The Control of Interceptive Arm Movements

De Sturing van Onderscheppende Armbewegingen

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General introduction

Abstract

In this first chapter I will briefly introduce some central themes of this thesis: eye-hand co-ordination, stability and flexibility of visuo-motor strategies, the hypothesis of equilibrium-point control and mass-spring models, and the problem to distinguish between the use of two different sources of visual information: position and velocity of a target. Subsequently, I will illustrate the problem of testing the hypothesis of equilibrium point control by discussing a well known (among specialists) set of experiments by Lackner and DiZio. Finally I will present or general methodology and a global outline of the thesis.

1.1 Aim of this thesis

This thesis is about how we control the movements of our hand when intercepting a target that moves on a surface somewhere within reach. This everyday act requires rapid and accurate co-ordination of what we see and how we move our hand. For example, imagine yourself sitting in a train, trying to stop a pencil that suddenly rolls towards the edge of the table because the train passes a railway point. Typically, it will take about half a second to catch the pencil. This is long enough to notice that there is a target that should be intercepted, to register the target's position and velocity, and to translate this information into a rapid and accurate movement of the hand. In the experiments described in this thesis, we let subjects perform an interceptive task under somewhat more controlled conditions. The subjects had to hit a virtual spider that appeared on a strong surface in front of them. The task also had in common with the above example that the hand's movement was sometimes mechanically perturbed. Instead of by the train's movement, the perturbations were administered directly to the subject's hand. With these experiments, we wanted to find out what kind of strategies normal human beings (the people who happened to be in the lab whenever I planned another experiment) use to control the movements in a rapid interception task. On the basis of the experimental findings we tested and improved existing mathematical models for interceptive movements.

With a strategy, I mean the choice of which of the available sensory information (for example the pencil's position) is used in the brain to control the hand's movements, and how the various sources of information are used. The difficulty is of course that a strategy cannot be measured directly. Instead, one can try to describe the observed behaviour by translating it into mathematical rules (i.e. a model), which can be tested by placing subjects in an appropriate experimental condition (Gottlieb et al., 1989). In this mathematical description and the experiments, we will concentrate on the hand's movements in relation to the visual information that we presented (and in chapters 2 and 7 also in relation to mechanical perturbations).

The project of which this thesis is a result was one out of four in a research program entitled "*Stability and flexibility of human movements*". The program consisted of two symmetry-axes: there were two projects about *rhythmic* movements (walking) and two about *goal-directed* (arm) movements. Two of the projects were about *healthy* humans and two were about *disabled* humans. In the first year, the title of the program resulted in some vivid discussions about the meaning of stability and flexibility. Some of the patients from the "rhythmic-disabled" project –of whom part of one leg had been amputated– displayed a very constant walking pattern, irrespective of the speed at which they walked, while others displayed asymmetric walking patterns that one would never encounter in normal subjects (Donker & Beek, submitted). So, were the first ones "stable" and were the latter ones "flexible"? And, which of the two kinds coped better with the handicap? In our enthusiasm, we had overlooked that stability and flexibility are not each other's antonyms. As illustrated by this example, I define *stability* of motor control as successfully using a single strategy to integrate sensory information into movements. Likewise, *flexibility* in motor control can be characterised by the ability to switch to a different strategy to use sensory information for movement control if this is required by the conditions. The opposite of *stability* in motor control could be called variability or the failure of a strategy to cope perturbations such as noise in the sensory motor system. The opposite of *flexibility* can be called rigidity, the failure to switch to a different strategy. Thus stability and flexibility both reflect adaptive, useful motor behaviour, whereas rigidity and variability reflect of non-adaptive, perturbed or noisy motor behaviour. The patients with a very constant walking pattern may have behaved rigidly, rather than stably. On the other hand, the asymmetric walking pattern of other patients was probably flexible rather than variable. When having two different legs (one artificial) it is probably efficient to develop an asymmetric walking pattern (Wagenaar & van Emmerik, 1994). It is usually difficult to distinguish between flexible and variable (noisy) motor behaviour and also to distinguish between stable and rigid motor behaviour (Donker & Beek, submitted). In **chapter 5**, this issue will be addressed for interceptive movements (de Lussanet et al., in press).

The above example illustrates a problem that one may encounter when studying stability and flexibility in a clinical case. The kind of answers that one will find depend directly on the theoretical understanding of the system for which one wants to solve a practical problem. This means that it is necessary to understand motor control in a healthy, normal condition in order to understand what is wrong in a clinical situation. This thesis will concentrate on the healthy, human motor control system, using a continuous interaction between experiments and theory.

The approach to choose is not self-evident: the kind of questions that one can answer depends on it. One possible approach to motor control would be a biomechanical approach (e.g. de Lussanet & Alexander, 1997). In the light of biomechanics, one will search for optimisation criteria (such as minimal energy or maximal speed) within constraints (such as the kind of muscles and muscle properties). Another approach could be neurological, in which case one could find out which brain areas are involved in the different stages of movement planning and execution and how. Alternatively one could study the dynamics of the evolving patterns (e.g. Haken et al., 1985, 1996), to find out how the sensory-neuro-motor system organises itself to produce complex behaviour. The latter approach is very suitable for the "rhythmic" projects. Although these models are quite similar mathematically to the equilibrium models (section 1.2) that we used in this thesis (**chapters 2, 6 and 7**), the underlying approach and the resulting questions are different.

As characterised with the above definition of stability and flexibility, the approach taken in this thesis will focus on the use of sensory information for the control of rapid interceptive movements. The important constraints for information are transmission rate and information capacity of the available channels. A famous example is Fitts-law, which describes the speed-accuracy trade-off in terms of the information constraints in performing a task as fast and as accurately as possible (for discrete movements: Fitts & Petterson, 1964). An example for an interceptive task is the debate on which visual information can be (and is) used to estimate the time until an approaching object will hit the eyes, or the hand (e.g. Rushton & Wann, 1999; Michaels et al., 2001).

However, this debate about approaching targets is not of interest for the experiments that we discuss in this thesis, because the targets of our experiments moved in a plane in front of the subjects. Instead, the important parameters are the target's position and velocity within the plane. Physically, the velocity is nothing else than the rate of change in position. However, since position and velocity can be derived from different visual cues, they can be processed independently in the brain. This was illustrated for example in Smeets and Brenner (1995a), where a moving background was shown to influence the subjects' perception of the target's velocity, but not of its position. Likewise, in the same study Smeets and Brenner showed that the hand's velocity was influenced by the velocity of both the target and the background. In addition, they showed with a model that the shape of the hand's path could be explained using only the target's changing position and no velocity information. Following this line of reasoning, the dependency of the hand's velocity on the target's velocity could reflect a compensation mechanism for the errors that result from the path not being suited to the target's velocity (Bairstow, 1987; Brenner & Smeets, 1996). This turned out not to be the case (Brouwer et al., 2000).

Another aspect of the use of velocity information in interceptive movements, the direction in which the hand moves, will be addressed in **chapters 3 and 4** (de Lussanet et al., 2001, submitted 1). It is not easy to find out whether or not velocity information influences the direction in which the hand moves, because the position of a rapid target changes faster than that of a slow one. This means that continuous use of positional information will give very similar results to the direct use of target velocity. Obviously, both positional and velocity information is picked up with the eyes. Therefore, it does matter what the eyes do during interception tasks. From studies on eye-movements it is clear that people can accurately pursue a moving target with their eyes. In pursuit eye movements, expectations play a role. When subjects are asked to follow a sequence of similar targets subsequently, the eyes' movements will anticipate those of the target, on the basis of the preceding targets' movements (Kowler et al., 1984; Kao & Morrow, 1994). Still, already the eye's initial acceleration depends on the present target's velocity, although this dependency saturates at a target velocity of about 10°/s (Carl & Gellman, 1987). Velocity information thus appears to be available at least for the control of eye movements.

1.2 The hypothesis of equilibrium point control

As a starting point to model the stability of motor control (**chapter 2**) we used the hypothesis of equilibrium point control of posture and movement (in short equilibrium hypothesis: Feldman, 1966). The hypothesis proposes that the ensemble of muscle and reflexes behave as a spring (Figure 1.1: upper row). The brain controls the equilibrium point of this "spring" (possibly in addition to parameters like co-contraction or stiffness and damping). Thus, according to the equilibrium hypothesis, the commands that descend from the brain do not encode forces but movement-related parameters such as positions or postures of the limb. This makes the hypothesis attractive, for it suggests that the brain does not need to perform complex inverse-dynamical computations to generate a movement. Instead, the dynamics of the movement arise automatically from the interaction of the mechanics of the limb with the set equilibrium position: the position to which one wants to move. The simplicity of this hypothesis provides a clear theoretical frame with which to study the responses to different visual input and to mechanical perturbations, as we will do in **chapters 2, 6 and 7**.

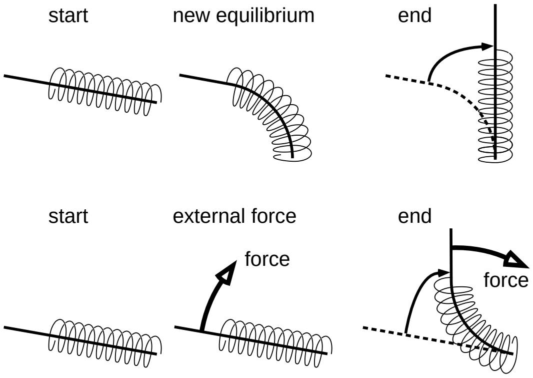

Figure 1.1 In a mass-spring system, a movement will result from changing the spring's equilibrium position (upper panels), but also when exerting an external force (lower panels). The first one is a voluntary action of the subject (for example as a reaction to a changed target position) whereas the latter can be achieved by exerting a force on the endpoint.

Feldman proposed the equilibrium point hypothesis on the basis of the observation that the unloading of a joint in a postural task causes the joint to rotate over an angle that is a function of the amount of unloading and the amount of co-contraction of the antagonist muscles prior to the unloading (Asatryan & Feldman, 1965). Later, the experiments by Bizzi and his colleagues (e.g. Polit & Bizzi, 1979; Bizzi et al., 1984) showed that deafferented rhesus monkeys can move their unseen limb accurately to a target, even when the limb is mechanically perturbed before or during the movement, which is consistent with the hypothesis.[1]

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[1] Bizzi and his colleagues originally stressed the importance of the spring-like behaviour of the muscles themselves, i.e. without the contribution of reflexes. Later they acknowledged the additional importance of reflexes (McIntyre & Bizzi, 1993). In the introduction of **chapter 2** we will give some arguments for lumping the contributions of muscles →

We can roughly divide the models for equilibrium point control (here called *mass-spring models*) into two categories: those with a controlled, moving equilibrium point (Feldman & Levin, 1995; Shadmehr et al., 1993; Gribble et al., 1998; Flash, 1987; Smeets & Brenner, 1995a, b) and those with a stationary equilibrium point in combination with pulse step control (Barto et al., 1999; Gottlieb, 1994). In the latter ones, the equilibrium point is set beyond the target in the pulse phase, before it is set at the target at the beginning of the step phase. These models can be seen as a specific solution for a problem that the first group of models tend to suffer from: they work well only for slow movements. To solve this problem, Latash & Gottlieb (1991) proposed a model that strictly belongs to the first group because the equilibrium point moves, but that effectively functions like one of the second group. In their view the equilibrium point's trajectory is recursive for fast movements. They reconstructed a trajectory that first moved towards the target, and then reversed its direction before approaching the target more slowly (Latash & Gottlieb, 1991, called it an "N-shaped trajectory"). This model comes very close to a (slightly smoothed) pulse-step model. We will come back to this issue in section 6.3 (Fig. 6.4).

In this thesis, we will concentrate on linear mass-spring models from the first category. Figure 1.1 illustrates that the movement that is predicted as a result of a changed equilibrium position is the same as the movement that is predicted as a result of an external force on the end effector. This prediction is even valid when the equilibrium position changes gradually over time, as long as the applied equilibrium trajectories are the same. Until now only the mechanical manipulation of the equilibrium position has been used to validate equilibrium models (e.g. Latash & Gottlieb, 1991; Gomi & Kawato, 1997; Bizzi et al., 1984; Bellomo & Inbar, 1997). We chose to use both manipulations in one experiment to test the equilibrium hypothesis (**Chapter 2**).

1.3 Has the equilibrium hypothesis already been rejected?

A problem of the equilibrium hypothesis is that there is little direct evidence in favour of it. The parameters that are supposed to be controlled (such as the equilibrium position) have not been measured directly (but see Houk, 1989). On the other hand, the ongoing discussion about the validity of equilibrium-point models (Feldman & Levin, 1995, and responses to it; Feldman et al., 1998; Gottlieb, 2000; Jaric & Latash, 2000), shows that it is not easy either to give any final arguments against equilibrium control.

Gomi & Kawato (1996, 1997) fitted a linear mass-spring model to perturbed movements and reconstructed an equilibrium trajectory that was very

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and reflexes under one set of model parameters. We basically have two arguments to do so. Firstly, incorporating both muscles and reflexes doubles the number of parameters to be fitted or estimated otherwise. Secondly, it would be very inefficient from a physiological point of view if the ensemble of muscles and reflexes can not be controlled (by the brain) as a single lumped unit. There is evidence suggesting that reflexes linearise the muscles' behaviour (**chapter 2.1**).

different from the limb's actual trajectory. They concluded that this is evidence against equilibrium control. Remarkably, the recursive equilibrium trajectories were qualitatively similar to those reconstructed by Latash and Gottlieb (1991) who drew the opposite conclusion. Latash and Gottlieb (1991) proposed instead that the threshold length ("lambda") for the activity of individual muscles changes in simple ramps. Gribble et al. (1998) showed that Gomi and Kawato's result (as well as that of Latash & Gottlieb, 1991) could be an artefact that was caused by using a linear model. Bellomo and Inbar (1997), using a very different method and a non-linear model (lambda model), reconstructed similar, recursive equilibrium trajectories in addition to complex "lambda trajectories" for the individual muscles. On the basis of this result they rejected the two versions of the lambda model (Feldman & Levin, 1995; Latash & Gottlieb 1991). In **chapter 6**, we will show that the finding of a recursive (N-shaped) equilibrium trajectory can be due to using a model with the wrong kind of damping.

There has been another attempt to reject the equilibrium hypothesis to which I never read a convincing defence. Therefore I will give it some more attention here. In a series of very elegant experiments, Lackner and DiZio (1994; DiZio & Lackner, 1995) let subjects make reaching movements that were perturbed by coriolis force. Coriolis forces occur during movements made in a rotating environment. They are only present while the subject moves and they are perpendicular to the direction of the movement and proportional to the speed of the movement. The subjects first made prerotary reaches while the room was stationary. Then the room started to rotate around a vertical axis and the subject had to sit perfectly still. Subsequently, the subject made a series of perrotary reaches, after which the room stopped to rotate. Finally, the subject made a series of postrotary reaches. The room was dark so the subject did not get any visual or tactile feedback. Lackner and DiZio discussed a number of variations on this basic experiment. In one experiment, subjects were asked not to touch the table at the end of the reach (Lackner & DiZio, 1994). In another study, DiZio and Lackner (1995) measured the transfer of adaptation to the non-adapted arm. In that experiment, they let subjects make the first postrotary reach with the hand that had been still while the room was rotating.

The averaged paths of the basic experiment are reproduced in the first two panels of Figure 1.2. Lackner and DiZio quantified the influence of the perturbation as lateral endpoint error (defined with respect to the last prerotary reach) and the curvature (the maximal deviation from a straight line between the start and the end of the path). Significant deviations were evident in the curvature and the endpoint of the first perrotary movement (Lackner & DiZio, 1994). Both parameters adapted rapidly and at the same rate over the subsequent movements, largely eliminating the influence of the coriolis perturbation. On the basis of two additional experiments, they argued that the adaptation of the endpoint and of the curvature reflect two different processes. Firstly, in the experiment in which the subjects were asked not to touch the table surface, the curvature did adapt whereas the (small) endpoint error did not adapt at all (Lackner & DiZio, 1994). Secondly, in the study on the transfer of the adaptation to the non-exposed arm, DiZio and Lackner (1995) showed that the adaptation of the endpoint error transferred whereas the adaptation of the curvature did not. Lackner and DiZio (1994, DiZio & Lackner, 1995) therefore concluded firstly, that the lateral movement endpoint and the shape of the trajectory are controlled independently and secondly that the perturbation does affect the movement's endpoint. Both are strong arguments against equilibrium point control.

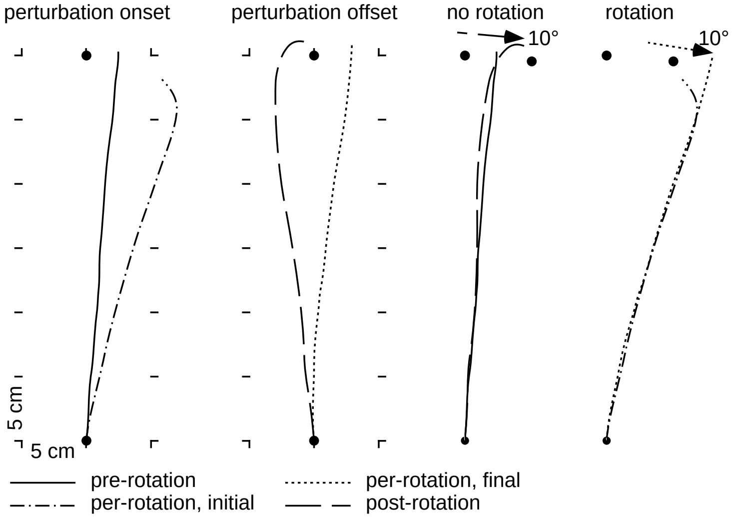

Figure 1.2 Top view of average reaching movements (11 subjects) made in darkness towards a just-extinguished target (redrawn from DiZio & Lackner, 1995: Fig. 1). The movement time was about 450 ms, the peak velocity about 950 mm/s. The room rotated10 rpm counter clockwise in the perrotary movements. Shown are the average final reach before the room started to rotate, the first and last perrotary reaches and the first postrotary reach. The influence of the perturbing coriolis force on the shape of the reaching movements is shown in panels **perturbation onset** and **perturbation offset**. Note that the trajectories in these panels start in the same direction. The amount of adaptation over the 40 perrotary reaches is shown for the same trajectories in panels **no rotation** and **rotation**. The trajectories of the final perrotary reach and the first postrotary reach were rotated rightwards (10°) about the starting position, corresponding with an adaptation of 10° leftwards. Note that the shape of the trajectories in these panels is remarkably similar over the first 25 cm (about 300 ms).

However, I argue that both conclusions are wrong, because Lackner and DiZio used the wrong parameters to analyse their results. Firstly, the curvature during the perturbed movements is not a measure of how the subjects *planned* to move, because it also measures the influence of the perturbation and the effect of the subject's corrections in reaction to the perturbation (the movements lasted long enough for subjects to make corrections). Thus, changes of the curvature in subsequent perrotary movements cannot be caused (entirely) by adaptation. Secondly, the lateral endpoint error reflects where the hand touched the table. As the subjects could not see the table surface, however, the hand may not yet have reached the equilibrium position when the finger was stopped by the table. In the first perrotary reach and the first postrotary reach, the hand moved in the wrong direction due to the change in room rotation. As a result, the hand approached the target from the side (Fig. 1.2 first two panels). This would result in a larger lateral endpoint error if the hand touched the table surface before reaching the equilibrium point. Indeed, the endpoint errors in the first perrotary reaches and the first postrotary reaches were large (3.9 cm), compared to the endpoint error in the experiment where the subjects made no final contact with the table surface (1.6 cm).

Fortunately, there is a much simpler explanation for Lackner and DiZio's results. This is that only the *direction* in which the movements started adapted over the subsequent perrotary movements, whereas the *shape* of the trajectories was not affected by the perturbation (and not the initial direction because at the start of the movements, the coriolis force was still zero). The first two panels of Figure 1.2 (Lackner and DiZio, 1994, basic experiment) show the influence of the onset and of the offset of the perturbation, when no adaptation could yet have occurred. The perturbation did not affect the direction in which the movements started, but did affect the shape of the first part of the trajectory. In contrast, the shape of the first 25 cm (about 300 ms) did *not* change during the adaptation phase (Fig. 1.2, last two panels). What had changed was the direction in which the movements started (10°). In addition, the curvature in the last 5 cm was different in the first perrotary reach and the first postrotary reach, which is not surprising because the subjects were allowed to make corrections.

