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Visuomotor delays when hitting running spiders

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Abstract

In general, information about the environment (for instance a target) is not instantaneously available for the nervous system. A minimal delay for visual information to affect the movement of the hand is about 110 ms. However, if the movement of a target is predictable, humans can pursue it with zero delay. To make this prediction, information about the speed of the target is necessary. Our results show that this information is used with a delay of about 200 ms. We discuss that oculomotor efference is a likely source of information for this prediction.

Introduction

When using information about ones environment to guide limb movements, one has to realise that several aspects of the visuomotor transformation cause the limb movement to lag behind the information. The time for information to reach ones body can be neglected; activating sensor organs, transport of sensor signals, processing in the central nervous system, transport of effector signals, contraction of muscles and acceleration of limbs all take time. For the best perception-action coupling, the effective delay should be as low as possible.

In (Smeets & Brenner, 1995a,b), we compared trajectories of the hand towards moving spiders with trajectories towards static spiders which were hit at the same position. The trajectories were clearly different, from which we concluded that information on the position of the spider was continuously used during the hitting movement. The use of this information was quite effective, as the subjects hit the moving spiders as accurately as the static ones. We modelled this interaction between the movement of the target and the hand with a simple mass-spring model. Our result was a good correspondence between model and experiment. However, to obtain such a good correspondence, we had to assume that the visuomotor delay was zero. The zero delay is compatible with the good performance in this task, but is not physiologically plausible.

In a subsequent study (Brenner & Smeets, 1997), we measured the visuomotor delay directly by studying the effect of the (static) spiders starting to move or making a jump after the hand had started moving. We found that after about 110 ms, the trajectory of the hand started to deviate in the direction of the spider's motion. For the targets starting to move, the delay was 10-20 ms longer, probably due to the gradually increasing displacement. We argued that this delay is based on continuous measurement of the position of the target, without information on its motion. This 110 ms delay is too long to obtain acceptable trajectories using the model of Smeets & Brenner (1995a,b).

The two values for the visuomotor delay (0 and 110 ms) are clearly different. This could in principle be due to inaccurate modelling of the interaction between target and hand. For the present purpose, we assume that the zero-delay is real. Presumably, it is realised by not using the directly perceived spider position, but a predicted position using information on the spider's motion. We showed recently (Brenner et al., 1997) that using new information on the target's speed to influence the speed of the hand takes more than 200 ms. We argued that this 90 ms longer latency is due to the fact that it takes more time to measure a change in velocity than to measure a position. If so, an update of the prediction of the target's current position on the basis of the new speed would also take about 200 ms.

For the response to a change in target velocity of a moving target, we have now 2 hypotheses. The first hypothesis is that the actual target position is followed: a change in target speed will affect the hand motion after the visuomotor delay of 110 ms. The second hypothesis is that the perceived position is a prediction which takes into account the velocity of the target; a change in velocity has to be detected before it can affect this position, after which the minimum visuomotor delay takes an extra 110 ms, in total about 200 ms.

Methods

The apparatus used in this experiment is described in more detail in several papers (Brenner & Smeets, 1997; Smeets & Brenner, 1995a,b); a full description of the present experimental set-up and experimental protocol will be given by de Lussanet et al. (1988). Spiders appeared at unpredictable moments on a screen; either running to the right (starting on the left side) or static at various positions. Subjects were asked to hit each spider as fast as possible using a rod which they held in their right hand. A motor exerted a lateral force of 4N on the hand.

During some trials, the task was made more difficult by a change of the speed of the spider or a change in the external force. In this report, we will only analyse the trials in which the spider moved and the force was constant. Each of these three conditions was presented 13 times to each of our 6 subjects. In the trials in which the velocity changed, this change (from 12 cm/s to either 6 cm/s or 18 cm/s) occurred about 85 ms before the reaction time. This to ensure that the reaction to the change in velocity occurs during the movement.

Results

Subjects started to move their hand 285±30 ms (mean ± standard deviation) after the spider appeared, and hit the screen 270±30 ms later. The spiders changed their velocity 85±20 ms before the hand started to move, so that all subjects had more than 300 ms to adjust their movement to hit the spider. The subjects had the impression that in some trials the spiders moved faster and in others slower, but did not notice that the spider velocity changed during some trials.

In *Figure 1*, we show the average lateral velocity of the hand. The velocity of the hand started to change about 200 ms after the spider velocity changed.

