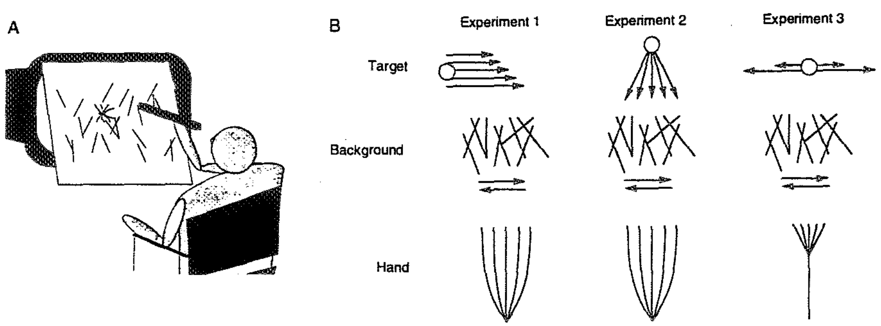

Figure 1. (A) The experimental set-up. Subjects sat in front of a screen onto which a target and a background were projected. (B) Both target and background could move (shown schematically in front-view), which influenced the hand's trajectory (shown schematically in top-view). In experiment 1, we varied the apparent speed of the target, by varying the target's motion, and by moving the background. In experiment 2, we varied the apparent direction of motion of the target by varying the target's motion and by moving the background. In experiment 3 the target and the background remained static until the hand started moving. Thereafter, either the target, or the background could start to move.

and Smeets, 1994; Smeets and Brenner, 1995). The distinction appears to be between position and motion, rather than between perception and action.

In the first part of experiments 1 and 2, we asked the subjects to indicate the perceived position, speed and direction of motion of the target with the computer mouse. In the second part of these experiments, we asked the subjects to hit the moving target as quickly as possible with a rod. We presented the same stimuli as in the first part of the experiments. Subjects received visual feedback about their performance after each trial.

To investigate whether spatial information influences ongoing ballistic movements, a third experiment was carried out. In this experiment, the target and background remained static until the hand started moving. Thereafter, either the background or the target could start moving, either to the left, or to the right. If the background moved to the left, the target appeared to move to the right, and vice versa.

All figures show results averaged over all subjects and trials. These were 6-12 subjects who each performed 5-15 trials for each condition (numbers depend on the experiment).

RESULTS

The perceived target motion in experiments 1 and 2 is shown in Fig. 2. The perceived position is independent of motion of the background, whereas the perceived speed and the perceived direction of motion are influenced by motion of the background. This is in line with our expectation: position is perceived egocentrically; motion is perceived (partially) allocentrically. Having a good perceptual characterization of our stimulus, we can now describe how this perceptual information is used in motor control.

Our subjects started to move their hand about 300 ms after the target appeared on the screen. They accelerated their hand almost continuously towards the screen. After about 300 ms, their hand was decelerated by the screen when they hit it. The direction in which the hand moved at motion onset depended on the position of the target, but was independent of its perceived speed (Fig. 3A). However, the perceived speed did influence motor control: the maximum velocity of the hand (and thus the movement time) depended on the perceived target speed (Fig. 3B).

One could conclude from experiment 1 that only egocentric information is used to direct the hand towards the target. To examine whether this is so, the role of another allocentric source of information was evaluated in experiment 2: the direction of target motion. Fig. 3C shows that the direction in which the hand moved at movement onset depended on the (allocentrically perceived) direction of target motion. We therefore reject the hypothesis that only egocentric information is used to direct the hand.

In experiment 3, the target was stationary when it appeared on the screen. Once the subjects moved their hands, it started to move. Subjects always adjusted the movements of their hands (Fig. 4). If the background moved instead of the target, the response of the hand was later, smaller, and in the opposite direction than the target appeared to move. Thus, the allocentrically perceived direction of motion is not used for the on-line control of fast movements. The latency of the response to target motion was always less than 150 ms; examination of the lateral acceleration showed that the latency of response to a change in target position was 110 ms (Brenner and Smeets, 1995). The maximum speed of the arm movements was independent of whether the target started to move. The control of an ongoing movement is therefore based on purely egocentric information on the target's position.