In all three of the above experiments the “adaptation” of the lateral endpoint error saturated at 1-2 cm with respect to the prerotary level. These final perrotary movements were not curved towards the target, indicating that the endpoint error was not detected by the movement control system, which explains why there was no more adaptation. If indeed endpoint errors of less than 2 cm were not detected by the subjects, this also explains why there was a persistent, non-adapting perrotary endpoint error (1.6 cm) in the experiment without terminal table contact. It also explains why the small transfer of the movement direction to the non-exposed arm (DiZio & Lackner, 1995) did not lead to a curved trajectory.

I conclude that just one thing adapted in the course of the subsequent perrotary reaches (the initial movement direction), so there is no proof of two separate feedback systems in the adaptation process. Secondly, that the large endpoint errors probably resulted from the finger making contact with the table surface, because they were almost absent in the experiment where the subjects did not touch the table surface. Thirdly, that there probably was a small transfer of the adaptation in the initial movement direction to the non-exposed arm, which did not result in a curved path because the error remained within non-detectable range. Finally, the small endpoint errors in the first perrotary and the first postrotary reaches without terminal contact provide strong evidence in favour of equilibrium point control (provided that the small effect on the movement endpoint could not be detected by the motor control system).

The above conclusions do not imply that there are no serious problems with the hypothesis of equilibrium point control (e.g. Smeets, 1991). The fact that the initial movement direction was adjusted during subsequent perrotary reaches is in conflict with equilibrium point control, for it implies that either the shape of the equilibrium trajectory had adapted (which is unlikely if the shape of the hand's trajectory over the first 25 cm did not change at all), or the mapping between the individual muscles and the activation of individual muscles should have adapted (equally unlikely for the same reason). Perhaps the simplest explanation for the results could be made with a pulse-step equilibrium model (see section 1.2), in which case only the direction of the pulse needed to adapt. In conclusion, there is no final evidence either in favour or against equilibrium control. In my opinion, it is a valuable hypothesis, because of its simplicity and its ability to describe both the maintenance of posture and generation of goal-directed movements. There are motor behaviours though, for which other kinds of models appear to be more useful (for example exerting a force, making a high jump or adapting to changed mechanical behaviour of the limb). **Chapters 2, 6 and 7** will be devoted to applications of mass-spring models of the first category (section 1.2) that seem to work reasonably well for goal directed movements.

1.4 Methodology of the thesis

In the above it will have become clear that we aim at an interaction between a model based approach and an experimental, model-free approach. The advantage of a model is that it can be used to make falsifiable predictions and that one can use it to study the movement dynamics as a whole rather than at a subset of movement parameters that are more or less interdependent (which is risky: c.f. section 1.3; Smeets, 2000). The disadvantage of a model is that it easily tempts the observer to only studying the phenomena that are defined within the model.

In the experiments that we treat in this thesis, the subjects were asked to hit each target (a spider) that appeared on the screen in front of him or her (Fig. 2.1). When the subject held his or her hand stationary within the starting region, a target appeared that was either stationary or that moved to the right. We analysed the hand's trajectory towards the screen. With the mass-spring model we will describe the left-right component of the hand's movement (i.e. the same direction in which the targets moved). In the model-free analyses, the direction in which the movement starts will be an important parameter. The fact that the initial movement direction is an important parameter in goal directed movements was illustrated in the previous section (see Fig. 1.2).

1.5 Outline of the thesis

In **chapter 2** we started with the mass-spring model that Smeets and Brenner presented earlier (1995a). We aimed to test this model with mechanical perturbations (similar to those of Latash & Gottlieb, 1991), and visual perturbations for which the model predicted the same effect on the hand's trajectory (see section 1.2). In the process of analysis and writing we realised that the model could not account for visuo-motor delays between the visual perturbation and the hand's first reaction for which we proposed a solution (see also Smeets, Brenner & de Lussanet, 1998). Also, we realised that our understanding of how a target's velocity influences the hand's movement (section 1.1) was wrong. We therefore studied the influence of the target's velocity. We first showed that the target's velocity continuously influences the hand's velocity (Brenner, Smeets & de Lussanet, 1998). As outlined above, subjects do not seem to predict the position where the target will be intercepted on the basis of its velocity, because the trajectories towards a moving or a stationary target that are hit at the same position start in a different direction (van Donkelaar et al., 1992; Smeets & Brenner, 1995a). In **chapter 3** (de Lussanet, Smeets & Brenner, 2001) we addressed the question of whether the velocity of the preceding target influences the direction in which the hand moves, as was suggested by Smeets and Brenner's (1995a) model. In **chapter 4** we addressed the question whether the velocity of the present target does influence the direction in which the hand moves (which is in contrast to the suggestion of Smeets & Brenner's, 1995a, model). Whereas in **chapters 3 and 4** we approached the behaviour of healthy human subjects from the viewpoint of *stable* movement strategies as defined in the beginning of this chapter, in **chapter 5** (de Lussanet, Smeets & Brenner, in press) we concentrated specifically on *flexible* behaviour. Flexibility in motor control, in the definition that I gave in the beginning of this chapter, will be revealed if a movement towards the same target in the same conditions is made differently when the set of targets preceding it was different. For example, if the preceding targets had a different average velocity or if the hand's previous movements were perturbed. In **chapter 6**, we present a mass-spring model with a kind of damping that is new for models of equilibrium point control. We will conclude the thesis (**chapter 7**) with the analysis of an improved version of the experiment of chapter 2. We will use the model of **chapter 6** to predict the influence of mechanical and visual manipulations on the left-right component of the hand's movements.

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2

A double test for the applicability of simple mass-spring models for understanding movement control

Abstract

The question we treat in this study is whether a mass-spring model for the control of fast arm movements predicts the responses to perturbations during such movements. The model we used has previously proved to be very good at describing differences between the paths of the hand in different conditions (Smeets & Brenner, 1995a, b). In the present study, subjects had to hit targets in a frontoparallel plane as fast as possible. Two kinds of perturbations were applied. One was a gradually changing force on the hand (mechanical perturbation). The second was a change in the velocity of the target, leading to a gradual change of the estimated interception position (visual perturbation). Half the trials were perturbed. Subjects did not notice the perturbations and succeeded in hitting most targets. Model parameters derived from unperturbed trials were used to predict the influence of the perturbations. Neither the responses to visual perturbations, nor those to mechanical perturbations were predicted adequately with the fitted model parameters. In the case of mechanical perturbations, the responses could not be reproduced by any combination of parameters. The findings imply that changing the position of the hand with respect to the target (by mechanical perturbation) is not the same as changing the target's position with respect to the hand position (by visual perturbation). We conclude that a linear model for unperturbed movements cannot predict reactions to perturbations.

2.1 Introduction

It is widely accepted that the (human) motor system is composed of elements with (damped) spring-like behaviour. Examples are tendons, muscle fibres and reflex loops. The force-velocity and force-length properties of muscles, the pattern of motor unit recruitment, and reflex loops, are all highly non-linear (e.g. Hill, 1938; Asatryan & Feldman, 1965; Gielen & Houk, 1984; Gottlieb & Agarwal, 1988; Shadmehr, Mussa-Ivaldi & Bizzi, 1993). However, this does not mean that their behaviour cannot be described by a simple linear system. It has been shown that the combination several non-linear elements may result in a system that behaves more or less linearly. Tax and Denier van der Gon (1991) modelled muscle activation using the non-linear size principle and non-linear twitch summation. In their model, the ensemble of these two non-linear subsystems behaved more or less linearly. At a higher level, the non-linear stretch reflex and non-linear stiffness combine to provide a more linear muscle stiffness (Nichols & Houk 1976). Many researchers have successfully modelled entire movements assuming that the motor system behaves approximately linearly (e.g. Latash & Gottlieb, 1991; Gomi & Kawato, 1997; Plamondon & Alimi, 1997).

Even if a system is not linear in the entire operating range, it can be described with a linear model within a small enough range (e.g. Hogan, 1985). This notion was the basis of the modelling approach used by Smeets and Brenner (1995 a, b). They studied how subjects use visual information to guide hits towards stationary targets and targets moving at different velocities. Trajectories towards stationary targets, and trajectories towards moving targets that were hit at the same position, were different in curvature (underlining the fact that visual information influences fast movements continuously, McLeod, 1987). Smeets and Brenner described the systematic differences between conditions with a linear mass-spring model. By only modelling the (small) differences between conditions, they eliminated the strongly non-linear aspects of the movements. The model described the data well using a single set of spring parameters for trials towards both moving and stationary targets.

However, behaviour within a limited range of a non-linear system cannot always be fitted with a linear model. Brenner and Smeets (1997) gave an example of behaviour that clearly cannot be simplified in this manner. They examined hitting movements towards static targets that sometimes either started to move or made a jump, shortly after the hand started moving. In that experiment, subjects did not react proportionally to the size of the perturbations, but always with the same (large) correctional acceleration. We suggest three possibilities why a linear model cannot explain Brenner and Smeets' (1997) results. The first one is that the reactions to the perturbations were not within the linear range of the motor system. The second is that the perturbations were so obvious that subjects intervened (changed their strategy). The third explanation is that responses to perturbations are controlled differently than movements themselves.

The first two explanations reflect violations in the proposed operating range of the linear model. The third explanation has more fundamental implications, because it indicates that using mass-spring models is mere curve fitting, with very limited physical or physiological meaning. In the present experiment we tested this third hypothesis.

A basic assumption for describing the response with an equilibrium point model (such as Smeets & Brenner's mass-spring model) is that moving the target away from the hand (as discussed above) is equivalent to pulling the hand away from the target. This equivalence has been used many times (e.g. Feldman, 1965; Flash, 1987; Latash & Gottlieb, 1991; Gomi & Kawato, 1997). Naturally, if we apply a force on a hand (with upper arm fixed) it is displaced in the direction of the force (Asatryan & Feldman, 1965). Translated to an equilibrium-point hypothesis, this means that a subject's reaction to a perturbing force and that to a change in target position are indistinguishable, provided that the subject does not change strategy. This prediction can be tested.

In the present study we compared responses to unexpected target displacements with responses to equivalent force perturbations. We tried to avoid the non-linear range of Brenner and Smeets' (1997) experiment. To reach this goal, we chose perturbations for which the hand remained within the (linear) range of voluntary movements. Moreover, we ensured that subjects could not intervene, by using perturbations that were too small to notice.

2.2 Materials and methods

As in Smeets and Brenner (1995a), we studied hitting movements towards stationary and moving targets. In part of the trials with moving targets (50 % of all trials) there was either a mechanical or a visual perturbation. We determined two system parameters by fitting the model to movements towards static targets. These parameters were used to predict the reactions to perturbations. This method provided us with two independent tests (visual and mechanical) for the applicability of mass-spring models to perturbed movements. We will start this section by describing the experimental set-up. Subsequently we will describe the model and, based on the model prediction, the experimental conditions; and finally we will derive the measures used for data analysis.

2.2.1 Equipment

The visual stimulus was as described by Brenner, Smeets and de Lussanet (1998). Subjects were sitting in a darkened room in front of a screen, on which a target appeared that they had to hit with a Perspex rod (Fig. 2.1). The target was a spider animation with a realistic shape, and natural movements. The screen was tilted 30° backwards (top of the screen farther away from the subject) to make the hitting more comfortable. Images were computed with a graphic workstation (Silicon Graphics, Onyx CMN A011).

The hitting rod (22 cm long, 1.7-cm diameter) was held with the tip in the direction of the screen, like one would hold a pencil. The position of two active infrared markers on the long axis of the hitting rod was measured at 250 Hz (Optotrak 3010, Northern Digital Inc., Waterloo, Ontario). The position of the tip of the rod (hereafter referred to as "hand position") was extrapolated from the positions of these markers. An electric servomotor (MC23AS) provided a controlled, rightward force on the hand. A thread (Twaron ripcord 840 ddex Z6, Akzo Nobel, the Netherlands, non twined to minimise strain, but instead treated with hairspray to prevent fray) connected the rod to a 40 cm lever, mounted on the axle of the motor. The force did not deviate more than 4° from the lateral direction, throughout a hit. The force in the thread (and thus on the rod) was measured by a miniature force transducer (Wazau CMDZ, Berlin, Germany, weight 6 g, 0-300 N). The force on the rod was regulated with a proportional regulator. The force built up with a time constant of 12 ms and a static friction of 3% at 2.0 N. During the entire experimental session, there was a constant pre-load of 2.5 N (in order to enable perturbations in two directions, by either pulling or releasing). This pre-load was not disturbing to the subjects.

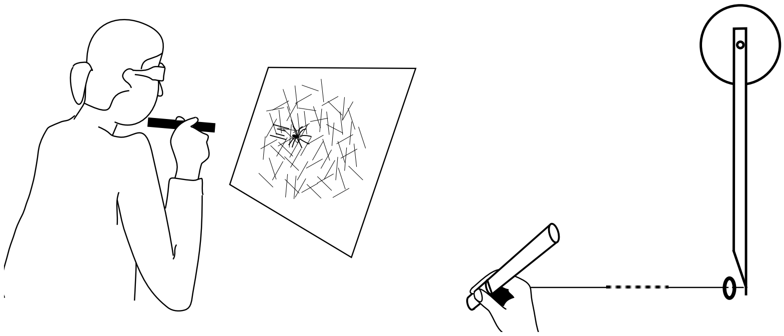

Figure 2.1. The experimental set-up (not to scale). Subjects were sitting in front of a transparent screen (Macrolon, 44 × 36 cm) on which they saw a stereo image consisting of red, randomly placed lines on which a yellow spider appeared. The spider was either stationary or running to the right, and it was to be hit with a rod. A servomotor generated force to the right, on the rod through a 3-m long thread.

2.2.2 Instructions and feedback

Instructions and feedback were as in Brenner, Smeets & de Lussanet (1998). Six subjects (including the authors) were allowed to position themselves so that they could hit the screen in a comfortable way. One subject (JB) was left handed, but all subjects used their right hand to hit. Subjects were told they would see static and walking spiders that they had to hit as soon as possible after appearance.

Before each trial the subject's hand was guided to the starting range by means of a 3-D arrow and written messages that appeared on the screen ("hand more to the left", etc.). This starting range was an invisible sphere of 5 cm radius around a position 40 cm away from the hitting screen. A spider counted as “hit” if the centre of the tip of the rod was within 18 mm from the centre of the spider. If the spider was hit, it looked squashed. If the spider was missed, it ran away in the direction opposite to which the error was made. For example, if the subject hit below the spider, it would run upwards. Each subject was allowed to practice until he or she felt comfortable with the task.

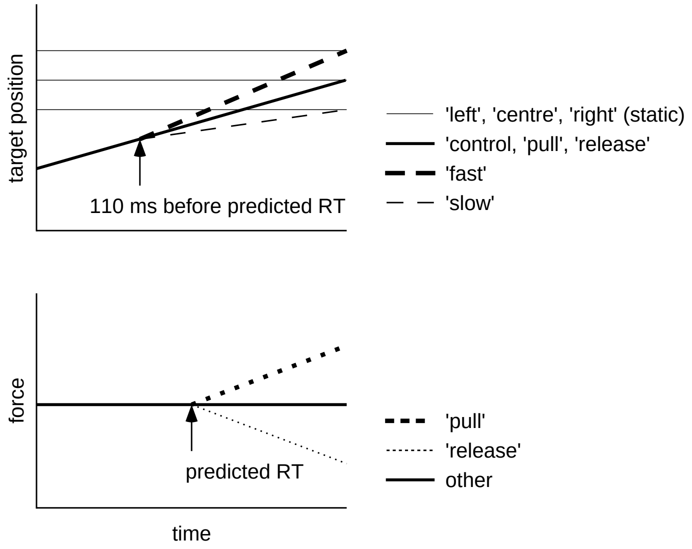

Figure 2.2. Experimental conditions.

2.2.3 Experimental conditions

Subjects had to hit 104 spiders of eight conditions (thirteen per condition), in randomised order in. The experiment took about 20 minutes. Figure 2.2 shows the conditions. There were three conditions with stationary spiders and five with moving ones. In four of the latter there were perturbations (50% of all trials), whereas the fifth (‘control’) was unperturbed.

We designed the perturbations in such a way that the mass-spring model predicts qualitatively the same deviations from the average trajectory for both kinds of perturbations. A complication is that the external force perturbs the movement directly, whereas the visual perturbation can only affect the movement after a delay (from retina to muscle force about 110 ms: Brenner & Smeets, 1997). We compensated for this delay by letting the visual perturbations start 110 ms earlier than the mechanical perturbations.

When the subjects held the hand stationary within the starting range, the target appeared. The hand’s left-right position at that moment was defined as position 0 cm. The *moving* spiders always appeared at position –7.0 cm, running at 12 cm/s to the right. Before each trial, the subject’s reaction time (RT) was predicted by the computer program that ran the experiment. This predicted RT was calculated as the average of the RT in the previous trial (when the hand had moved 5 mm from its start) and the previous average RT. In conditions ‘pull’ and ‘release’, the force started to change at a constant rate[2] of 5 N/s, beginning at the predicted RT. In conditions ‘fast’ and ‘slow’, the target’s speed changed at 110 ms before the predicted RT to 18 and 6 cm/s respectively.

The *stationary spiders* (‘left’, ‘centre’ and ‘right’) appeared at the final position of the last presented ‘slow’, ‘control’ or ‘fast’ spider respectively. In this way, the range and variability in positions of static targets was artificially equated to that of moving targets’ final positions.

2.3 The model

As we outlined in the Introduction, our model is a simple linear damped mass-spring system, a choice that is justified by modelling only a restricted part of the movement (Smeets & Brenner, 1995a, b). The model only describes the subjects’ small lateral deviations from their average path towards the screen. The general equation of motion for a damped linear mass-spring system is

$$M\ddot{x} + B\dot{x} + K\left(x - p(t)\right) = F(t). \tag{2.1}$$

The left-hand side gives the dynamic behaviour of the hand: the time dependent deviation, x, and its first and second time-derivatives ($\dot{x}$ and $\ddot{x}$). The mass (M), the viscosity (B) and the stiffness (K) are assumed to be constant during the complete session (and thus during each trial). Note that the mass, viscosity and stiffness are abstract parameters, not approximations of the complex physiology of the multi-joint arm. The variable $p(t)$ is the continuously updated position where the subject *predicts* that he will hit the target; $F(t)$ is the perturbing external force. As the model only applies to variations that arise during the movement, F and p are defined relative to their average values at movement onset.

The number of constant parameters in (2.1) can be reduced to two: the Eigenfrequency of the spring ω, and the time constant of damping τ, so that

$$\begin{aligned} \omega &= \sqrt{K/M - \left(B/2M\right)^2}, \\ \tau &= 2M/B. \end{aligned} \tag{2.2}$$

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[2] In pilot experiments we determined appropriate values for the perturbations, using various velocity- and force perturbations. We found that subjects still reacted proportionally to a velocity perturbation, when the velocity changed by 60 mm/s (in contrast to the larger visual perturbation in Brenner and Smeets 1997, where subjects appeared to react maximally). With a force changing at a rate of 5 N/s, the hand movements remained within the range of those in the static conditions. Therefore, we used these values in the present experiment. The naive subjects were asked after the experiment whether they noticed perturbations (in the instruction we only told them that they were to hit stationary and running spiders). They did not notice force perturbations on their hand, nor changes of spider velocity. They only noticed that *not all spiders had the same speed*, and that *the force was not entirely constant*.

For (unperturbed) static targets, p is constant and equal to the target's position. The perturbing force F is zero, so that (2.1) is homogeneous. The boundary conditions are $x(0) = \dot{x}(0) = 0$ (the hand starts at $x = 0$, with zero velocity). We only solve the model for the underdamped range (as overdamped movements will undershoot the targets). Filling in the boundary conditions and (2.2), gives the solution:

$$x = p - p\ e^{-t/\tau}\left(\cos(\omega t) + \frac{\sin(\omega t)}{\omega \tau}\right), \qquad (2.3)$$

where τ and ω are found by fitting the model (2.3) to trials towards static spiders, in which p is assumed to correspond with the real target position.

Some insight into the model is gained by regarding two border values for the parameters. Firstly, without damping ($1/\tau = 0$), p will be reached when the lateral velocity of the hand is maximal, meaning that a slightly faster or slower hit results in a large error. Secondly, in the critically damped case ($\omega = 0$), the lateral velocity is small at the end of the movement, so the error is less sensitive to when the screen is hit, but the target will never be reached.