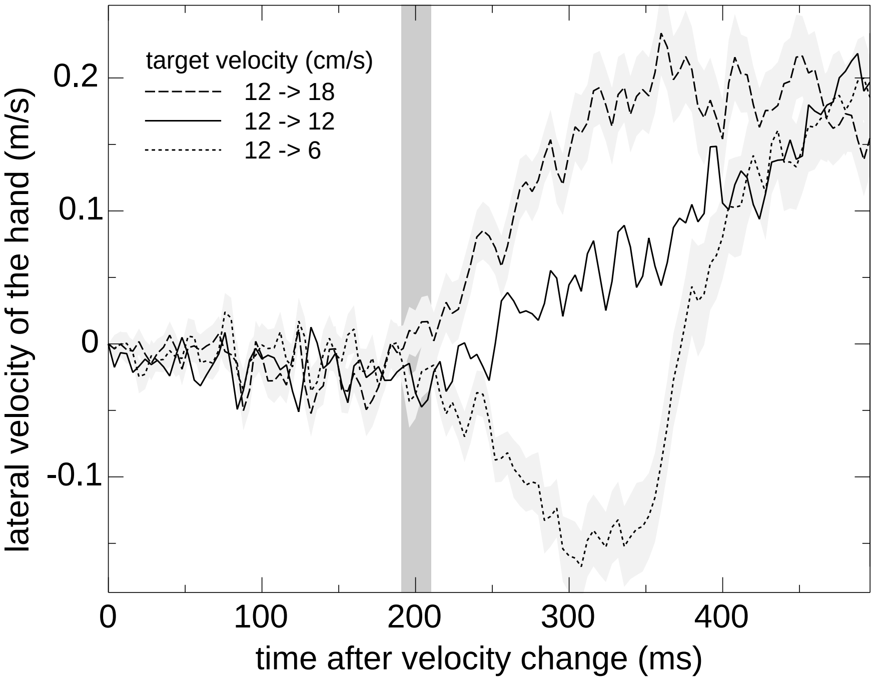

Figure 1. The lateral velocity of the hand plotted as a function of the time after the spider changed its speed to 18 cm/s (dashed curve) or 6 cm/s (dotted curve). This change took place on average 85 ms before the onset of hand motion. The light grey area indicates the standard error of the mean velocity. The continuous trace is the lateral velocity in the trials in which no perturbation occurred. The latency of the response (indicated by the dark grey bar) is about 200 ms.

Discussion

The latency for responding to a change in target-motion that we found in this study (200 ms) supports the second hypothesis: the hand moves towards a predicted position, based on information on the target's speed. To be sure of this conclusion, we have to be sure that this 200 ms delay does not differ from 110 ms only due to experimental differences. The experiments were done using the same equipment with the same instruction to the subjects. One difference is that the change in target speed of the present study was 6 cm/s, whereas in Brenner & Smeets (1997), it started to move at either 12 or 24 cm/s, or jumped (instantaneous speed 240 or 480 cm/s). This is not likely to be the explanation for a latency of clearly more than 130 ms to a the change in target motion, because the latency for the slowest movement in that study was only about 20 ms longer than the one for the largest jump. Therefore, the latency of the response to a change in target velocity must be longer than to motion onset because they are based on a different mechanisms. According to our second hypothesis, the response to a change in velocity depends on the prediction of the target position using velocity information. What can the basis of this predictive mechanism be?

Before discussing how the prediction takes place, it is important to realise that it is not the future that is predicted, but the present. This prediction is only used to compensate for the delays in the nervous system. Predicting the present has been found many times in pursuit tasks. If a target moves unpredictably, the hand follows the target with a delay of more than 200 ms (Koken & Erkelens, 1992; Miall et al., 1986). In our view, this lag is a combination of a pure visuomotor delay (about 120 ms) and a phase-lag due to the low-pass filtering characteristics of the musculo-skeletal system (about 1Hz). If the target-motion is sinusoidal, this lag can be reduced to less than 20 ms (Koken & Erkelens, 1992, Vercher & Gauthier, 1992). For periodic movements, the delay can be minimised by comparing visual and/or proprioceptive information of the sinusoidal motions of target and hand. However, for 'ballistic' movements as in our experiment, this comparison cannot be used.

How can we pursue a target moving at a constant speed with zero delay? For eye movements, this zero delay is rather simple to achieve: the retinal position and retinal slip of the target give instantaneous information about the difference between the predicted and actual target motion. Probably, the neural command ("efference copy") for the pursuit eye-movement is also used to guide the limb movement (figure 2). The visuomotor delay of the eye is about 90 ms (Brenner & Smeets, 1998). This is about 20 ms shorter than for the hand, due to the different lengths of the efferent pathways. So the use of a copy of efferent oculomotor signals will reduce the visuomotor delay to about 20 ms. What is the experimental evidence that the efference copy is indeed used as a prediction of the present target position?