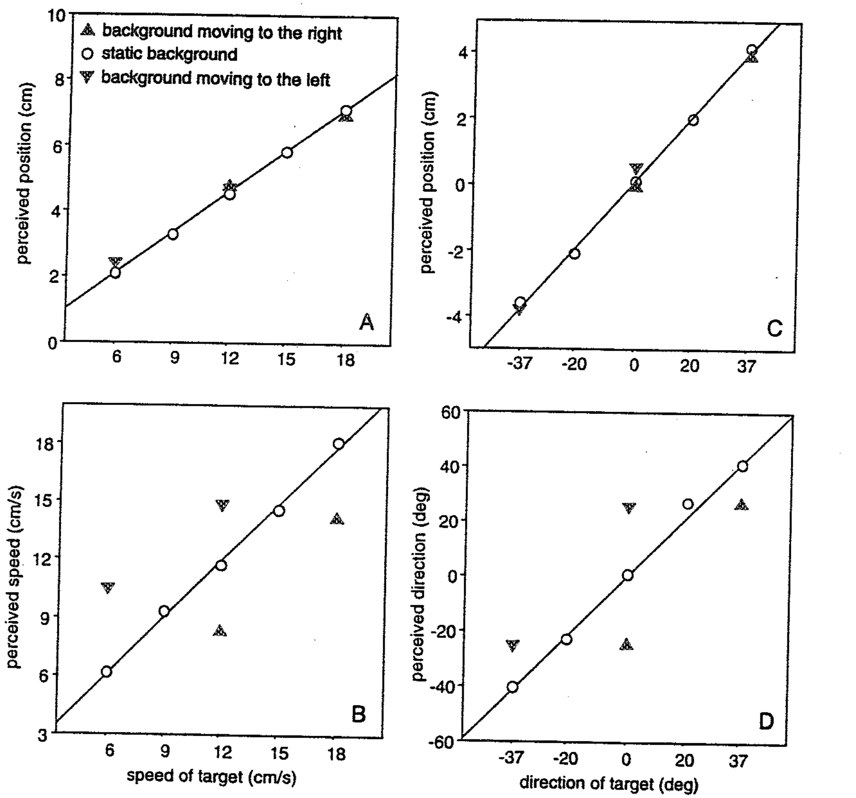

Figure 2. Perception of spatial information. (A) Subjects were asked to indicate the positions at which targets moving at different speeds disappeared (experiment 1). These positions were perceived correctly, irrespective of background motion. (B) Subjects were asked to match the targets' speed (experiment 1). Background motion induced large errors in the perceived speed. (C) Subjects were asked to indicate the positions at which targets moving in different directions disappeared (experiment 2). The different positions at which the targets disappeared were again perceived correctly, irrespective of background motion. (D) Subjects were asked to indicate the directions in which targets moved (experiment 2). Background motion induced large errors in the perceived direction.

DISCUSSION

We started this work with the idea that the distinction between allocentric and egocentric information would be useful to describe visuo-motor behavior. Our work shows that these sources of information are used differently during the planning and the execution of movements. During the control of ongoing movements, only egocentric information (perceived position) was used. In the planning stage, our subjects used both allocentric and egocentric information. Perceived direction (allocentric) and perceived position (egocentric) were used to predict where the target would be hit; perceived speed was used to control when the target was hit. The planning stage (reaction time) takes about 250 ms longer than the time needed to adjust ongoing movements (110 ms).

On-line control of movements can only be useful if the delay in using the sensory information is short. It therefore seems to be a good strategy to only use information which