When the spider moves, we suppose that subjects use the expected spider velocity[3] (v) to predict p (Smeets & Brenner, 1995a). In accordance with the 1995a paper, we assume that v is equal to the average velocity of the moving spiders (in the present experiment this is equal to the spiders' initial velocity). During the movement, p depends on the current spider position (s), on v and on MT–t (i.e. the remainder of the movement time):

$$p(t) = s(t) + v\cdot(\mathrm{MT} - t). \qquad (2.4)$$

so p changes gradually in time if $v \neq \dot{s}$. Replacing $s(t) = s(0) + \dot{s}\ t$ ($\dot{s}$ is the actual spider velocity) and subsequently $s(0) + \mathrm{MT}\cdot v(t) = p(0)$, and multiplying by K, equation (2.1) becomes:

$$M\ddot{x} + B\dot{x} + K\ \left(x - p(0) - t\ (\dot{s} - v)\right) = F(t), \qquad (2.5)$$

As the initial velocity of moving targets is always the same, $K\cdot p(0)$ is always the same. Therefore, the force perturbation must be $F(t) = K\ t\ (\dot{s} - v)$ to predict that the subjects' reactions are the same. This is a force that changes at a constant rate of $K\cdot G$ N/s (where $G = \dot{s} - v$).

As a result of the time dependent right-hand side, (2.1) becomes non-homogeneous for moving targets. The way to solve this kind of equation can be found in many textbooks on mathematics, and is reproduced in Smeets & Bren-

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[3] The perceived velocity is not the same as the time derivative of the perceived position, as there are several illusions that influence just one of these percepts. Likewise, the expected velocity is not a time derivative of some position measure.

ner (1995a). After applying the boundary conditions, the non-homogeneous solution of (2.5) becomes:

$$x = \hat{v}\,t + \hat{x} - \mathrm{e}^{-t/\tau}\left[\hat{x}\,\cos(\omega t) + \left(\frac{\hat{x}}{\omega\,\tau} + \frac{\hat{v}}{\omega}\right)\sin(\omega t)\right] \qquad (2.6)$$

with

$$\hat{v} = G + \dot{s} - v$$

$$\hat{x} = p(0) + \frac{\hat{v}}{\frac{1}{2}\tau\,\left(\omega^2 + \tau^{-2}\right)}$$

2.4 Analysis

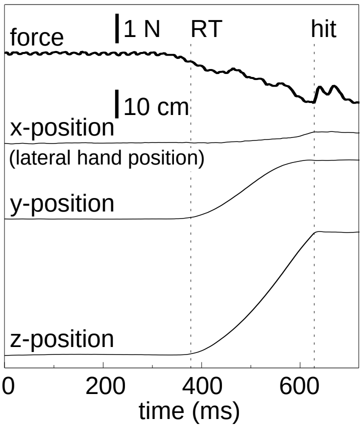

Figure 2.3. A single trial (subject JS). Force and the hand's *x*-, *y*- and *z*-positions during a trial with decreasing force. *x* is rightwards (the direction in which the target moved); *y* is upwards and parallel to the hitting screen; *z* is forwards and orthogonal to the hitting screen. Time = 0 is when the spider appeared.

For the analysis, the RT is defined as the moment when the *z*-component of the velocity of the hand, low-pass filtered at 10 Hz, exceeds 0.1 m/s. For this filtering we used a 4th order numerical Butterworth filter, applied back and forth in time to prevent phase shifts. Filtering was only used to determine movement onset. Figure 2.3 shows a trace of the hand in three components to the same scale. Note that the lateral component (*x*), which is the component that we study here, is much smaller than the forward component (*z*).

Of the hand's lateral movements we studied the deviations from each subject's average trajectory. For this, each trial was time-normalised over the MT (151 samples), so that the trials (with slightly different MTs) could be averaged. The average path of the 39 trials with static targets was subtracted from each individual path. By this method, the paths towards static targets ‘centre’ became more or less straight and those towards the other static targets were symmetric around the ‘centre’ paths. Lateral hand deviations in trials towards moving targets were also computed by subtracting the average path towards static spiders.

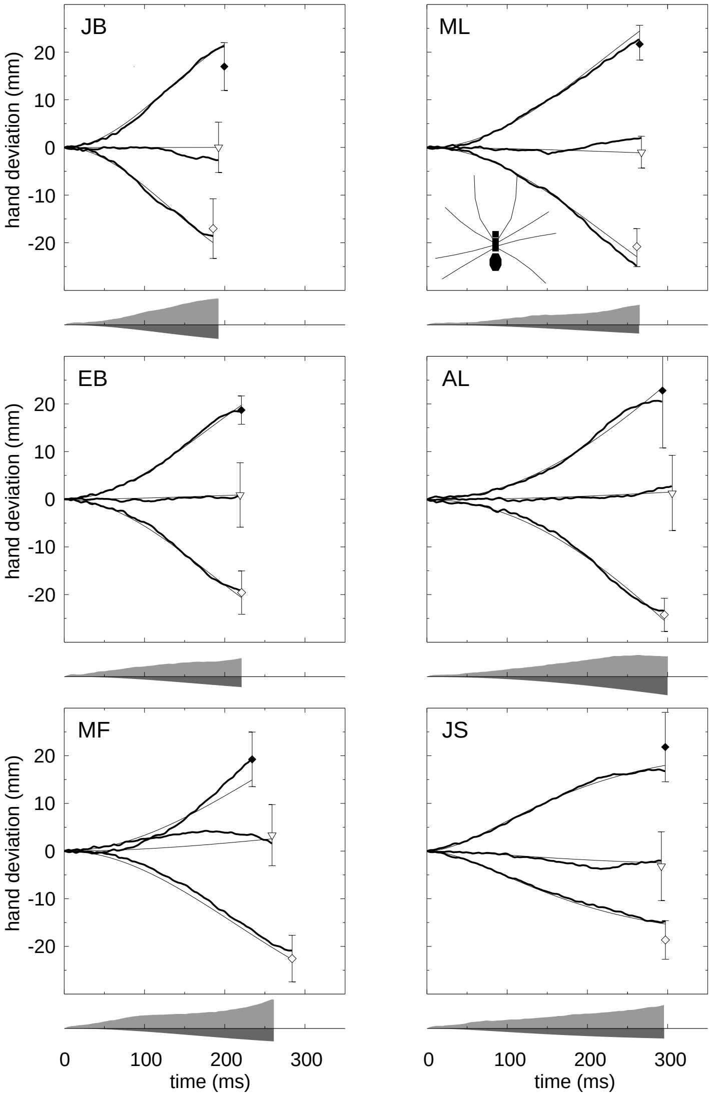

Figure 2.4. Average lateral hand deviations (*thick lines*) and average model predictions (*thin lines*) for the three conditions with static spiders (n = 13 for each condition). At time t = 0, the hand started to move. The grey curves at the bottom of each panel give the standard error of mean (SE), averaged for the three conditions (upwards for the experimental hand deviations, downwards for the model predictions). Symbols give the average spider position with standard deviations (SD). In the upper right panel, the spider is drawn to the scale of the figure. Subjects are ranked by MT.

The trials with static targets were fitted to the model by minimising the summed square difference between the model and average hand deviations over all time samples[4]. As a measure of the accuracy of the fitted parameters, we calculated the standard error of ω and of $1/\tau$ obtained from fits of the separate trials (not the averaged trials) of the conditions ‘left’ and ‘right’.

The fitted parameters (together with target position and speed and changes in force) were used as input for the model to predict the individual paths of all eight conditions. As a measure of the quality of these model predictions, we used the standard deviation (SD) of the difference between experimental hand deviations and predicted deviations for the 151 samples per trial.

Table 2.1. Model parameters in conditions with static spiders. Subjects are ranked by average movement time (MT). Note the almost reversed order of ω (in accordance with the curves in Fig. 2.5).

Subject	MT (ms)	ω (1/s)	1/τ (1/s)
JB	193	10.7	1.8
EB	221	8.0	1.0
MF	259	6.0	0.6
ML	263	6.8	0.5
AL	294	4.9	–0.7
JS	297	0.0	10.6

2.5 Results of fitting the parameters

Figure 2.4 (thick curves) shows the average lateral hand deviations for each subject in the static conditions. The thin curves show predicted average trajectories, computed with the parameters fitted to the average experimental trajectories (Table 2.1). For most subjects, the average predicted hand deviations (thin curves) resemble the experimental ones. Some subjects (e.g. subject AL), made an inward curvature at the end of the trajectory, which cannot be fitted by the model. The standard error of mean (SE) curves show that the different spider positions had significant effects on the trajectories, even though the effects were small (about 2 cm on a movement distance of 40 cm). The SEs of the predicted trajectories are caused by variability in the static spiders’ positions between trials. Thus, about half the SE in the experimental trajectories is due to the variation in spider position.

Table 2.1 shows a trend for smaller Eigenfrequency ω with longer MT, which can be expected if damping is small. In subject JS, the Eigenfrequency was

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[4] Our model does not account for variability in the subjects’ behaviour. Therefore, we fitted the average hand deviation in each condition, instead of the individual trials. For each fit, the average paths of one subject to the three static targets were fitted at once. This we did by constructing a position array and a time array that each contained the data points from all three average paths. These two data arrays were used as input for the fitting procedure (Levenberg-Marquard method, Press et al, 1996), resulting in one set of parameters for all three paths at once.

zero, which means that this subject behaved as a critically damped oscillator (Fig. 2.4: note that he hit the targets systematically too close to the centre). In the other subjects, the damping was small ($|\tau| >> MT$). With low damping, the lateral target position is reached at time $\pi/2\omega$ (i.e. a quarter period of a cosine function). Figure 2.5 shows the parameter settings with which the model predicts that the static targets are hit for three MTs. For each τ, there are different solutions for ω (two thick lines shown), but for none of the subjects was the parameter solution close to the larger value of ω. A detailed analysis of the shapes of the trajectories with different parameterisations will be given in section 2.9.2.

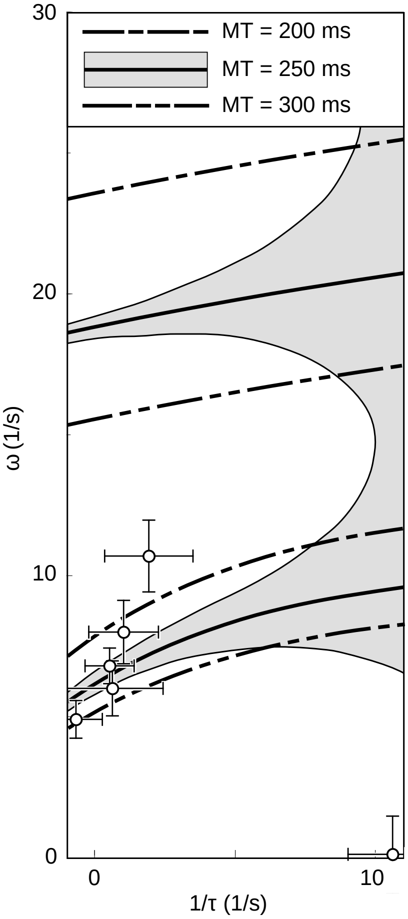
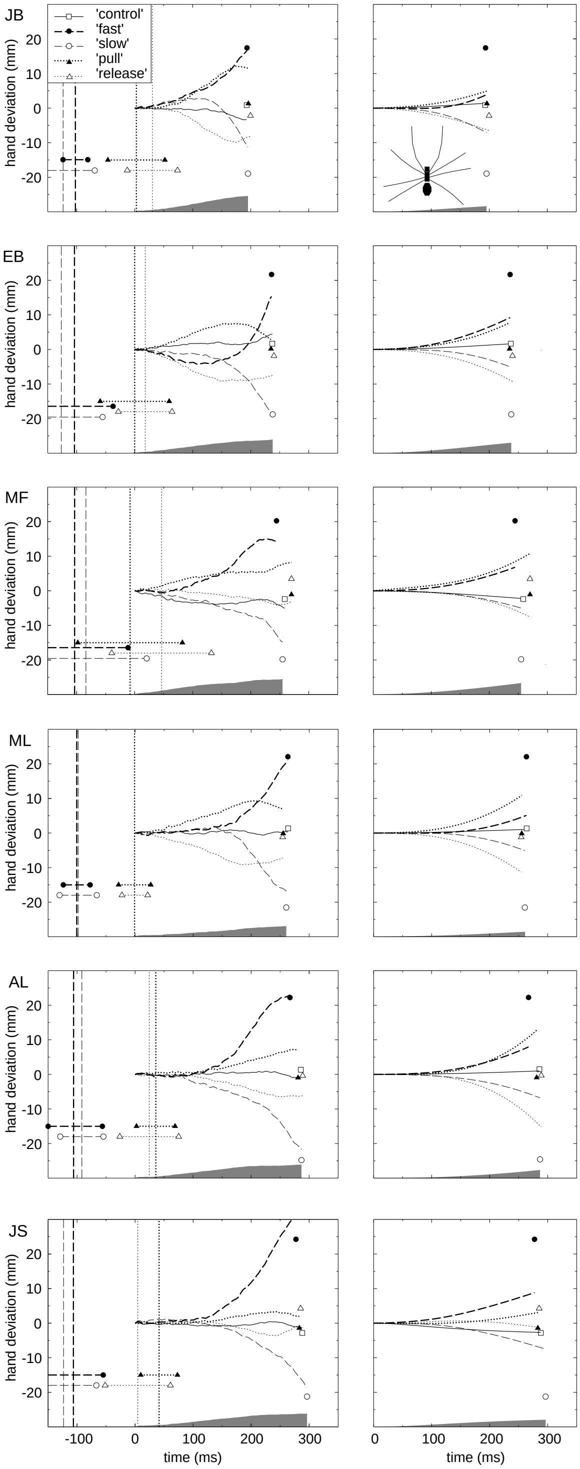


Figure 2.5. Model parameters based on the static conditions (*open circles*; with SEs) for the six subjects. *Thick lines* give parameters for which the model predicts that static targets are hit, for MTs of 200 ms, 250 ms and 300 ms. Within the grey area are the parameter settings with a hit error < 2 mm (MT = 250 ms). The open circles correspond with the values in Table 2.1.


JB
EB
MF
ML
AL
JS
'control'
'fast'
'slow'
'pull'
'release'
hand deviation (mm)
20
10
0
-10
-20
-100
0
100
200
300
time (ms)

← **Figure 2.6.** Average lateral hand deviations (*left panels*) and average model predictions (*right panels*) for the five conditions with running spiders (N = 13 in each condition). At time $t = 0$, the hand started to move. The *grey curves* at the bottom of each panel give the SE, averaged for the five conditions. *Vertical lines* (with SD) give the average time of the start of perturbation. Symbols at the end of the curves give the average final spider position and time of hit. The spider (left upper panel) is drawn to the scale of the figure.

2.6 Results of the perturbations

Figure 2.6 (left panels) shows the average lateral hand deviations for the five conditions with running spiders. The variation in the start of perturbation (vertical lines) resulted from variability in RT. Due to this variation spider positions differed between conditions and subjects. This partly explains apparent differences between subjects, and asymmetries of the trajectories. The SDs of the final spider position (not shown), were comparable with those in the static conditions, because the static spiders were placed on the final positions of moving spiders. Movements in the ‘control’ condition followed a similar path as those in condition ‘centre’ (i.e. little hand deviation), indicating that the modelling assumptions about an expected target velocity were valid.

Even though the change of spider velocity occurred on average 110 ms before the RT, the first effect on the hand’s path was clearly after the RT in all subjects. As the force started to change at the RT, we could not compare the trajectories for the two kinds of perturbations directly in the manner we had intended. Such a large delay gives a non-trivial problem to the model, which we attempt to solve below.

2.7 How to model the visuomotor delay

Figure 2.7 shows how a delay influences the perceived target positions and the resulting expected interception positions (p). The first example (Fig. 2.7A), represents the model presented above. There is an immediate reaction to the position mismatch of the target. This cannot be the case, however, because there must be a delay in the reaction of the hand to changes in the speed of the target. Figure 2.7B shows the effect of a 200 ms delay. The subject perceives the target at a position at which it had been some time earlier. With such a delay, the hand paths on non perturbed trials cannot be fitted anymore (the model predicts for example that subjects always hit behind the ‘control’). Figure 2.7C presents a solution to this problem (Smeets, Brenner & de Lussanet, 1998). The subject predicts the present target position on the basis of its velocity. As a result he reacts in accordance with the position the target would have been at had nothing unexpected happened. About 200 ms after the target changed speed, the subject switches to a new prediction of the present target position. It is this last kind of visuomotor delay that we used in our model predictions for targets that change velocity. For these predictions we used the non-homogeneous solution: equation (2.7).

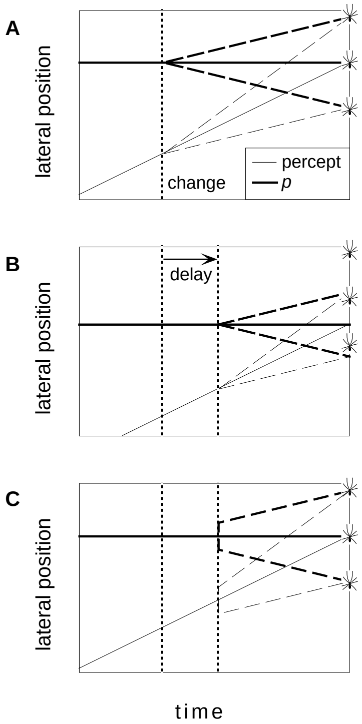


Figure 2.7. The visuomotor delay. *Thin lines*: perception of the target position, *thick lines*: *p*, where the subject predict to intercept the target. Continuous lines: the target moves at constant speed, dashed lines: the target changes speed at time "change" (left vertical line). **A** No delay: the target is always perceived where it actually is. **B** A constant delay: the target is always perceived where it was some time earlier, so subjects miss the targets. **C** There is only a delay after an unpredictable event (i.e. a change in target velocity). Before the event, and after the processing delay, the subject compensates for the visuomotor delay.

2.8 Model predictions

The parameter values found from the trials with static targets (Table 2.1) were used to test the model in conditions with moving targets. Figure 2.6 (right panels) shows the predictions for conditions with visual perturbations ('slow', 'fast') and with mechanical perturbations ('release', 'pull'). The asymmetries in the model predictions are all due to asymmetries in the final spider positions.

Figure 2.8 shows the hitting errors, defined as positive to the left for conditions 'left', 'slow' and 'release', and positive to the right for the other conditions. The figure shows that in 'slow' and 'fast' the predicted error was much more negative than the experimental values (significant in paired t-test, $P < .001$). For all subjects, the model strongly underestimated the amount of correction made with the 'fast' and 'slow' targets, but the shape of the predicted trajectories was good. The predicted error was not significantly different in the static and mechanically perturbed conditions ($P > .1$). However, with mechanical perturbation all subjects (except MF) had a strong final correction towards the target, which was not predicted by the model. Thus for mechanical perturbations, the general shape of the predicted trajectories was wrong.

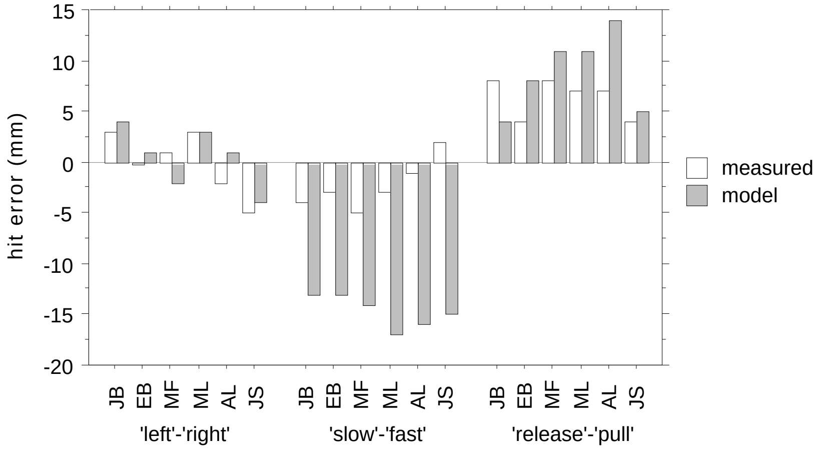


Figure 2.8. Systematic hit errors (mm): experimentally found (measured) and predicted values (model) for the three types of conditions. In conditions ‘left’, ‘slow’ and ‘release’, hitting to the left of (behind) the target is positive error. In conditions ‘right’, ‘fast’ and ‘pull’, hitting to the right of (in front of) the target is positive error. Only in the ‘slow’ – ‘fast’ conditions, the model predictions differed significantly from the results.

Table 2.2 gives the SDs (see Analysis) of the model predictions for static conditions (from which the model parameters were fitted), and for conditions with moving spiders. The SDs for ‘control’ are almost as low as those for the fitted conditions (static spiders) are. In the perturbed conditions, the SDs are generally higher, especially with visual perturbations (‘slow’ and ‘fast’). With the mechanical perturbations, the SDs were not as much higher, but there the curvature of the predicted trajectories did not match the experimental trajectories (Fig. 2.6).