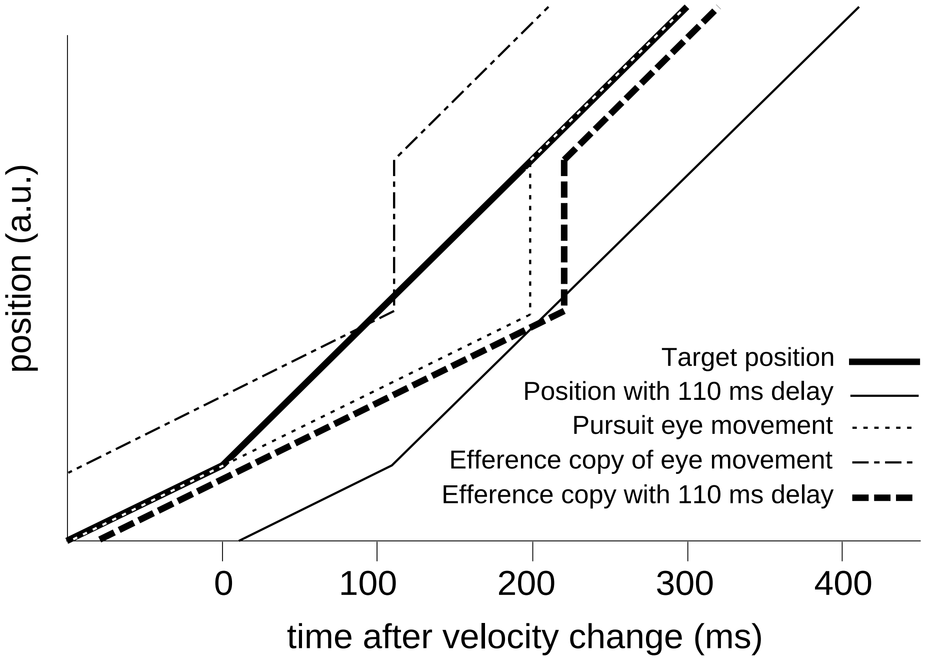

Figure 2. A predictable (e.g. constant) target motion can be pursued ocularly with zero delay. The use of the efference copy of this eye movement as a prediction of target motion can reduce the error in perception-action coupling tremendously, compared to a physiological delay. This holds even when unpredictable events (like a velocity change) occur.

The first argument in favour of this model is that the remaining visuomotor delay for arm movements towards targets moving at a constant speed is very small (20 ms), which corresponds to the results of the model calculations by Smeets & Brenner (1995a,b). Furthermore, smooth pursuit eye movements respond with a latency of 180 ms (or more) to a change in target velocity (van den Berg, 1988). Taking into account the 20 ms longer efferent pathways for arm movements, this latency is the same as the 200 ms latency we find in this study for the response of an arm to a change in target velocity. Further support for this hypothesis is found in experiments of van Donkelaar & Lee (1994). They compared manual tracking of a moving target in a condition in which the target was pursued using smooth eye movements with tracking in a condition in which the target was pursued with saccades. In the latter case, subjects were unable to track the target with an approximately zero delay.

The advantage of this scheme is that it does not have to take into account the actual delay: by using the occular position command as a prediction of the target position for arm movements, the pure visuomotor delay is compensated except for 20 ms. As we argued above, the pure delay is only a part of the effective delay, because the spring-like properties of the muscles cause a low-pass filter like behaviour of the visuomotor system. To describe how we can intercept moving targets, a model of these characteristics has to be used (as proposed in Smeets & Brenner 1995).

Prediction of the present is a different matter than prediction of a future event. The main difference is that the brain knows when the present will happen, but not the time of a future event. Probably, that is the reason why prediction of future events seems so very poor, and subjects rely on continuous control to intercept moving targets (Brenner & Smeets, 1996; Mcleod & Dienes, 1996; Peper et al., 1994; Smeets & Brenner, 1995a,b). We showed that the subjects predict a future target position when hitting moving targets (Smeets & Brenner, 1995b). However, they do not predict on the basis of the actual target velocity, but on an “expected velocity”. Or, phrased in another way: they always move towards a position in front of the target, independent of the speed of the target. This strategy is probably acquired during the experiment. Thus, although the speed of the target is used to predict the present (and cancel out most of the visuomotor delay), it is not used to predict the future.

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