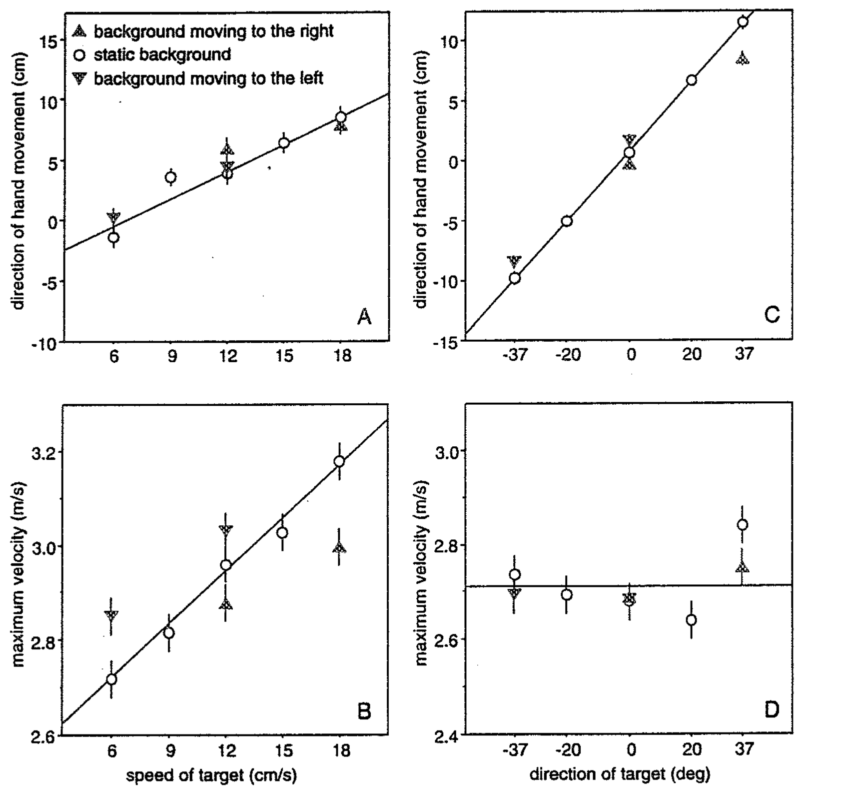

Figure 3. The use of spatial information for planning goal-directed arm movements. The direction of the movement of the hand is expressed as the intersection-point between the tangent to the trajectory and the surface on which the target moved. The maximum velocity is the maximum of the velocity-component orthogonal to this surface. Error bars indicate the average of the individual subjects' standard error of the mean. (A) When the speed of the target was varied (experiment 1), the direction in which the hand started to move was independent of motion of the background, and thus independent of the perceived speed. The direction of the hand movement did depend on the target's position at reaction time and thus indirectly on the target's speed (see Fig. 2A). (B) The maximum speed of the hand during the movement depended on the background motion in the same way as the perceived speed did (see Fig. 2B). (C) When the target's direction of motion was varied (experiment 2), the direction of the hand at movement onset did too. Note that the range of directions of hand movement was much larger than in the first experiment (Fig. 3A). This is because the direction of the hand at movement onset is influenced both by the position of the target at reaction time (see Fig. 2C) and by the extrapolation of its position using the perceived direction of motion (see Fig. 2D). The latter is evident from the fact that the direction of the hand movement depended on the motion of the background. (D) The maximum speed of the hand during the movement does not depend on the direction of target motion.

is in the same frame of reference as the motor-commands (Paillard, 1991). This saves the time needed for the nervous system to transform information. During the preparation, more time is available. Why we do not use all the available information to estimate where the target will be hit is not that easy to explain. It is important to realize that the target can only be hit at a certain position, if it is hit at the right instant. The strategy our subjects chose was to determine the position on the basis of position and direction, whereas the timing was based on the perceived speed. In this way, space and time can be determined independently (Brenner and Smeets, 1994b).

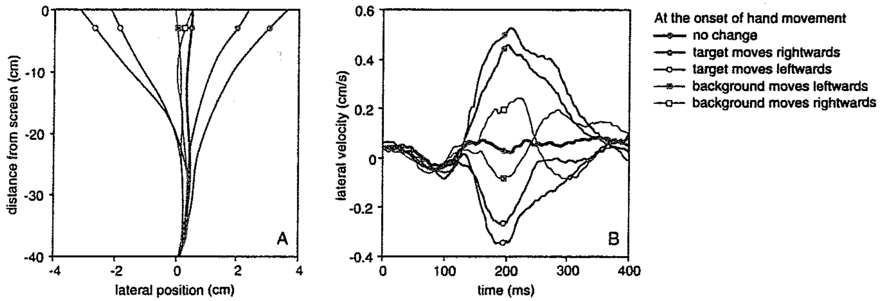

Figure 4. The use of spatial information for adjusting ongoing movements. Open symbols: target appears to move rightwards; closed symbols: target appears to move leftwards. (A) Average trajectories of the hand towards the screen. The target started moving when the hand was about 38 cm from the screen. (B) The lateral velocity as a function of time after the target started moving. The effect of background motion is small and opposite to the effect one would expect on the basis of the apparent motion of the target.

Our results question the notion of ballistic movements. Some authors claim that some kinds (or some parts) of movements cannot be changed by sensory information (reviewed by Jeannerod, 1988). It has been argued that fast goal-directed arm movements must be ballistic because the first 100 ms of an EMG-pattern of such a movement is not influenced by proprioceptive information about that movement (Wadman et al, 1979). However, proprioceptive information can change fast goal-directed movements at any instant during the movement (Smeets et al., 1990, 1995). The only reason that some (parts of) movements seem to be ballistic is that the sensory-motor loop (both visual and proprioceptive) has a delay of more than 100 ms. Recently, Pratt and Abrams (1994) claimed that the acceleration phase of a goal-directed movement is ballistic. The movements in our experiments only consisted of an acceleration phase, but were modifiable by changes in visual information during the movement. We conclude therefore that the title of this chapter is inadequate: goal-directed movements are never ballistic.

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