Table 2.2. Quality of model prediction, expressed as the SD (mm) of the difference between the experimental and predicted hand paths.

subject	static spiders	‘control’	‘slow’ & ‘fast’	‘release’ & ‘pull’
JB	0.7	1.9	4.4	3.7
EB	0.4	1.1	4.7	3.4
MF	1.5	2.2	4.3	1.3
ML	0.9	0.5	5.0	2.8
AL	0.6	0.5	6.5	1.9
JS	0.5	1.4	6.0	1.3
average	0.8	1.3	5.1	2.4

2.9 Discussion

2.9.1 Quality of the predicted responses

In the above we tested the limitations of a linear mass-spring model of motor control using visual and mechanical perturbations. For both of them, the mass-spring model that we tested makes clear predictions, based on the responses in unperturbed trials.

The model parameters were obtained by fitting the model to the trajectories toward static targets (with no perturbation). The obtained values were within the very wide range (compare Beek, Rikkert & van Wieringen, 1996; Kelso, 1995) of values found previously in perturbation studies (Flash, 1987; Gomi & Kawato, 1997) and in studies with trajectory fitting (Smeets & Brenner, 1995a, b). Parameter values varied from critically damped to non damped. The trajectories that were calculated for static targets using the fitted parameters described the shape of the average hand deviations well, underlining that it is reasonable to use the linear approximation. For the ‘control’ condition, any set of parameters will result in a straight path like condition ‘centre’. However the fact that the experimental trajectories also are straight, affirms our assumption that subjects use an expected target speed to predict where they will hit the target (equation (2.4)).

Responses to visual perturbations (Fig. 2.6, left panels) started with a delay of about 200 ms, which was considerably more than the 110 ms that we expected. Elsewhere, we showed (Smeets, Brenner & de Lussanet, 1998) that the first effect of a change of target velocity on the lateral movement component of the hand is 200 ms after the change (90 ms longer than to target motion onset). This is in agreement with the present experiment.

Using the visual information with such a delay in our model would yield very small responses. Even with the discontinuous compensation (section 2.7), the model underestimated the subjects’ responses (Fig. 2.6). This failure to predict the responses to visual perturbations could mean that a mass-spring model is not suitable for predicting the response to changes in target speed. Alternatively it could mean that in the present experiment the assumption of constant parameter settings for all kinds of targets did not hold. Subjects could, in fact, clearly recognise two kinds of targets: static spiders and moving ones. The difference between static and moving targets was so obvious that subjects may have used two distinct strategies, i.e. with parameters optimal either for static or for moving targets. We will discuss this below (section 2.9.2).

By implementing a discontinuous reaction in the visuomotor delay with visual perturbations we introduced a non linear element in our model. The fact that a linear model cannot describe the visuomotor delay, does not mean that it cannot work for mechanical perturbations. However, the subjects’ responses leave us to suspect that it indeed cannot.

One could wonder why we did not consider to implement a reflex delay in the same way that we implemented the visuomotor delay. However a basic assumption of equilibrium models is that muscle mechanics and reflexes cooperate (on different time scales) to obtain the required behaviour. Evidence for this assumption is that reflexes compensate for later deviations in the muscle mechanics (Nichols & Houk, 1976). Thus, implementing a reflex delay would conflict with the basic assumptions of equilibrium-point models.

Moving targets, either unperturbed or with visual or mechanical perturbations, were not distinguishable for the subjects when reacting, so we expect the same parameters for all moving targets. Below we investigate whether the model could have predicted the right responses for all conditions had different parameters for static and moving targets been allowed. For this we show the predictions of the model for a wide range of parameter settings.

2.9.2 Possible responses

Figure 2.9A shows ranges of the model parameters τ and ω, for which the spider is predicted to be hit when static, with visual perturbation and with mechanical perturbation. With low $1/\tau$ and low ω the ranges do not overlap, whereas with high $1/\tau$ and ω, targets of all conditions can be hit. The exact position of the areas depends on the MT and RT, but their relative positions remain almost the same. The circles indicate the parameter settings of the modelled trajectories shown in Figure 2.9B.

With the parameters of panel 7, all targets are hit. Thus, subjects could have hit all targets with one set of parameters. However, the shape of the trajectories in panel 7 does not match the experimental ones. The responses to static targets do match trajectories with parameters close to those of panel 1 and 5, whereas those to visual perturbations match the paths close to panel 2 and 6. None of the panels in Figure 2.9B shows a hand deviation that matches that of the force perturbation.

Thus, using one set of movement parameters for static targets and a different set for moving ones, could explain the subjects’ responses to visual perturbations. However, as such parameters do not explain the responses to mechanical perturbations, allowing for two sets of parameters does not explain the poor predictions of the model.

Using a similar analysis as in Figure 2.9, one can understand why the model did work in a previous experiment (Smeets & Brenner, 1995a). In that experiment, both static targets and targets moving at different constant speeds were used. The optimal parameter settings for hitting targets moving at a constant velocity (not shown in Fig. 2.9A) almost completely overlaps with ones for static targets (light grey in Fig. 2.9A), so the same parameters could describe both conditions. The reason why the parameters that work for static targets also yield good performance for targets moving at constant speed is that by the time the hand starts to move, the predicted final target position has already changed considerably. If, on the other hand, the target velocity changes just before the hand starts to move, the predicted final target position has not yet changed on the RT. In that case a successful trial needs (in terms of the model) a much larger ω.

In the ‘pull’ condition (Fig. 2.9B), the predicted hand deviations increase monotonically during a hit. This is because there is a constantly increasing force. Unless the parameters change during the hit (viz., are non-linear) the modelled hand deviation cannot curve back to the target, in contrast to what we found in the experiment. The conclusion must therefore be that the hand deviations we found with the mechanical perturbation cannot be fitted with a linear model.

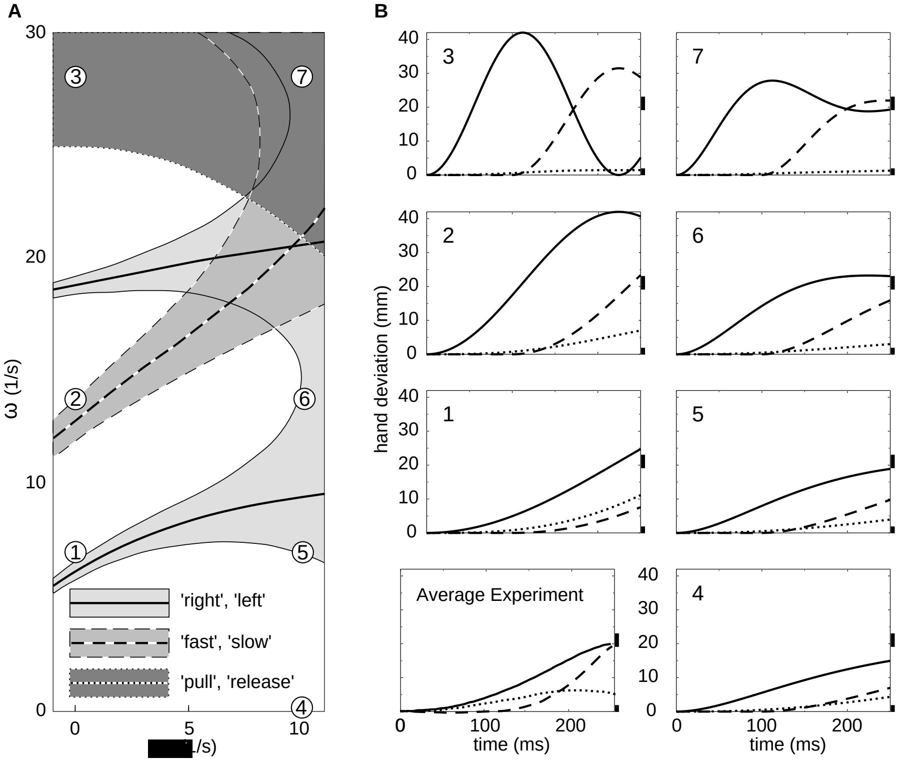


Figure 9A. Ranges of parameter settings for which our model predicts that the targets will be hit. *Thick lines* show parameter settings that result in hand deviations with zero hit error. Within the *grey areas* are the parameter settings with a hit error < 2 mm. The three areas (corresponding to our 3 conditions) only coincide with high damping (1/τ) and high Eigenfrequency (ω). This is the region where all targets are hit according to the model. **B** Model trajectories for the parameter settings that correspond with the circles in panel A. The bars on the right axis show the ranges of 2 mm hit error. In the *lower left panel* (*Average Experiment*) each curve is averaged over all subjects. *Continuous lines:* static spiders; *dashed lines*: ‘fast’, ‘slow’; *dotted lines*: ‘pull’, ‘release’. Predictions are made for RT = 300 ms, MT = 250 ms, and visuomotor delay = 210 ms (see Fig. 7C). Different values shift the areas in panel A, and the curves in panel B slightly, but the amount of overlap and the general shape hardly change.

2.9.3 Relation with other experiments

Our result is not the first one to show that a dynamic model that describes movements well, fails to predict responses to small perturbations. Oscillating movements can usually be described well with relatively low-parameter mass-spring oscillators (Haken, Kelso & Bunz, 1985). Kay, Saltzman and Kelso (1991) applied brief force perturbations to rhythmic finger movements and found that the perturbed movement could no longer be described with the regular low-parameter oscillator. They observed that “the movement temporarily speeds up in response to the perturbation, which would occur if the stiffness of the system temporarily increases”. From their results one cannot decide whether a subject switches to a different movement task, or that the same movement behaves differently if the hand is pulled away mechanically.

Smeets, Erkelens and Denier van der Gon (1990) measured EMG responses to load perturbations during fast arm movements. Their subjects responded with a latency of about 35 ms to these unpredictable perturbations. To describe the reactions with a servomechanism (i.e. correction signal based on position or velocity error), a negative delay in the feedback would have been needed. This is of course not physiologically possible, so the authors concluded that the responses could not be described with a standard servomechanism.

2.9.4 Relation with other models

The objectives for using models can be divided into two main categories. In the first, the main purpose is to examine whether selected physiological mechanisms can explain the behaviour, whereas in the second, the purpose is to give a simple description of the behaviour. These two categories are not exclusive. In the first, the models are based on physiological elements like muscles and reflex loops (Bullock & Grossberg, 1991; St-Onge, Adamovich & Feldman, 1997; Gribble, Ostry, Sanguineti & Laboissière, 1998). A disadvantage of this way of modelling is that it can be difficult to fully understand the model’s behaviour. This is a major drawback, because some complex models can generate almost every behaviour within the physiological range of parameters.

The present study follows the second category of models, in which the objective is to make the model simple enough to retain full insight into its behaviour (Hogan, 1985; Haken, Kelso & Bunz, 1985; Latash & Gottlieb, 1991; Shadmehr, Mussa-Ivaldi & Bizzi, 1993; Smeets & Brenner, 1995b; Gomi & Kawato, 1997). This implies that not too much effort is put into programming realistic physiological parameters, but rather to summarise them in simple (often linear) parameters at the behavioural level.

Our finding that a model for unperturbed movements failed to predict mechanically perturbed movements agrees with previous findings (see previous section). This raises doubt concerning the use of perturbations to obtain parameters for models of the second category. Reconstructing trajectories from parameters that are derived from perturbed postures (Flash, 1987) or perturbed movements (Latash & Gottlieb, 1991; Gomi & Kawato, 1997) may lead to wrong conclusions.

2.9.5 Conclusion

We wanted to find out whether human visuomotor reactions may be approximated as a linear system (mass-spring model). For this, we studied the effect of modest, unpredictable perturbations during fast hitting movements. In a linear mass-spring model changing the equilibrium position (by changing the estimated interception position) is equivalent to changing an external force on the hand. In our experiment however, the responses to these two kinds of perturbations differed considerably. We conclude therefore, that linear mass-spring models cannot be used to integrate responses to visual and mechanical perturbations, even within the range that is linear for non-perturbed movements.

Acknowledgements

The Netherlands Organisation for Scientific Research (NWO) is gratefully acknowledged. This research was conducted while the first author was supported by a grant of the Foundation for Behavioural and Educational Sciences of this organisation (575-23-002). We thank the Department Physics of Man, University of Utrecht, who kindly lent us the electric motor. We thank Dr. P. J. Beek, Dr. C. van den Berg and Dr. R. G. J. Meulenbroek for their valuable comments on the manuscript.

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3

The effect of expectations on hitting moving targets: influence of the preceding target's speed[5]

Abstract

When hitting a target that is moving, the time for planning the interception is limited. Instead of waiting for all the necessary information about the target's position and speed before starting to move, subjects could use their previous experience with similar targets to make initial guesses and adjust as new information becomes available. In the present study we examined whether the speed of the preceding target influences a hitting movement. Subjects hit moving targets that appeared on a screen about 40 cm in front of them. The targets moved at 6, 12 or 18 cm/s. Both the hand's initial movement direction and the final hitting error depended on the speed of the preceding target. We conclude that people control the way they hit moving targets on the basis of the speed of the preceding target.

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3.1 Introduction

In order to hit a target, people have to determine where to move and how. This takes time. If the target moves, one has to anticipate where the target will be by the time it is reached. To anticipate where to hit a moving target, one may rely on visual information about where the target is and how fast it is moving. However, in such a task, speed information does not seem to influence the hand's initial movement direction (Smeets & Brenner, 1995). The reason for this may be that it takes about 200 ms to use speed information (Brenner et al., 1998), which is about as long as the whole reaction time. It may be more efficient to use speed information from previous experience to build an expectation of where and how fast the target will move, and only to rely on new visual information to correct these expectations (Smeets & Brenner, 1995).

The results that we present here are based on the first experiment of an ongoing study in which we examine the influence of target speed on hitting movements. In the present paper we analysed the data to study the influence of the preceding target's speed on the movement.

3.2 Methods

The apparatus and experimental procedure were described in more detail in several previous papers (Brenner et al., 1998; Smeets & Brenner, 1995; Brouwer et al., 2000). In short, subjects sat unrestricted in front of a strong 35 x 45 cm screen that was tilted backwards by 30°. The target was an 18-mm long spider that appeared when the subject's hand had been at the starting position, 40 cm from the screen, for 1-2 s. Subjects were told that they had to hit each spider as soon as it appeared. Each target moved at a speed of 6, 12 or 18 cm/s (1 cm/s ≈ 1 deg/s). Targets of 6 cm/s appeared 7 or 5.5 cm to the left of the hand's lateral position, targets of 12 cm/s appeared 8.5, 7 or 5.5 cm to the left of the hand and targets of 18 cm/s appeared 8.5 or 7 cm to the left of the hand. Half the targets moved at 12 cm/s, one-quarter at 6 cm/s and one-quarter at 18 cm/s.

For hitting, subjects held a rod in the way one holds a pencil. A target was hit if the tip of the rod came within 18 mm of its centre. Subjects received visual feedback about whether they hit the target. Fourteen subjects (including two of the authors) volunteered to hit 80 targets. Except for the authors, the subjects were naive with respect to the purpose of the experiment.

The movements of the hitting rod were measured at 250 Hz (Optotrak 3010, Northern Digital Inc., Waterloo, Ontario). The *reaction time* (RT) was the interval between the moment the target appeared and the moment the hand moved faster than 0.1 cm/s towards the screen. The *movement time* (MT) was the interval between when the hand moved faster than 0.1 cm/s and the moment the hand hit the screen. The *initial movement direction* was the angle between the tangent of the hand's path and a line perpendicular to the screen, after the hand had moved 2.5 cm. The *hitting error* was the horizontal distance (positive to the right) from the centre of the target to the centre of the tip of the rod.

In order to examine the influence of the speed of the preceding target, we had to make sure that effects were not due to differences of the present target. Therefore, we examined whether three experimental variables influenced the movement parameters: the present target's position at RT, the speed of the present target, and the speed of the preceding target. We calculated the correlation of each movement parameter with these variables using a covariance analysis (which is a special form of multiple regression analysis, Fig. 3.1). In addition to the continuous variables, we included 13 binary independent variables in the analysis: each contained ones for the trials of one of the subjects and zeros for all other subjects. By this method, the differences in offset between subjects were captured by the coefficients of the 13 binary variables, while one single coefficient was obtained for all subjects for each of the three continuous variables. The present target's position at the RT is correlated with its present speed, so the coefficients that are found for these variables are not informative. However, since we are not interested in the influence of the present target, this was not a problem. We only report the coefficients for the previous speed. The coefficients represent the slope, and therefore have the dimension of this variable divided by the dimension of target speed (cm/s).

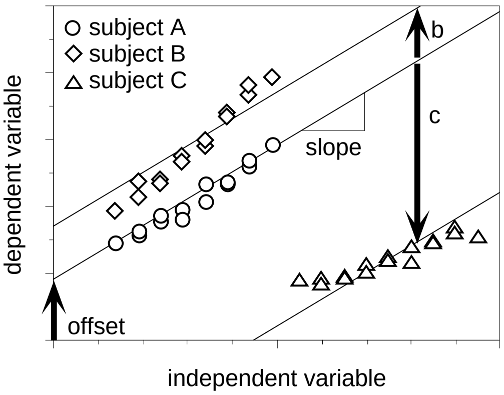

Figure 3.1. Illustration of the method of covariance analysis on fictive data from three subjects. The method results in a single regression slope for all subjects and in coefficients (b, c) for the differences in offset between the subjects.

For plotting the relation between the movement parameters and the speed of the present and of the preceding target, we first averaged the values within subjects, and then across subjects. We had to do this because the number of occurrences of each combination of present and previous speed differed between subjects due to the random order of presentation.

3.3 Results

Figure 3.2 shows the influence of the speed of the preceding target and that of the present target on each movement parameter. If the preceding speed has an effect on the parameter, the lines have a slope. This is so for the initial movement direction and the hitting error. If the present target's speed (or the correlated present target's position) has an effect, the lines differ in intercept, as is clearly the case for the MT and the initial movement direction. Figure 2D also shows that the previous speed has a larger effect on the hitting error than the present target has (the lines more or less overlap, but clearly have a slope).

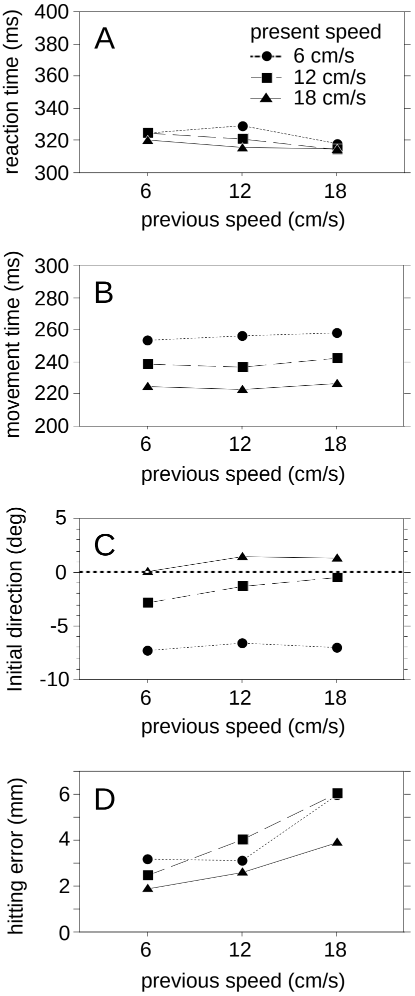

Figure 3.2. Influence of the preceding targets' speed for each present target's speed. The preceding target's speed had a significant effect on the initial movement direction and on the hitting error.

We tested the statistical significance of the slopes in Figure 3.2 with the covariance analysis. As explained in “Materials and methods”, the only coefficient that is relevant and meaningful for the scope of the present study is the coefficient for the preceding target’s speed. The effect of the preceding speed was highly significant ($P < .001$) for the initial movement direction (0.17 ± 0.05 deg·s/cm, slope ± standard error) and for the hitting error (29 ± 7 ms, slope ± standard error). The expected small effect on the RT (apparent in Fig. 3.2A) was not significant ($P = .07$). Hitting errors were not large: on average 90 % of all trials were hit by the subjects.

3.4 Discussion

Our results show that the speed of the preceding target did affect the initial movement direction and the hitting error. This result was not unexpected because Smeets and Brenner (1995) already proposed that subjects make use of an expected speed to hit a moving target. To our knowledge influences of the preceding target’s speed have never been observed for arm movements. Also, the results imply that the range of target speeds should influence the interception movement. This was indeed found by Van Donkelaar et al. (1992) and by Brouwer et al. (2000). A different effect of the preceding trial on arm movements was found by Jaric et al. (1999). In their experiment in which there was an unexpected change in the load on the arm between some trials, the MT and peak velocity depended on the previous load.

The influence of the present (and of the previous) target’s speed was not significant, though the magnitude was about the same as found in earlier studies (e.g. Smeets & Brenner, 1995), where it was significant. The present target’s speed apparently has a relatively large influence on the hand’s initial movement direction. This effect is a bit misleading, because it reflects the summed influence of present target position and speed on the initial movement direction (on the RT the 6 cm/s targets were on average more to the left than the 18 cm/s targets). The highly significant effect of the preceding target's speed on the hitting error is surprising at first sight, as the *present* target’s speed did not seem to influence the hitting error (Fig. 3.2D). We can interpret the influence of the preceding target’s speed on the hitting error as being a result of the effect that the preceding target’s speed has on the initial movement direction. If this effect of the preceding target on the initial direction is never fully compensated, it may still be present in the hitting error. The mass spring model of Smeets and Brenner (1995) illustrates this interpretation. According to this model, the effect of the expected speed decreases during the movement, but does not completely disappear due to the inertia and damping of the arm. Following the same line of reasoning, we can understand why the previous target’s speed did not affect the MT. The MT depends on the hand’s velocity, which is corrected on the basis of the *present* target’s speed (e.g. Brouwer et al. 2000). Thus there is no need to let the previous speed influence the MT.

In the present experiment we used visual targets. This means, that the information for making the arm movement is likely to be based on where the eye is looking. Some interesting examples of the influence of previous trials on eye movements may therefore be related to the effects that we found in the present study. Kowler and Steinman (1981) showed that anticipatory eye movements are made when subjects fixate a target that they expect to jump. When the direction of the jump was unknown, the direction of the anticipatory movement was correlated to the direction in which the previous two or three targets jumped. Kowler, Martins and Pavel (1984) showed that even the saccadic latency and the size of the saccade were influenced by the direction of the previous targets' jump. Not only saccadic eye movements, but also smooth pursuit movements have been shown to be influenced by previous movement cycles of a target (Kao & Morrow, 1994).

How far back the influence of previous targets on a present movement goes may affect the amount of variability one may find in a randomised experiment. If, for example, the expected speed from Smeets and Brenner’s (1995) model is the average of many previous targets’ speed, it can be regarded as a constant that does not impose extra scatter on the data. If, however, only the speed of the preceding target influences the movement, as would be closer to Kowler and colleagues’ (1984) findings for eye movements, this would cause extra variability in a randomised experiment. A covariance analysis including the second preceding speed did not reveal any effect, suggesting that the influence of the target before last is very small at best.

3.5 References

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4

The use of velocity information in fast interception of stationary and moving targets[6]

Abstract

In the present study we ask whether a target’s velocity is considered when planning a fast hit. Subjects had to hit targets that moved at different velocities from left to right across a tilted screen (starting with the hand 40 cm away from the screen). The targets appeared at different positions, so that they reached a similar position at the subject’s reaction time despite their different velocities. The direction in which the hand initially moved depended on the target’s velocity, as long as the targets moved slower than 12 cm/s. This indicates that velocity information was used for deciding where to aim. The initial direction differed in initial movement direction, A quantitative analysis showed that the initial movement direction was appropriate for the actual velocity of the target. The initial direction of movements towards faster targets did not depend on the target’s velocity.

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[6] This chapter was submitted to Journal of Experimental Psychology: Human Perception and Performance

4.1 Introduction

In order to intercept a moving target, our hand must reach a position that depends both on the target's velocity and on when the target is reached. To intercept a stationary target, one simply needs to aim for its position. To intercept a moving target, one can best aim ahead of it. This makes the interception of moving targets more complicated than the interception of stationary ones. Nevertheless people are remarkably good at intercepting moving targets (e.g. Bootsma et al., 1990; McLeod & Dienes, 1993). Intercepting fast targets is more difficult than intercepting slower ones (Fayt et al., 1997), so that stationary targets seem to fall within a continuum of targets speed rather than forming a separate class.

In the present study, we examine to what extent subjects consider the target's velocity when they aim ahead of moving targets. It is well established that subjects aim ahead of moving targets (van Donkelaar et al, 1992; Smeets & Brenner, 1995), but some of the evidence suggests that subjects only distinguish static from moving targets (Smeets & Brenner, 1995), relying on the velocity of previous targets to control the distance ahead of the target that they aim (de Lussanet et al., 2001). The fact that subjects are successful in hitting targets is explained by the fact that subjects continuously correct the hand's movement direction on the basis of the target's position.

In the above it was supposed that people make a (continuously updated) prediction of where they will intercept a moving target. For catching it is commonly believed that people predict when the target will arrive at a given position (Lee, 1976; Rushton & Wann, 1999), whereas this is not evident for interception. In many studies it has been proposed that people do not plan the place and time of interception independently but that these emerge from the strategy (McLeod & Dienes, 1993; Lenoir et al., 1999; Lee et al., 2001; Michaels et al., 2001).

In the latter case we expect to see an influence of target velocity on the initial movement direction, but the magnitude of this influence is difficult to predict, because target velocity may influence various aspects of interceptive movements to different degrees.[7] The prediction therefore depends on one's model. Examples of parameters that are influenced by target velocity include the reaction time (Tynan & Sekuler, 1982; van Donkelaar et al., 1992; Smeets & Brenner, 1995), and movement velocity or duration (van Donkelaar et al.,

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[7] In fact there are different kinds of sources of velocity information (e.g. Peper et al., 1994). The first kind of velocity information comes from the movement of the target on the retina, the other from the rotations of the eyes that follow the target. If the target approaches the eyes, the retinal velocity is the expansion of the target on the retina (looming), and the other is the change in disparity between both eyes that fixate the target (Rushton & Wann, 1999). If the target moves but does not approach the eyes, both sources give physically the same information, though they may lead to different behaviour (e.g. the reaction time: Smeets & Brenner, 1994).

1992; Brenner et al., 1998; Brouwer et al., 2000). However, these influences do not necessarily result from a single control mechanism. There are findings, for example, suggesting that the hand's acceleration and direction of movement are controlled separately (Bairstow, 1987; Brenner & Smeets, 1997). The velocity dependence of the reaction time may reflect the fact that movement at lower speeds takes longer to detect (van Doorn & Koenderink, 1982; Tynan & Sekuler, 1982), rather than being a control strategy.

Static and moving targets that are hit at the same position have different positions when the hand starts to move. In spite of this, the direction in which the hand initially moves differs little for such targets (Smeets & Brenner, 1995). This demonstrates that people already aim ahead of a moving target at the onset of the hand's movement. It does not mean though, that the hand's initial movement direction depends on the target's actual velocity (Brenner and Smeets, 1996). Smeets and Brenner (1995) found that an illusory increase or decrease of the target's velocity failed to influence the shape of the path toward that target. Van Donkelaar et al. (1992) designed an interception task so that targets of different velocities reached approximately the same positions by the time the hand started to move. They compared series of trials in which all targets had the same velocity (predictable) with series in which targets of the various velocities were presented in random order (unpredictable). They found that target velocity had a modest influence on the initial direction of the interception when it was unpredictable, and a strong influence when it was predictable. Thus, these studies suggest that the initial movement direction mainly depends on the target velocity on previous trials, rather than on the current one. In contrast to this conclusion, however, there is also some direct empirical evidence that subjects do consider target's velocity (van Thiel et al., 2000).

We designed two methods, one qualitative and one quantitative, to address the question of whether information about the target's velocity has a direct influence on the hitting movement. The qualitative method compares the hand's movement paths in different conditions. This method resembles the one used by van Donkelaar et al. (1992). They compared the paths in sessions in which each target velocity was presented in a separate block of trials with paths in sessions in which the velocities were presented in random order. One drawback of this method is that individual subjects display a large between-session variability (chapter 5: Fig. 5.7). We improved the method by including a reference within the same experimental session. Just like in van Donkelaar et al. (1992), there were targets of different velocities that reached the same position about the time the hand started to move. In addition, there were targets of each velocity that reached a different position at that time. Thus the hand's trajectories towards targets that differed only in position could serve as a reference for those towards targets of different velocities and a similar position around the reaction time. Around the time when trajectories towards targets that differ in position only diverge, the trajectories towards targets that differ in velocity (but not in the position when the hand starts to move) will also start to diverge if the current target's velocity is used to guide the hand.

In the experiments we used targets of different velocities, that moved from left to right on a screen in front of the subjects. We chose the targets' starting positions so that targets of different velocities reached the same position around the subjects' reaction time while others reached the same position around the time when the subjects hit the screen. Thus, if the current target's velocity is used appropriately, the trajectories towards the targets that are hit at the same position will have the same shape. On the other hand, if the current target's velocity does not guide the hand, the trajectories towards the targets with the same position at the reaction time will start in the same direction, even if the targets differ in velocity.

A restriction of the qualitative method is that it is not suitable for statistical testing. It is also sensitive to differences in the subjects' reaction times, when comparing movement paths towards targets of different velocities. Therefore we also used a second, quantitative measure. This method was based on the hand's initial movement direction. The effect of a difference in target velocity was scaled to the effect of a difference in position only on the initial movement direction. This number was used for statistical testing.

In order to restrain the length of the experimental sessions (to avoid influences of fatigue), we restrained the number of velocities tested within an experiment to two-four. To increase the range of velocities tested, we carried out a number of experiments. We thus covered the range from static to rapid targets, where the upper constraint was the size of the hitting screen and the time that it took subjects to reach the targets. In addition we changed the velocity intervals, to test if subjects could classify the velocities presented and thus use different strategies for each velocity. Another control was to enlarge the number of target positions, to test if the effect of velocity were correlated with the targets' position around the reaction time.

4.2 General methods

4.2.1 General Experimental Set-up

Subjects were the authors, our colleagues and medical students (20-64 years old; 30% female; two subjects hit with their left hand). Most subjects did not take part in all experiments. Except for the authors, the subjects were naive with respect to the exact purpose of the experiments. Subjects sat on an adjustable chair in front of a transparent hitting screen (Macrolon, Lexan) on which the stimuli were presented (Figure 4.1). The screen was tilted 30° backwards (top of the screen farther away from the subject) and was fixed in a strong construction so that it could easily withstand a hard blow. The target was a 3D-spider animation with a realistic shape, and natural movements. It was presented on a background of randomly orientated 4-cm lines, as if walking on a surface of fir-needles. The targets were hit with the tip of a rod (22 cm long, 2.1 cm diameter) that was held like a pencil between thumb and fingers.

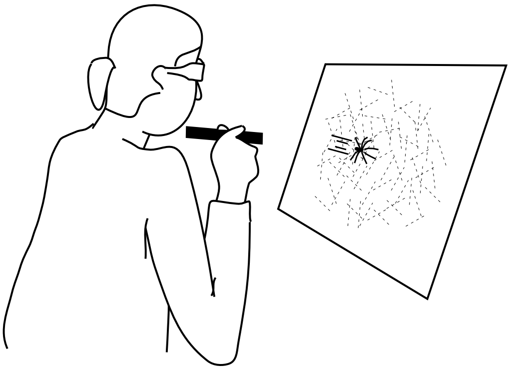

Figure 4.1. Schematic view of the experimental set-up.

The position of the rod's tip (we will simply speak of "the rod") was recorded at 250 Hz (Optotrak 3010, Northern Digital). The rod's position was calculated from the position of two active infrared markers that were fixed to the long-axis of the hitting rod. In addition, the positions of the subject's eyes in space were calculated from another three infrared markers fixed to spectacles worn by the subjects.

The stimuli were presented at 120 Hz on a monitor behind the screen. They were computed with a graphic workstation (Silicon Graphics, Onyx CMN A011). Subjects saw the stimuli on the screen. To achieve this, subjects wore liquid crystal shutter spectacles (StereoGraphics, CrystalEyes 2). A stereo-image was calculated for each frame using the positions of the subject's eyes with respect to the screen. During the experiment, the delay in adapting the visual image to changes in the positions of the eyes was 21 ± 3 ms (mean ± standard deviation (SD): see Brenner et al., 1998). In the off-line calculations, we were able to determine the moment when the target appeared with the 4-ms resolution with which the position of the rod was determined (method: see Brenner et al., 1998).

4.2.2 Instructions and feedback

Subjects were told that they had to hit each stationary or moving spider with the tip of the rod, as prescribed above. They were to hit the target as soon as possible. They were to minimise not only their movement duration, but also their reaction time. Subjects were free to position themselves (and the chair). They all spontaneously chose a starting position with the hand beside the shoulder, and thus viewing the screen slightly from the side. From this position, one cm on the screen corresponded to 0.8-1 degree of viewing angle.

Before each trial the subject had to move the tip of the rod to within 5 cm of a pre-set position 40 cm away from the screen. This starting position was opposite the screen's vertical midline, at the same height as the screen's centre. If the rod was not within the starting range, a 3D virtual line sticking out of the screen indicated the starting position, and a written instruction appeared to guide the hand towards there. The rod's exact starting position varied between trials. The position at which a target appeared on the screen was adjusted to the rod's starting position. The spider appeared when the rod had been stationary within the starting range for a random period of 1-3 seconds (mean velocity < 0.005 m/s).

The spider was hit when the centres of the rod's tip and of the spider came within 18 mm of each other. If the spider was hit, it looked squashed. If the screen was hit outside this 18-mm range, the spider was missed. It then ran away in the direction opposite to where the error was made. For example, if the subject hit below the spider, it would run upwards. After each trial, the background was refreshed.

Each subject practised until he or she felt comfortable with the task (usually 10-20 trials). The room lights were turned off, so the subject could not see the computer monitor but only the stereo-image that it generated. An experiment of 80 trials lasted 10-15 minutes.

4.2.3 Data analysis

In one out of a total of 78 experimental sessions (6 experiments, 12-14 subjects), the subject did only 58 trials (instead of 80) because the experiment stopped prematurely due to a software error. Of the 6818 trials by all the subjects, 141 were discarded because either the infrared markers became invisible before the screen was reached, or the rod was already moving when the target appeared. We verified that the percentage of misses was not related to target velocity (linear regression on the subjects' percentages per kind of target; $\alpha = 0.05$). Note that the misses were included in the analysis.

The targets always appeared at the same vertical position with respect to the rod. Therefore, we do not expect adaptations to the targets' position or velocity in the vertical component of the movement path. We analysed the projections of the movement on a plane perpendicular to the screen (and parallel to the target's path), where we do expect adaptations to target velocity and position. The reaction time (RT) was defined as the time between the target's appearance and the time when the rod's velocity towards the screen exceeded 0.1 m/s. The end of the movement was defined as the moment when the rod hit the screen. The movement time (MT) was defined as the time between start and end of the rod's movement. For the analysis we defined the origin of the movement as the rod's position at the RT.

We used the Savitzky-Golay method (Press et al., 1992) for smoothing the data. This method performs a least-square fit of a polynomial to points within a moving window. We used a second order polynomial and a window of 11 samples (5 before and 5 after the data point). The position and direction of the path in the centre of the moving window are respectively the second and third term of the polynomial. The advantage of this method over conventional filtering is that it does not yield overshoots before and after a sharp change in velocity.

Average paths of the rod were calculated for each movement condition and each subject. For this, the lateral movement component of each hitting movement was resampled to 151 points with equal intervals on the axis perpendicular to the screen. Each point was calculated as the linear interpolation between the two nearest time samples. Average paths were calculated from these resampled paths. To give an impression of the accuracy of the overall mean of these trajectories, they were printed with a thickness of one standard error of the mean path (SE). This SE was calculated as the *average intra-subject SE* / $\sqrt{N}$; with N subjects. Note that this measure does not represent the variability of the paths. The variability would be a meaningless measure because it would reflect variability between subjects, as well as in RT and MT, etc.

The direction in which the rod initially moved was determined in the tenth sample (out of the 151) in each subject's average paths. This was at about 2.5 cm towards the screen from the rod's initial position, corresponding with 68 ± 12 ms (mean ± SD) after the RT. We chose this definition as a compromise. The direction of movement should be determined as early in the movement as possible, because around that time the target's positions were equated (relative to the hand). Moreover, the hand should not yet have moved far because otherwise the direction of motion will also depend on the movement's past. However, the direction should not be determined too early to avoid measuring only noise. We used each subject's average paths in order to be less sensitive to such noise at the beginning of the movement.

4.2.4 Qualitative estimate of the influence of the target's velocity

As we outlined in the Introduction, we used targets of the same velocity that appeared at different position, ones of different velocities that reached the same position around the time that the hand started to move and ones that reached the same position around the time that the hand reached the hitting screen. We can make some clear predictions about the hand's paths. Firstly, if velocity information influences the hand's initial movement direction, the paths towards targets of different velocity (that reach the same position at the reaction time) will start in different directions. If a subject appropriately uses velocity information already at the movement's start, the hand's movement will start as if the subject aims directly at the position where the target will be when hit. Therefore the paths of the rod should coincide when the targets are hit at the same position, despite the difference in the targets' position at the RT. On the other hand, if differences in target velocity do not influence the initial movement direction at all, the paths towards targets of different velocities will start in the same direction if those targets reach the same position around the time when the hand starts to move.

4.2.5 Quantitative estimate: the initial adjustment

For each subject and target velocity, we calculated a quantitative measure for the influence of target velocity on the initial direction of the rod's movement, the *initial adjustment*. To calculate this initial adjustment, we made use of the linear relationship that exists between the rod's initial movement direction (see above) and the target's current position[8]. We derive the initial adjustment in the Appendix. To give a brief definition in words: (1) Compare the direction in which the hand initially moved for targets of the same velocity that appeared at different positions. (2) Calculate the relation (slope) between the hand's initial movement direction and the target's current position. (3) Compare the hand's initial movement direction for targets of different velocities. (4) Translate this into a difference in target position from relation 2. (5) Compare this with the difference in velocity and divide by the movement time to obtain a value expressed in cm/s.

To limit the number of comparisons, each target velocity was compared only to the average velocity. In two of the experiments (4 and 6) 12 cm/s is used because none of the targets moved at the average velocity.

4.2.6 Statistics

If the targets' velocities do not influence the initial movement direction, the initial adjustment will be zero. We tested (one-tailed t-tests; $\alpha = .05$) whether the initial adjustment differed from zero for each target velocity (except for the reference for which there is no difference by definition). For velocities below the reference we tested whether the value was significantly below zero. For velocities above the reference we tested whether the value was significantly above zero.

The RT and the MT both depend on the target's velocity (RT: van den Berg & van den Grind, 1989; MT: Brouwer et al., 2000). This is well known and the initial adjustment was calculated in a manner that takes this into account (see Appendix). To give the reader an impression of these dependencies, we give the slopes (of a special form of multiple regression analysis, known as covariance analysis) for the first experiment.

4.3 Experiment 1

We analysed the rod's initial movement direction towards targets that appeared at different positions with different velocities. The data of experiment 1 were also used in a different analysis (de Lussanet et al., 2001), in which we showed that the rod's initial movement direction and the final hitting position with respect to the target were significantly influenced by the velocity of the *preceding* target. In the present study we concentrated on the influence of the current target's velocity, but for comparison we also averaged the trajectories to reveal the influence of the preceding target's velocity on the rod's movement trajectory.

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[8] For predicting the initial direction of movement from the target's position, Brenner and Smeets (1996) used the position 110 ms before the start of rod movement (a change in target position influences the path of the rod after a delay of 110 ms). However, later we (Smeets, Brenner & de Lussanet, 1998) proposed that subjects compensate for this visuomotor delay as long as nothing unexpected (like a jump of the target) occurs, so we here use the position of the target at the moment when the initial movement direction is defined.

4.3.1 Methods

Eighty targets appeared in random order at a position that was defined with respect to the hand's current position (Table 4.1). The principle methods were as described in the 'General methods' section. One of the fourteen subjects was excluded from the analysis because he did not reveal a consistent relation between initial movement direction and target position (so we could not calculate a meaningful initial adjustment).

For the additional analysis of the influence of the preceding velocity, each subject's paths were averaged by the velocity and position of the present target and the velocity of the preceding target (7 kinds of targets × 3 velocities = 21 average paths; each subject's first trial was omitted). The 21 paths were averaged again (across subjects) by the preceding and present target's velocity (resulting in 9 paths, one for each preceding and present velocity). The averaging was done in two steps for reasons of balance: a subject's (seven) experimental conditions were not preceded by each of the three possible velocities for the same number of times. Subjects for whom the targets of one of the seven conditions were never preceded by one of the three velocities were excluded for that specific present velocity. (For example, if for a subject the trials with a left 6 cm/s target were never preceded by a target of 12 cm/s, none of the paths for 6 cm/s present targets were included for that subject. However, that subject's paths for 12 and 18 cm/s present targets may be included.)

Table 4.1. Positions (cm) of the targets at various times after appearance. Position = 0 is the hand's lateral position when the target appeared. Targets with the same position are printed in the same format.

velocity (cm/s)	6	6	12	12	12	18	18
N	10	10	15	10	15	10	10
0 ms	**-4.5**	-3.0	*-6.0*	**-4.5**	-3.0	*-6.0*	**-4.5**
250 ms	-3.0	**-1.5**	-3.0	**-1.5**	*0.0*	**-1.5**	*0.0*
500 ms	-1.5	0.0	0.0	1.5	*3.0*	*3.0*	4.5

4.3.2 Results

Figure 4.3A shows average paths towards the 5 targets that are shown with thick lines in Figure 4.2. On average subjects hit slightly in front of what we defined as the centre of the targets. The targets' positions at the RT and time of hit are marked by arrowheads. On average, each of the targets was close to one of three positions at the RT. This shows that the chosen starting positions were adequate. The RT (Table 4.2) depended slightly on target velocity, with a slope of –0.07 s^2/m (P = .02; this is 4 ms per 6 cm/s). The RT was slightly longer than the 250 ms to which we had suited the targets' positions. In the extra time the 6 cm/s and the 18 cm/s targets on average moved another 0.20 and 0.43 cm respectively as can be seen in Figure 4.2. The MT (Table 4.2) depended on target velocity with a slope of –0.27 s^2/m (P < .0001).

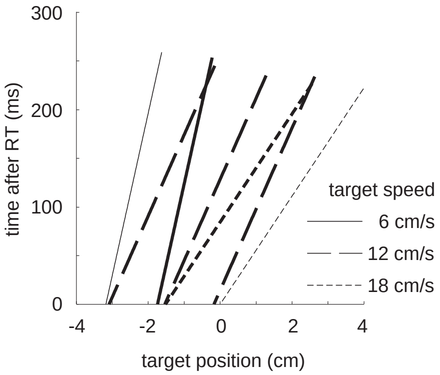

Figure 4.2. Average target positions in experiment 1. Time = 0 is when the hand started to move. Position = 0 is the hand's lateral position when the target appeared. The ends of the lines show the average time when the screen was hit in each condition. Thick lines are the target motions that belong to the movement paths shown in Figure 4.3A.

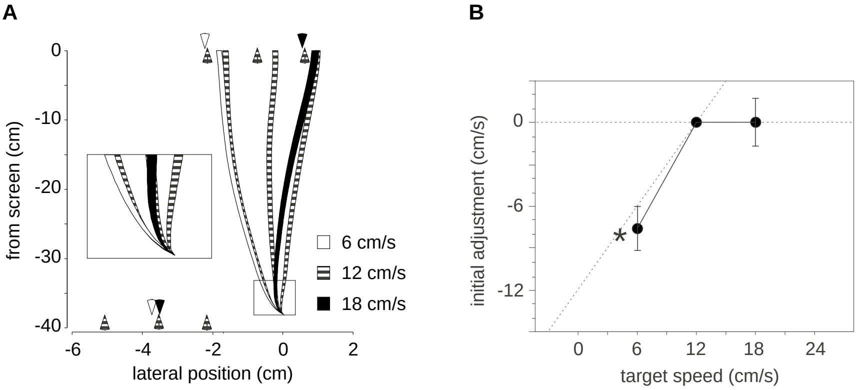

Figure 4.3. Panel A: Average paths of the rod in experiment 1 for the targets indicated by thick lines in Figure 4.2. The thickness of the paths denotes the standard error (SE) of the mean path (see Data analysis). Arrowheads show each target's average position at the RT and the MT. Note the different scales on the axes, and note that the paths towards one 6 cm/s and one 18 cm/s target are not shown. The inset shows a magnification of the first 5 cm of the trajectories. **Panel B:** The initial adjustment with respect to 12 cm/s targets (with inter-subject SEs). The dashed diagonal line shows the appropriate change in initial movement direction for the difference in target motion. The initial adjustment for 6 cm/s is significantly *below* zero (indicated with the asterisk, *); for 18 cm/s it is not significantly *above* zero.

The *qualitative analysis* (Figure 4.3A) gave both possible results. On the one hand, the path towards the 6 cm/s target (white curve) coincided with that to the 12 cm/s target with a similar final position (left striped curve). This indicates that the subjects *did* adjust for the difference in target velocity. On the other hand, the path towards the 18 cm/s target (black curve) started in the same direction as that towards the 12 cm/s target with a similar position at the RT. This indicates that the subjects did not adjust for the difference in velocity between 12 and 18 cm/s.

The *quantitative analysis* (Figure 4.3B), that includes all seven conditions, gave the same result. This is not evident, because the quantitative method is based on the results of individual subjects. The initial adjustment at 18 cm/s was close to zero. The initial adjustment is calculated relative to 12 cm/s, so the initial movement direction towards 18 cm/s targets did not reflect the fact that 18 cm/s targets will move further than 12 cm/s targets while the rod moves towards the screen. On the other hand, the initial adjustment at 6 cm/s was significantly below zero (–8 cm/s; P = .002). Thus the initial movement direction towards 6 cm/s targets did reflect the fact that 6 cm/s targets will move less far than 12 cm/s targets during the rod's movement (diagonal line). The range for the initial adjustment was –21.8 to +1.5 cm/s at 6 cm/s and –18.4 to +17.0 cm/s at 18 cm/s.

Table 4.2. The reaction time and movement time in all experiments (ms; mean and inter-subject standard deviation, SD). The average intra-subject SDs were 39 ms (RT, experiment 1) and 24 ms (MT, experiment 1).

experiment	reaction time	SD	movement time	SD
1	279	26	242	81
2	286	27	216	45
3	267	37	232	72
4	281	27	227	44
5	266	26	233	50
6	270	33	215	58

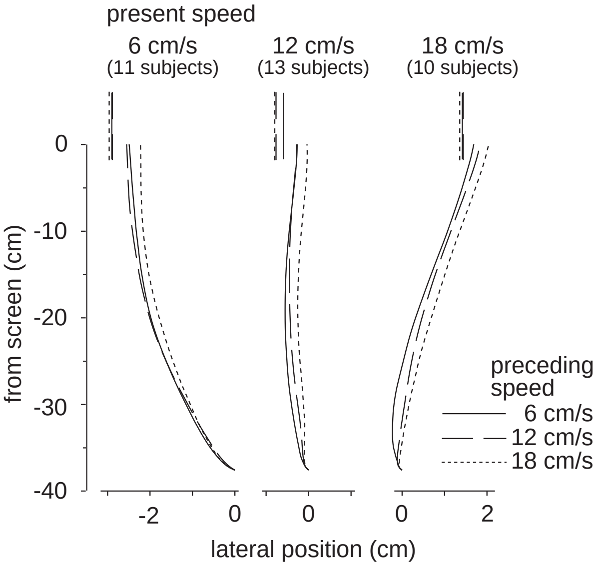

Figure 4.4. The movement trajectories averaged by the velocity of the present and previous target in experiment 1. For clusters of three paths the present target's velocity was the same. For paths with the same style the previous target had the same velocity. Note that each cluster of three paths was calculated over a different number of subjects. The vertical lines at the top show the target's average final positions.

The qualitative influence of the *preceding target's velocity* is shown in Figure 4.4. The vertical lines show that the targets of each velocity on average were hit at almost the same position. The three paths towards 6 cm/s targets started in the same direction: the preceding target's velocity did not influence the initial movement direction. The paths towards 12 cm/s and 18 cm/s targets reveal a systematic influence of the velocity of the previous target on the initial direction. Subjects aimed further ahead when the preceding target was faster.

4.3.3 Discussion

The results for the analysis of the target's velocity were very clear and were the same for both the qualitative and the quantitative method. The results were unexpected, however, because the influence of the target's velocity was only present with slow targets. Therefore, we have to find out why there was a difference between slow and fast targets before we can conclude that the initial adjustment between 6 and 12 cm/s was indeed caused directly by the difference in velocity.

One way to interpret the results is that subjects rightly judged (and used) the velocity of the 6 cm/s targets, but not the velocity of the faster ones. If the target was a fast one the subjects could have used the velocity of the preceding target instead (Figure 4.4). On average, the velocity of the preceding targets was 12 cm/s. In this view, one would indeed expect the initial adjustment to be the same for 12 and 18 cm/s targets, because with those targets the hand would on average start in a direction as if the velocity was 12 cm/s. For the 6 cm/s targets one would expect an initial adjustment of –6 cm/s (i.e. the difference between 6 and 12 cm/s).

Van Donkelaar et al. (1992) used an interception task similar to ours. In one of their experiments, the RT was decreased by using a go-signal. The initial direction of the hand's paths in that experiment was not correlated to the targets' velocity or position. In our experiment, the RT was shorter for fast targets than for slow ones. Could this explain why the velocity of fast targets did not influence the hand's initial movement direction, while that of slow targets did? The correlation between RT and target velocity (5 ms per 6 cm/s) was very much smaller than the decrease in RT (>100 ms) imposed by van Donkelaar et al. (1992) and cannot explain that the effects in our data were so large.

In the control experiments below, we will check that there is a linear relationship between target position and initial movement direction (experiment 2). Secondly, in this first experiment one could argue that the subjects treated the 6 cm/s targets as a special case. this is a possibility, because the relative difference in velocity between 6 and 12 cm/s is larger than that between 12 and 18 cm/s. This could have made the trials with 6 cm/s targets 'pop out' among the trials with higher velocities (experiment 3). Finally, we need to know whether the asymmetry in how subjects move towards slow and fast targets shifts with the range of target velocities used in the experiments. It may for example depend on the average of the preceding targets' velocities (experiments 4 and 5).

4.4 Experiment 2: target position does not explain the effects

One could argue that the difference in the influence of target velocity in the initial movement direction was an artefact caused by the fact that in experiment 1 most fast targets were more to the right than most slow targets. This was so for the entire duration of the hand's movement (Fig. 4.2). In this experiment we want to rule out this possibility by presenting the targets on more positions.

4.4.1 Method

Four targets of 6 cm/s and four of 12 cm/s were each presented on ten trials. The targets of the same velocity appeared at different positions, 1.5 cm apart, in such a way that after 250 ms each 6 cm/s target had the same position as one of the 12 cm/s targets. Further methods and analysis were the same as in experiment 1. Twelve volunteers took part in this experiment.

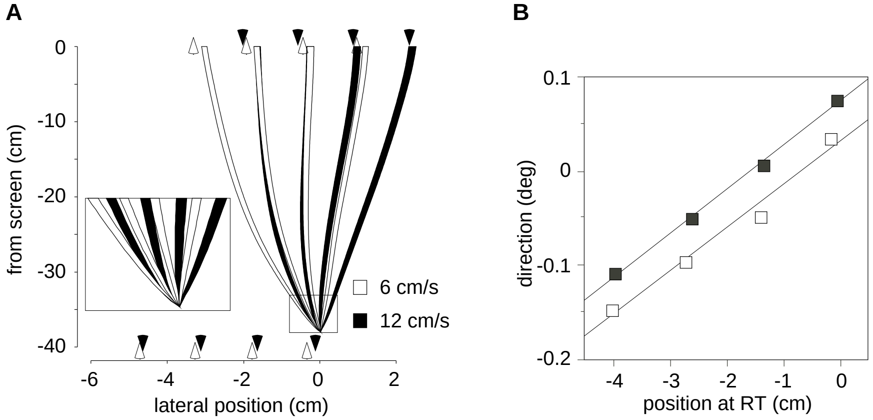

Figure 4.5. Panel A: Average paths of the rod in experiment 2 for four targets of 6 cm/s (white) and four of 12 cm/s (black). See Figure 4.3A for further explanation. **Panel B:** The relation between the target's average position at the RT and the average initial movement direction. 6 cm/s: slope = 0.046°/cm, R2 = 0.98; 12 cm/s: slope = 0.047°/cm, R2 = 0.99.

4.4.2 Results and conclusion

The RT and MT are given in Table 4.2. Figure 4.5A shows that target velocity did influence the initial movement direction towards 6 cm/s targets relative to 12 cm/s targets, though not as much as in experiment 1. The initial adjustment between 6 and 12 cm/s was –3.9 cm/s and was significantly below zero. We will come back to this result later (section 4.7.3).

Figure 4.5 also shows that there was no difference in the effect of velocity between left and right targets. This means that the influence of the targets' velocity on the direction of the rod's movement was constant for the range of target positions that we used in our experiments. We can conclude that in experiment 1 the fact that the slowest targets were hit differently than the faster ones was not due to the difference in the targets' average positions.

4.5 Experiment 3: relative velocity differences did not make the slowest targets 'pop out'

In experiment 1, the targets' velocities differed by 6 cm/s, so the *relative velocity difference* between the fastest targets was smaller than that between the slowest targets. This may have helped the subjects to distinguish the slowest targets as a separate class. Such a strategy would not be the same as using the slowest targets' correctly perceived velocity, but rather one of making an exception for how to hit the most deviant targets.

In the following experiment targets of intermediate velocities were added, so the relative velocity difference between the slowest targets and the next slowest targets was smaller. Moreover, there were more different velocities, which made "the slowest targets" less conspicuous. We hypothesise that adding these intermediate velocities should not interfere with the movements made to 6, 12 and 18 cm/s targets. For these velocities, the qualitative and quantitative results should be equal to those of experiment 1. If, on the other hand, our hypothesis is wrong, the initial adjustment between 6 and 12 cm/s should be closer to zero, and the trajectories towards 6 cm/s targets should start in the same direction as the faster targets with the same position at the RT.

4.5.1 Method

In this experiment the seven conditions of experiment 1 (Figure 4.2), were combined with two conditions with targets of 9 and 15 cm/s. The 9 and 15 cm/s targets each appeared at positions that made them reach the same position as the central 12 cm/s target after 250 ms. In 30 of the trials targets moved at 12 cm/s. Targets with velocities of 6, 9, 15 and 18 cm/s were each presented in 20 trials. Twelve volunteers took part in this experiment.

4.5.2 Results

Figure 4.6A shows that the average paths towards the 6, 12 and 18 cm/s targets were very similar to those in experiment 1. This means that the initial direction did not depend on the number of intermediate target velocities. Figure 4.6B confirms that the initial direction accounted for the velocity difference between the 6 and 12 cm/s targets. For none of the velocities was the initial adjustment significantly below zero (for 6 and 9 cm/s: $P = .08$ and $P = .10$ respectively). However, for both 6 and 9 cm/s targets the initial adjustment was almost exactly as predicted if velocity information was accounted for. The RT and MT are given in Table 4.2.

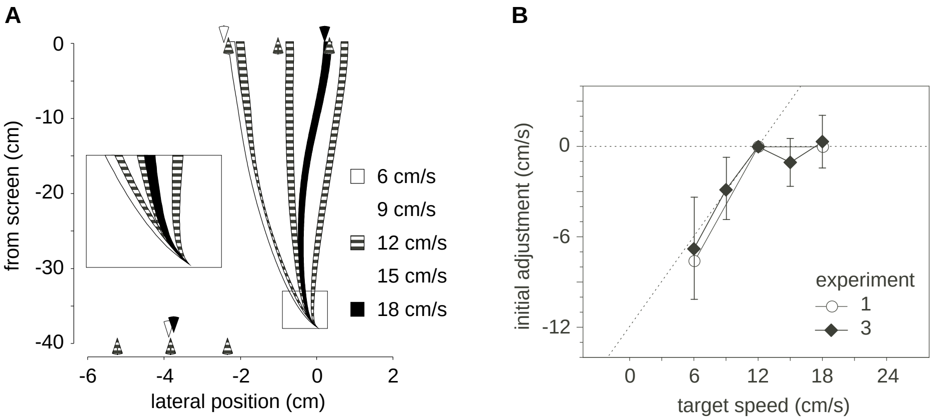

Figure 4.6. Panel A: Average paths of the rod in experiment 3. Note that the paths to one of the 6 and one of the 18 cm/s targets are not shown. **Panel B:** The initial adjustment with respect to 12 cm/s targets (filled symbols). The initial adjustment is not significantly below zero for 6 and 9 cm/s targets, and not significantly above zero for 15 and 18 cm/s targets. See Figure 4.3 for further explanation.

4.5.3 Discussion

The results confirm the hypothesis. The path towards the 6 cm/s target clearly started in the same direction as the left 12 cm/s target. Also, the initial adjustment was –6 cm/s, which is the value that is expected if velocity information is used optimally. It is a bit surprising though that the initial adjustment with 6 cm/s targets was not significantly below zero. In the present experiment there were fewer 12 cm/s targets (30 compared to 40 in experiment 1) and fewer subjects (12 compared to 13 in experiment 1), but these differences cannot explain the between-subject SE being twice as large.

4.6 Experiment 4 and 5: the influence of low and high velocities

In the first experiment, the rod's initial movement direction was influenced by the velocity of 6 cm/s targets relative to 12 cm/s, whereas it was not influenced by the velocity of 18 cm/s targets relative to 12 cm/s. With experiment 3 we showed that this was not caused by the relative velocity difference between 6 and 12 cm/s being larger that that between 12 and 18 cm/s. The alternative hypothesis, that we will test in experiments 4 and 5, is that there is an absolute limit to the velocity that is used by the subjects to plan the initial movement direction. To test this, we repeated experiment 1 two times: once with all targets 6 cm/s slower (experiment 4) and once with all targets 6 cm/s faster (experiment 5). If the hypothesis is right, the initial adjustment between the slowest targets in experiment 1 (6 and 12 cm/s) and 4 (0 and 6 cm/s) should be the same. Also, the initial adjustment between the fastest targets in experiment 1 (12 and 18 cm/s) and 5 (18 and 24 cm/s) should be zero.

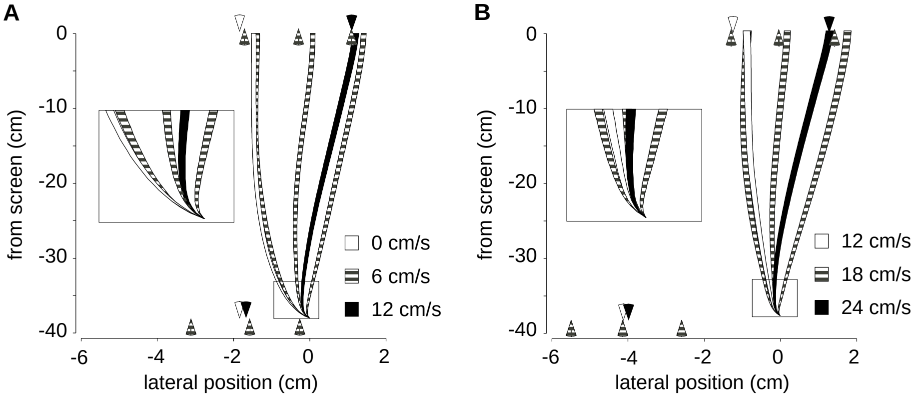

Figure 4.7. Average paths of the rod in experiment 4 (**Panel A**) and experiment 5 (**panel B**). Note that the paths to only one of the slowest targets and one of the fastest targets and all intermediate targets are shown. See Figure 4.3A for further explanation.

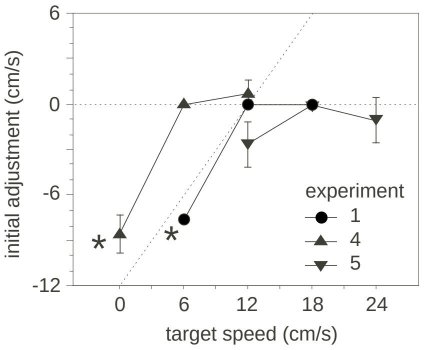

Figure 4.8. The initial adjustment for experiments 1, 4 and 5, each time calculated with respect to the targets of intermediate velocity (respectively 12, 6 and 18 cm/s). * initial adjustment is significantly < 0. See Figure 4.3B for further explanation.

4.6.1 Methods and results of experiment 4

The targets were as in experiment 1, but with velocities of 0, 6 and 12 cm/s. With respect to experiment 1, all targets appeared 3.5 cm more to the right. Fourteen volunteers took part in this experiment.

In experiment 4, the positions of the targets when hit and the relative positions at the RT were very similar to those in experiment 1 (compare arrowheads in Figures 3A and 7A).

The average path towards the stationary target (Figure 4.7A) almost coincided with the path towards the 6 cm/s target that had a similar position when hit. The path towards the 12 cm/s target, however, started in the same direction as that towards the central target of 6 cm/s (which was at a similar position at the RT, Table 4.2). The initial adjustment between 0 and 6 cm/s (Figure 4.8) was significantly below zero (P = .0003). Between 12 and 6 cm/s the initial adjustment was almost zero (P = .47). Thus, the qualitative and quantitative methods gave the same result.

4.6.2 Methods and results of experiment 5

The targets were as in experiment 1. However, all targets appeared 2 cm more to the left, and moved at 12, 18 or 24 cm/s. The same fourteen subjects of experiment 4 took part in experiment 5. One of them was excluded because he did not reveal a consistent relation between target position and initial movement direction.

The average path towards the shown 24 cm/s target (Figure 4.7B, black curve) started in the same direction as that towards the middle 18 cm/s target (middle striped curve). For these two targets, the positions coincided at the RT (Table 4.2; see arrow heads). This means that the rod's initial movement direction was not correlated with the difference in velocity between 18 and 24 cm/s targets.

The left and the central 18 cm/s targets (arrowheads in Figure 4.7B) had the same position as the 12 cm/s target at the RT and the time of the hit respectively. The path towards the 12 cm/s target started in a direction in between these targets. The initial adjustment (Figure 4.8) between 12 and 18 cm/s and that between 24 and18 cm/s did not differ significantly from zero (P = .17 and P = .62 respectively). The initial adjustment at 12 cm/s was on average –2.4 cm/s, less than half the difference between 12 and 18 cm/s. Thus, the qualitative and quantitative methods gave the same result.

4.6.3 Discussion

The hypothesis is confirmed. The initial adjustment between 0 and 6 cm/s (experiment 4) was the same as between 6 and 12 cm/s in experiment 1. As for the initial movement direction, stationary targets are thus not a special case. Also, the initial adjustment was zero between 18 and 12 cm/s (experiment 1) as well as between 24 and 18 cm/s.

Note that the initial adjustment between 0 and 6 (experiment 4) and that between 6 and 12 (experiment 1) were almost the same (respectively –7.6 and –8.6 cm/s), but that both were below –6 cm/s (the value expected with complete adjustment). This is not too surprising because the initial adjustment was based on the remainder of the movement time, whereas the initial movement direction was calculated after the first 2.5 cm of movement. The short (68 ms) movement history partially influences the direction of the movement after 2.5 cm, so the remaining MT may effectively be an underestimation. Another possible explanation will be given in the General discussion.

The hypothesis was a minimal one though. We still have to explain the values for the initial adjustment between 12 and 6 cm/s (experiment 4) and between 12 and 18 cm/s (experiment 5). If there is indeed a sharp distinction between the influence of low and high target velocity on the hand's initial movement direction, the values that one will find for the initial adjustment will obviously depend on the transitional velocity. In experiment 1 we showed that the hand's initial movement direction depends strongly on the velocity of the preceding target if the present target is a fast one. Therefore, on average the initial movement direction towards fast targets (velocity > transitional velocity), will be the same as that towards a target that moves at the transitional velocity. Accordingly, the initial adjustment between a velocity above and a velocity below the transitional velocity will be the same as that between the lower velocity and the average velocity in an experiment.

In Figure 4.8, the initial adjustment was calculated with respect to the average target velocity in each experiment. The transitional velocity should thus be above 6 cm/s (experiment 1). The transitional velocity should also be below 18 cm/s (experiment 1). The initial adjustment between 12 and 6 cm/s (experiment 4) was positive, whereas that between 12 and 18 cm/s (experiment 5) was negative (these values did not differ significantly: unpaired t-test, $P>0.1$). Summing up, the transitional velocity should be just around 12 cm/s. Given the fact that the data were averaged over 14 subjects and that the subjects were free to position and move their head, the transition is remarkably sharp.

A transitional velocity of 12 cm/s is also in agreement with the results of experiment 2 and 3. In experiment 2 the average velocity was 9 cm/s so one would expect the initial adjustment between 6 and 12 cm/s (–3.5 cm/s) to be half the value in experiment 1 (i.e. $0.5*-7.5 = -3.7$ cm/s). Also, the values for the initial adjustment in experiment 3 agree remarkably well with those for experiment 1, and the value at 9 cm/s is almost exactly half the value at 6 cm/s.

4.7 Experiment 6: combining experiments 1 and 4

In the preceding experiment we proposed that the velocity of targets slower than about 12 cm/s does influence the hand’s initial movement direction proportional to the target’s velocity, but not that of targets of 12 cm/s and faster. In the latter case, the initial movement direction is on average as if the target’s velocity is the average of the experiment. This hypothesis is in agreement with the hand’s initial movement direction of experiments 1-5.

However, in the preceding experiments, the range of velocities was always small. A special feature of the hypothesis is that it predicts the large difference in initial adjustment between 6 and 12 cm/s between experiments 1 and 4 (Figure 4.8). For an experiment that combines the velocities of experiments 1 and 4 (i.e. 0, 6, 12 and 18 cm/s), the hypothesis predicts that the initial adjustment between 0 and 6 cm/s will be as in experiment 4. It also predicts zero for the initial adjustment between 12 and 18 cm/s, whereas it predicts the initial adjustment between 6 and 12 cm/s to be equal to the difference between 6 and the average velocity in the experiment.

4.7.1 Method

In experiment 6 we used the seven conditions of experiment 1 (Figure 4.2), but in addition there were three conditions with stationary targets. The stationary targets appeared at one of the three positions that the 12 cm/s targets reached after 250 ms. Thus there were ten conditions, that each consisted of 10 trials: three conditions with 0 cm/s and with 12 cm/s targets, and two with 6 cm/s and with 18 cm/s targets. Twelve volunteers took part in this experiment. One of them was excluded because he did not reveal a consistent relation between target position and initial movement direction.

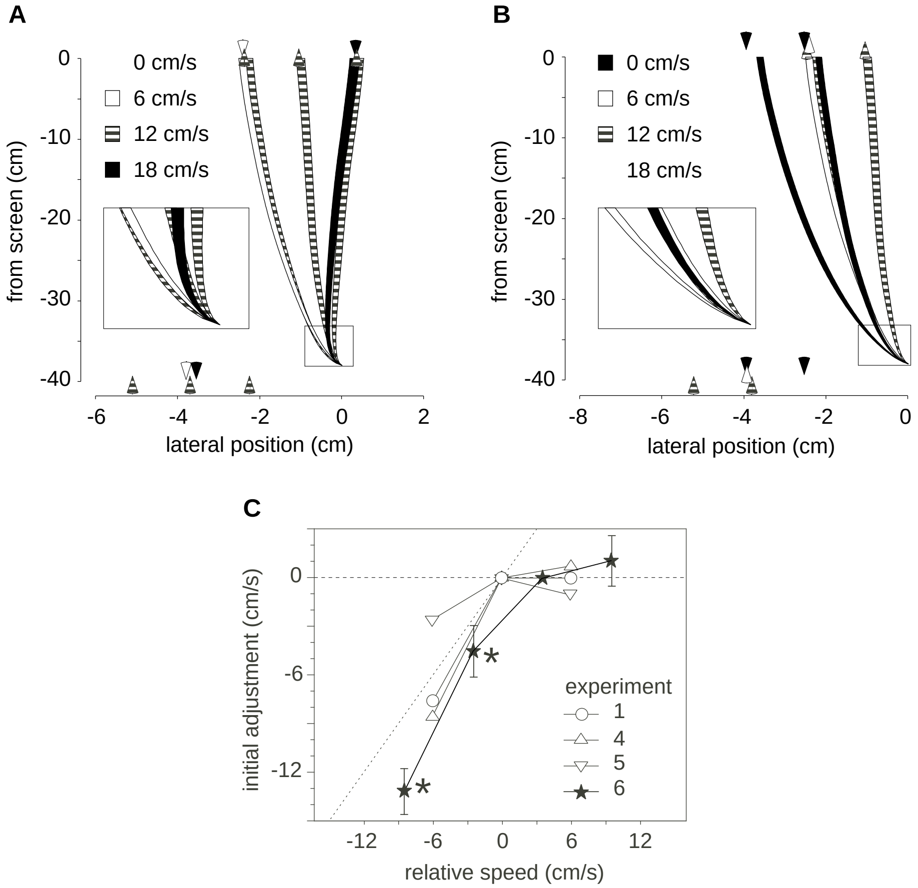

Figure 4.9. Panels A, B: Average paths of the rod in experiment 6. **Panel A:** Paths for the three targets of 12 cm/s (striped), one of 6 cm/s (white) and 18 cm/s (black). **Panel B:** Paths for the middle and right stationary targets (black), for the right 6 cm/s target (white) and for the left and middle 12 cm/s targets (striped). Note that just one target of the middle velocity (6 cm/s) is shown, in contrast to panel A and Figure 4.3. **Panel C:** The initial adjustment as a function of target velocity with respect to the average velocity. The initial adjustment was calculated with respect to the average velocity in experiments 1, 4 and 5, and with respect to 12 cm/s in experiment 6. The initial adjustment was significantly below zero for 0 and 6 cm/s targets, and not significantly above zero for 18 cm/s targets. See Figure 4.3 for further explanation.

4.7.2 Results

The path towards the 18 cm/s target shown in Figure 4.9A clearly started in a direction that corresponds with the target's position at the RT (Table 4.2). The path towards the 6 cm/s target (Figure 4.9A) started in a direction in between the left and middle 12 cm/s targets. Figure 4.9B shows a 0, 6 and 12 cm/s target that on average were hit at the same position. In addition it shows two paths towards targets hit at different positions. The paths towards the targets that were hit at the same position all started in the same direction.

In Figure 4.9C we displayed the initial adjustment in a slightly different way than we did in the preceding experiments. This, the initial adjustment is displayed with respect to the average velocity (i.e. respectively 12, 6, 18 and 8.4 cm/s in experiment 1, 4, 5, and 6). The hypothesis predicts that the initial adjustments with respect to the average velocity is zero for the velocities of 12 cm/s and higher (in Figure 4.9C for velocities above the average velocity and in addition: for 12 cm/s in experiment 5). The other data points are predicted to lie on a diagonal line through the origin with a slope of a little more than 1 (see discussion of experiment 5).

The initial adjustment in experiment 6 agrees well with the hypothesis. The initial adjustment between 0 and 12 cm/s and between 6 and 12 cm/s are significantly below zero (respectively –13.2, $P < .0001$ and –4.6, $P = .0017$) and lie on a diagonal line through the average velocity (= 8.4 cm/s; slope = 1.4). The initial adjustment between 18 and 12 cm/s (1.0 cm/s) did not differ significantly from zero ($P = .59$).

4.7.3 Discussion

The results of experiment 6 are in agreement with the hypothesis. For clarity, the results of experiments 2 and 3 were not plotted in Figure 4.9C. Inspection of the values found for these experiments shows, that they fit well in the range of the other experiments. The initial adjustments of experiment 3 were very similar to those of experiment 1. The initial adjustment in experiment 2 was –3.9 cm/s, and the average velocity 9 cm/s. The point for 12 cm/s targets would get zero initial adjustment, so the point for 6 cm/s targets would be at –3, –3.9 cm/s in Figure 4.9.

With slow targets, the paths towards targets that were hit at the same position overlapped (Figure 4.9B) whereas with fast targets, the paths towards targets with the same position at the RT started in the same direction (inset in Figure 4.9A). Likewise, the initial adjustment was as predicted by the hypothesis. In experiments 1 and 4 the slope of the diagonal line through the lowest velocity (6 and 0 cm/s) was 1.3 and 1.4 respectively. In experiment 5 we gave as possible explanation, that the initial movement direction (after 2.5 cm ≡ 68 ms) reflects the direction of the movement until that time, whereas in the initial adjustment we used the remainder of the movement time (equation (6)). A slope of 1 would have been obtained from a movement time of 220 ms, which is close to the average movement time in the three experiments. Another possible explanation will be given in the General discussion.

4.8 General discussion

The velocity of fast targets did not influence the initial movement direction. Note that it is well possible though, that later in the hitting movement target velocity did influence the direction of the hand. This cannot be answered from the data of this study, because later in the movement, targets of different velocities also have different positions. In addition, later in the movement the direction of the hand's movement depends partly on what happened earlier in the movement. That means that we cannot be sure whether differences in the movement direction later in the movement are due to differences in target position only or to differences in target velocity as well. It is known however, that the target's velocity continuously influences on the hand's velocity (Brouwer et al., 2000; Smeets et al., 1998; McLeod, 1987). Van Donkelaar et al. (1992) used an interception task similar to ours. In one of their experiments, the RT was increased by using a go-signal. The initial direction of the hand's paths of these delayed interceptions was stronger correlated to the targets' velocity. Thus, there are data that suggest that information about the target's velocity is used continuously and that it can have an influence later in a movement.

4.8.1 High velocity may take longer to judge

The finding that adjustment to velocity occurs when intercepting slow targets, but not when intercepting fast ones, needs an explanation. Ignoring the motion has larger consequences for fast targets than for slow ones. Moreover, if the limited time before the rod starts to move (the RT) is long enough to take the velocity of slow targets into account, this time should also be long enough for fast targets. Even more so, if we consider that high velocities take less time to detect than low velocities (Tynan & Sekuler, 1982; van Doorn & Koenderink, 1982). A possible explanation is that the initial movement direction is not influenced by the velocity of fast targets because *judging* the velocity (rather than *detecting* motion) may take longer for high velocities.

A similar effect has been found for smooth pursuit eye movements. The initiation of smooth pursuit eye movements to targets of various velocities is less correlated to the target's velocity if the target moves fast (more than 10-20 °/s) than if it moves more slowly (Carl & Gellman, 1987; Kao & Morrow, 1994). For fast targets smooth pursuit, initiation of the eye movement is more strongly correlated with the velocity of the previous target (Kao & Morrow, 1994). Thus the asymmetry in the use of velocity information for fast and for slow targets is not specific for interception.

This raises the possibility that it is due to high velocities generally taking longer to judge than low velocities. In the experiments of the present study, the subjects were looking at a stationary structured background when the target appeared, so the eyes were stationary. This means that at first, the velocity has to be judged from retinal information. Later, the eyes will follow the target and then the target's velocity should be judged from extraretinal information (the eyes' rotation) as well. There is evidence suggesting that humans have two independent mechanisms for detecting slow and fast retinal motion (Verstraten, van der Smagt & van de Grind, 1998). The transition between the dominance of these low- and high velocity detection mechanisms differed between subjects, but was around 10°/s in their study. It could well be that the mechanism for high velocity motion detection needs longer to *judge* the velocity.

4.8.2 Target detection, target position and target velocity are processed independently

Above we reasoned that the speed of a fast target takes *longer* to judge than that of a slow target. However, in all experiments, the RT was *shorter* for fast targets than for slow ones. This is an inefficient control strategy. The relation between the RT and the target's velocity was the same as that between the detection time of movement on a stationary background (van den Berg & van de Grind, 1989). Thus, if we could subtract the detection time from the RT, there would probably be no velocity dependency left. The detection of the target and the target's velocity appear to be processed independently for otherwise one would expect a longer RT with faster targets.

In the discussion of experiment 1 we mentioned an experiment by van Donkelaar et al. (1992) where the reaction time was decreased, but not the time that paths towards targets of different position and velocity started to go in different directions. Also, in our own experiments we observed that some of the subjects displayed such behaviour without any instruction to do so. These subjects had the shortest reaction times though the time when the paths towards targets at different position went in different directions was not notably different. These observations show that target detection and the target's position are also processed independently.

Finally, in the present study we have shown that with fast targets, the direction of the hand's movement (after moving 2,5 cm towards the screen) reflects the targets' difference in position, but not the difference in velocity, whereas with slow targets it does. This shows that even the target's position and the target's velocity are processed independently.

The independent processing has implications. Firstly, it implies that the subjects did not predict the position where they will hit a moving target. This means that the relation between the initial adjustment and the target velocity is not necessarily 1:1, because the initial adjustment was scaled on the basis of the influence of the targets' position. Indeed, the relation between target velocity and the initial adjustment was steeper than 1 (Figure 4.9C).

The findings may also have implications for other studies. In models for catching (Lee, 1976; Rushton & Wann, 1999) and for interception (Lee et al., 2001; Michaels et al., 2001) it has often been proposed that position and velocity information are processed together to control the movement. This appears incompatible with the independent processing of position and velocity that we observed. Moreover, there are models of catching (McLeod & Dienes, 1993), interception (Lenoir et al., 1999; de Lussanet et al., in preparation) and of grasping (Zaal et al., 1999) in which position and velocity of moving targets are treated as independent sources of information.

4.8.3 Relation with earlier studies

In the Introduction we stated that previous literature does not agree on whether target velocity influences initial movement direction. Now that we know that only low velocities influence the initial movement direction, this disagreement is understandable.

Brenner and Smeets (1996) reanalysed the data from Smeets and Brenner (1995, see section above). They did find an effect of target velocity for stationary targets (they treated interceptive movements towards stationary targets as a different group). For moving targets however, they found that the initial direction was independent of target velocity. This was presumably because they tested over all non-zero velocities (6, 9, 12, 15 and 18 cm/s) at once. They could only have found an effect for the two lowest velocities. In our present experiment 6 (of which the range of target velocities matches that in Brenner & Smeets, 1996), we would not have found a significant effect if we had tested over all non-zero velocities.

Van Thiel, Meulenbroek, Hulstijn and Steenbergen (2000) used the same measure as Brenner and Smeets (1996) for interceptive movements. They did find a clear effect of target velocity on the initial movement direction (0 cm/s not included). There are two explanations for the apparent discrepancy. The first is that they only used slow targets of 0, 6, 9 and 12 cm/s. This means that for most of their targets there should be an influence of target velocity. The second reason is that Van Thiel et al. found the significant effect over the data of healthy and hemiplegic subjects together. The effect was most prominent in the patients. For movements by healthy subjects hitting with their preferred hand, the effect appears to be about the same size as in Brenner and Smeets (1996, comparing the same velocities). It seems surprising that hemiplegic patients make better use of the target’s velocity than healthy subjects do. A possible explanation is that they need to use more information in order to compensate for their impaired co-ordination. The patients’ RTs were on average 112 ms longer, which is consistent with the suggestion that velocity information becomes available later. Apparently, in healthy subjects the control mechanisms for guiding the rod to the target are so good that these subjects do not have to increase the RT to be able to use target velocity for intercepting fast targets.

The role of the target’s velocity in the control of fast goal directed movements is complex. As we pointed out in the introduction, the visuomotor delay for target velocity is relatively long compared to the time between target appearance and the screen being hit (~200 ms compared to ~500 ms). We showed in the present study that the target’s velocity is used to control the initial movement direction, but only for the slower targets. With targets faster than about 12 cm/s the velocity of the previous target influenced how far ahead of the target the subjects aimed.

Acknowledgements

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4.10 Appendix

Below we derive the initial adjustment. First we will describe how we estimated the slope of the relation between target position and initial movement direction for each subject. Subsequently we will use this relation to calculate each subject's initial adjustment. The relation between target position and movement direction can only be calculated for targets with the same velocity. Therefore, targets of each velocity appeared at several different positions in all experiments described in the present study. The initial movement direction was calculated from each subject's average paths (one path for each target, see Methods). We used average paths instead of individual movements to reduce variability.

Let N be the number of pairs of targets (in a single experiment) with the same velocity but a different position of appearance. For example, in experiment 1 there were two conditions with 6 cm/s targets, three conditions with 12 cm/s targets and two with 18 cm/s targets. If we number these seven conditions, the $N = 5$ combinations of conditions i, j with equal velocity would be i, j {1 2; 3 4, 3 5, 4 5; 6 7}. Further, let θ_i be the initial direction (with respect to straight ahead) of the rod's average path in condition i, and let x_i be the average target position at that same moment (Figure 4.10A). For each subject we derived a single constant S for the relation between x and θ (Figure 4.10B):

$$S = \frac{1}{N} \sum_{i,j} \frac{x_i - x_j}{\theta_i - \theta_j}. \tag{4.1}$$

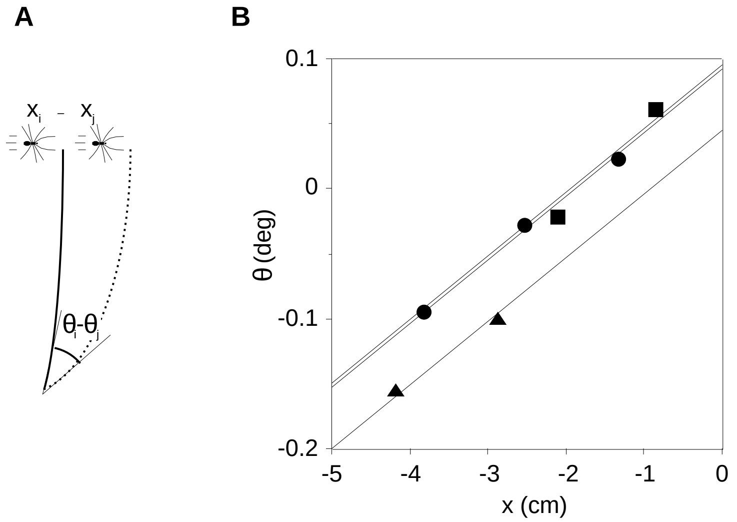

Figure 4.10. Panel A: Schematic view of two average paths with tangents for the initial movement direction, *θ*, and the current lateral position of the targets, *x*. The dotted path will intercept with the grey target (/) and the black path with the black target (/). **Panel B:** x and *θ* for all seven targets of experiment 1. Triangles: 6 cm/s. Circles: 12 cm/s. Squares: 18 cm/s. Lines show the slope *S*. For the sake of the presentation the values were averaged over subjects.

There was a significant (t-test, $\alpha = .05$) positive relationship between target position and initial movement direction in 75 out of a total of 78 experimental sessions (subject-experiment combinations). For the three cases where this relation was not significant, the subject's data were excluded from the analysis (i.e. in experiment 1, 2 and 6 one subject each). This relationship allows us to express differences in initial movement direction as differences in "aiming position" (x^{aim}), even for targets of different velocities. Let *k*, *l* be conditions with targets of different velocity. Then

$$x_k^{aim} - x_l^{aim} = S\ \left(\theta_k - \theta_l\right). \tag{4.2}$$

We assume that the subjects judge the difference in target position ($x_k - x_l$) correctly, so

$$x_k^{aim} - x_l^{aim} = x_k - x_l + \left(x_k^{adj} - x_l^{adj}\right), \tag{4.3}$$

where we interpret x^{adj} as the subject's adjustment to the targets' different velocities. As this adjustment is for target velocity and not target position, $\left(x_k^{adj} - x_l^{adj}\right)$ will be smaller for faster subjects. The reason for that is that with a fast subject, the targets have less time to move and the difference in final position between slow and fast targets will be smaller. We can correct this by dividing the subject's average remaining MT (rMT). By this we get the initial adjustment:

$$v_{k,l}^{adj} = \frac{x_k^{adj} - x_l^{adj}}{rMT}. \tag{4.4}$$

Equation (4.4) can be solved by filling in (4.2) and (4.3):

$$v_{k,l}^{adj} = \frac{S\ \left(\theta_k - \theta_l\right) - \left(x_k - x_l\right)}{rMT}. \tag{4.5}$$

We always present the initial adjustment with respect to the average of the conditions with the reference velocity *L* (three or four, depending on which experiment). So the initial adjustment for condition *k* becomes:

$$v_{k,L}^{adj} = \frac{\left(S\ \theta_k - x_k\right) - \left(S\ \bar{\theta}_L - \bar{x}_L\right)}{rMT}. \tag{4.6}$$

Note that for *S*, θ, *x* and rMT we used the values for each individual subject in the current experiment.

5

The relation between task history and movement strategy[9]

Abstract

In the present study we examine whether subjects hit identical moving targets differently when the task history is different. Twelve subjects each took part in four experimental sessions. Each session consisted of recurring targets that were the same in all sessions, randomly interleaved with context targets that differed per session. We compared the movements that subjects made towards the recurring targets. There were clear influences of the preceding target on the hitting movements within a session, and clear differences between movements towards the same targets between sessions, but the latter differences were not consistently related to the kind of sessions involved. This indicates that influences of task history are limited to the use of information from preceding trials rather than to changes in how information is used (movement strategy).

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[9] This chapter will appear as: de Lussanet, M. H. E.; Smeets, J. B. J. & Brenner, E. The relation between task history and movement strategy. Behavioural Brain Research (in press):

5.1 Introduction

How we move depends on what we want to do: on the task. For example, in a hitting task the hand's movement speed will depend on the instructions for speed and accuracy. However, the speed of the target and even that of the background on which the target moves will also influence the hand's speed (Brouwer, Brenner & Smeets, 2000; Smeets & Brenner, 1995). Many studies address how the task and the experimental conditions influence movements. One aspect of the experimental conditions that has received surprisingly little attention is the influence of task history (the preceding trials) on how a task is performed. This will be the focus of the present study.

In many cases it is conceivable that the task history influences subjects' expectations of the present conditions, and therefore influences which sensory information subjects use -and how-, to execute a movement. If task history thus influences how one moves, the choice of other conditions in an experiment will influence a subject's performance in a given condition. In other words, in a given condition subjects may perform differently in different experiments.

The idea that the task history may play a significant role in movement control is of course not new. For example, Smeets and Brenner (1995) formulated a model in which an important and functional role was proposed for the task history. In their interception task, the perceived target speed did not directly influence the direction in which subjects started to move, though subjects clearly aimed ahead of moving targets. They proposed that subjects base their prediction of where they will hit a moving target depends on the speed of previous targets. Indeed, the speed of the target in the *preceding* trial influences hitting movements (de Lussanet, Smeets & Brenner, 2001, chapter 3).

The above example clarifies what we mean with influences of task history. It is a difference in performance between trials of which the task and the present conditions are the same, but for which the task or the conditions in the preceding trials differ. We will continue with some more examples. Rossetti and Régnier (1995) let subjects point to remembered targets. They found that the distribution of the endpoints of movements to one target position was influenced by the distribution of the positions of the target in the other pointing trials. Thus, the endpoints of individual movements to targets at the same position were influenced by the target's position in preceding movements. In another example, the proportion of preceding trials with visual feedback influenced reaction time and grip opening in prehension movements (Jakobson & Goodale, 1991).

Sometimes an effect of task history was looked for but was not found. Proteau and Masson (1997) did a control experiment to show that there was no influence of task history in their main experiment. They were interested in the influence of unexpectedly moving the background on how subjects move a cursor to a line. In the control experiment the background never moved. Indeed they found no difference between the trials in the control experiment and those in the main experiment in which the background was stationary, even though in the latter the background had sometimes moved in preceding trials.

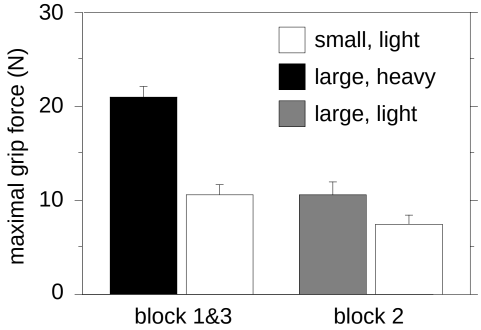

Figure 5.1. An example of the influence of task history (based on Table 1 in Gordon et al., 1991). Subjects lifted small and large boxes in three consecutive blocks. In block 2, the large boxes had the same weight as the small ones (300 g). In the others, the large boxes were heavier (1200 g). The maximal grip force when lifting the small boxes was lower when the large boxes were light (block 2), than when they were heavy (block 1&3). Error bars indicate standard errors of the mean.

Figure 5.1 gives an example of an influence of task history in a study that addressed the use of size cues in picking up objects. The figure is based on data from an experiment by Gordon, Forssberg, Johansson and Westling (1991). Subjects lifted small and large boxes in random order. The weight of the large ones differed between blocks. The interesting result in the context of task history, is that the weight of the *large* boxes influenced how the *small* boxes were lifted, although the small boxes always had the same weight. Grip force was higher for the small boxes when preceding trials included heavy boxes.

An explanation for the subjects' behaviour in three of the studies mentioned above (Rossetti & Régnier, 1995; Jakobson & Goodale, 1991; Gordon et al., 1991), can be sought in two directions. One explanation is that the subjects changed their movement strategy to cope with the different sets of experimental conditions. In this context, movement strategy is how information concerning the present target is used (and which information). This may be influenced by the variability and the mean of the relevant information in the preceding trials. For example, when a source of information is constant (when the same condition is presented in two subsequent trials) there is no need to process the information again. As a consequence, the reaction time for a given condition is shorter when the frequency with which that condition occurred in preceding trials is higher (Miller, 1991).

A second, very different explanation could lead to similar results in the studies mentioned before the above example. Subjects may partly have used information from the preceding trials instead of the most recent information (like in de Lussanet et al., in press). For this second explanation for influences of task history, we can give two more examples. Jaric, Milanovic, Blesic and Latash (1999) studied unidirectional movements with an inertial load on the hand, that sometimes unexpectedly differed from the load in the preceding trial. They compared movements for which the preceding 3-6 trials had been made with either the same load or a different one. Jaric et al. found small differences in the velocity profile of these movements. This means that information about the load in the preceding trials had been used to plan the present movement. A second example of the use from preceding trials are anticipatory movements. Anticipatory eye movements are made for example, when in previous trials a target jump occurred (e.g. Kowler, Martins and Pavel, 1984). These anticipatory eye movements depended on the direction of the jumps on the preceding 3-4 targets. In the same experiment, there was also an effect of the previous trials on the final gaze in the same direction as the anticipatory movements. Naturally, it is very unlikely that the influence on the final direction resulted from a change in movement strategy whereas the anticipatory movements did not.

The two explanations for an influence of task history will lead to effects on different time scales. A change of movement strategy will last longer than a few trials, and should therefore be revealed in differences in the movements for a given condition in different experiments. On the other hand, the use of information from preceding trials is more likely to last just one or a few trials. The studies mentioned above either cannot distinguish between these two explanations, or tested just one of them. The present experiment was designed to find effects in the movement strategy.

We presented different task histories in four separate experimental sessions. Two kinds of targets were identical in all the sessions (*recurring targets*). The movements toward these targets were analysed. The other kinds of targets differed between the sessions (*context targets*). They were presented to vary the task history of the recurring targets. Compared to the Reference session, those of the other sessions either contained more variability in the range of target speeds, or included perturbations of either the hand’s or the target’s position. In order to determine whether subjects hit targets differently with a different task history we compared how they hit recurring targets in each session with how they hit the same targets in the Reference session.

It is conceivable that subjects directly control movement speed and curvature of the movement path during fast interceptive movements. It is at least as likely though, that these aspects of the movement emerge from the control of other parameters, such as stiffness and damping (Smeets & Brenner, 1995), or reflex-gains (Flanagan, Ostry & Feldman, 1993). Different models assume different controlled parameters and therefore will predict different effects of task history on the movement (Jaric, Milanovic, Blesic & Latash, 1999). We chose for a general, model-free approach by analysing various parameters that describe the shape and timing of the movements.

A change of movement strategy can be revealed by comparing trials with recurring targets between the sessions. Within each session the features of the context targets were designed symmetrically around the recurring targets, so that direct influences of the preceding trials would cancel out when comparing between sessions. The latter kind of influences were examined by comparing trials within each session. Thus, we could distinguish between influences of task history that resulted from a change in movement strategy, and those that resulted from the use of information from the preceding trial.

5.2 Materials and methods

5.2.1 Apparatus and stimuli

The visual stimulus was as described by Brenner, Smeets and de Lussanet (1998). Subjects sat in a darkened room in front of a screen (44 × 36 cm) on which the targets were shown. They were to hit each target with a rod (Figure 5.2). The target was an animated spider of realistic shape and natural movements. The screen was tilted 30° backwards (top of the screen farther away from the subject) to make the hitting more comfortable. Images were presented with a graphic workstation at 120 Hz.

The hitting rod (22-cm long; 1.7-cm diameter) had a soft tip and was held with the tip in the direction of the screen, like one would hold a pencil. The position of the hitting rod was measured at 250 Hz with active infrared markers (Optotrak 3010, Northern Digital Inc., Waterloo, Ontario). The position of the tip of the rod was extrapolated from these markers' positions.

In one of the sessions, an electric servomotor (BBC Brown Boveri, MC23AS) provided a controlled, rightward force on the hand. A 3-m long thread (Twaron ripcord 840 ddex Z6, Akzo Nobel, the Netherlands; non-twined to minimise strain, but treated with hairspray instead to prevent fray) connected the rod to a 40 cm lever, mounted on the axle of the motor. The force in the thread (and thus on the rod) was measured by a miniature force transducer (Wazau CMDZ, Berlin, Germany; 0-300 N, weight 6 g) at 6 cm from the rod. The force on the rod was regulated with a proportional regulator. The force built up with a time constant of 12 ms and a static friction of 3% at 2.0 N.

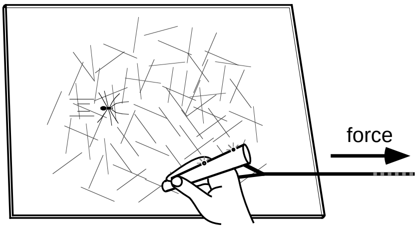

Figure 5.2. Experimental set-up. In one of the sessions, a servomotor generated a rightward force on the rod. The hand started 35-45 cm from the screen.

5.2.2 Subjects

Twelve subjects (including the authors) took part in four different experimental sessions on separate days. Later, twelve subjects performed a control experiment; nine of these subjects (including the authors) had also taken part in the main experiment. Apart from the authors, the subjects were naive with respect to the purpose of the experiments.

5.2.3 Procedure

The experimental sessions lasted about 15 minutes each. Subjects were to hit moving virtual spiders as quickly as possible after they appeared on the screen. They knew that they would obtain points for each hit: more points for faster hits, and no points for misses. At the end of each session subjects saw their score. Neither before nor after an experimental session were they told what kinds of targets were presented (but the perturbations of the hand in one session and of the target's position in another were clearly noticeable).

Before each trial, if necessary, the subject's hand was guided to the starting range by means of messages on the screen. This starting range was located at a distance of 35-45 cm from the screen. Within 0.5-2.0 s of the subject holding his or her hand stationary within this starting range, the target appeared. A trial ended when the hand reached the screen. The target appeared to be squashed if it was hit, or ran away in a direction opposite to a miss.

5.2.4 Sessions

The order of the four sessions in the main experiment was counterbalanced across subjects. The control experiment that we carried out later, consisted of three experimental sessions (on three different days) which were the same as the Reference session in the main experiment (see below). The nine subjects who had also participated in the main experiment did only two sessions in addition to the one which was the Reference session in the main experiment.

In each session the targets were presented in four equal blocks of thirty trials (without intervals between the blocks). Within a block, each of six kinds of targets was presented five times, in random order. The first block of 30 trials was excluded from the analysis in order only to analyse the trials in which the task history is clearly defined.

The sessions were designed to present the subjects with specific task histories. To make the results of the sessions comparable, two kinds of targets were presented in each of the sessions (*recurring targets*), while four other kinds of targets differed between sessions (*context targets*). The movements toward context targets were not analysed but were necessary to give a specific task history to the trials with a recurring target. The recurring targets moved at a speed of 15 cm/s, and they appeared either 8.5 or 4.5 cm to the left of the hand. We will refer to them as 'left recurring target' and 'right recurring target' respectively.

Figure 5.3 summarises the targets' properties in the four sessions (that we will from now on call by the name above each panel). We will use the results of the *Reference* session as a reference for the results of the three other sessions. In this session, the context targets appeared at a range of different lateral positions, but they all moved at the same speed (15 cm/s).

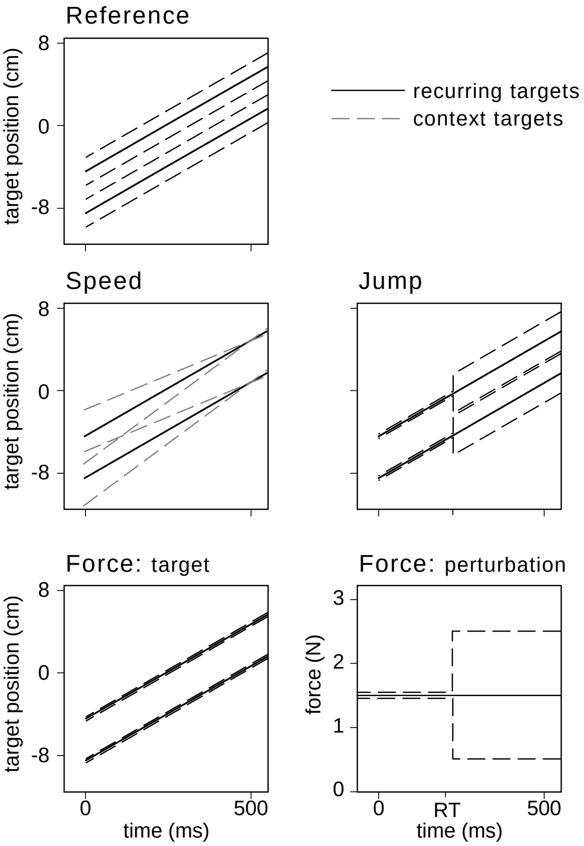

Figure 5.3. Characteristics of the four experimental sessions. *Continuous lines* depict the two kinds of recurring targets; *dashed* lines represent the context targets. The *first four panels* give spider position as a function of time (0 cm is the position on the screen opposite to the starting position of the hand). Targets moved at a constant speed until the screen was hit. The 5th panel presents the force development in the Force session: during the context trials there was a sudden pull on or release of the hand when the hand started to move.

In session *Speed*, the context targets had speeds of 10 and 20 cm/s. In session *Jump* and session *Force*, the context trials were perturbed. In session Jump, context targets jumped leftwards or rightwards when the subject’s hand started to move. In the session *Force*, there was a constant force of 1.5 N to the right on the hitting rod. During the context trials, this force suddenly decreased or increased by 1.0 N when the subject’s hand started to move. We must keep in mind that in session Force, the pre-load itself could affect the subjects’ movements, which of course is not an influence of task history.

5.2.5 Analysis

Of each session, only the 30 recurring targets of the last three blocks (5 targets of each kind per block) were analysed. Out of the 1440 hits towards recurring targets (4 sessions × 12 subjects × 30 trials), 31 were rejected mainly because the markers were invisible to the Optotrak or because the subject was already moving when the target appeared. In the control experiment 13 trials –out of 1080– were rejected for these reasons.

The *position* in the fore-aft direction (perpendicular to the hitting screen) and in the lateral direction were each numerically low-pass filtered without phase shift (Butterworth 4th order, back and forth in time, effective cut off frequency: 20 Hz). Movement initiation was defined as the moment at which the hand's velocity towards the screen exceeded 0.2 m/s. For this, the *velocity* was low-pass filtered (effective cut off frequency: 10 Hz). The exact position and the time of hitting the screen were extrapolated from the last three samples before the screen was reached. The timing of the perturbations (sessions Jump and Force) was obviously computed on-line, and therefore on the unfiltered data.

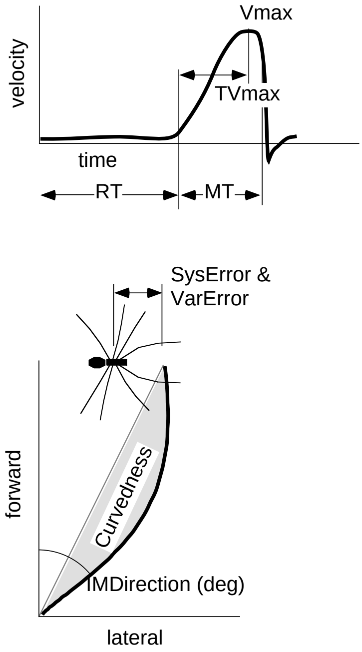

Figure 5.4. The movement parameters. In the analyses we used rTVmax = 100*TVmax/MT.

Figure 5.4 shows the movement parameters that we analysed. The reaction time (*RT*) is the time from the spider's appearance until the hand started to move. The movement time (*MT*) is the time from when the hand started to move until the screen was hit. *Vmax* is the maximal tangential velocity. The *rTVmax* is the time from RT until Vmax, divided by the MT.

The initial movement direction (*IMDirection*) is the angle between the direction perpendicular to the screen, and the line through the hand's starting position and the hand's position 5 cm closer to the screen. The *Curvedness* is the path's average deviation from a straight line between start and end (rightward is positive Curvedness). The systematic error (*SysError*) is the average lateral difference between the centre of the rod and that of the spider when the screen was hit. The variable error (*VarError*) is the standard deviation of this difference. We deliberately chose to include a relatively large number of movement parameters, although this implies that some parameters will be dependent (see section 5.3).

The two kinds of recurring targets differed only in position. Nevertheless, we cannot simply average the movements towards the two because there could be both mirrored and congruent influences of task history. With *congruent* we mean that an influence of task history is in the same direction for both kinds of targets, so that the effect remains visible when the movement parameter is *averaged* over both kinds of recurring targets. This would for instance be the case if the MT would decrease in sessions in which the hand was sometimes unexpectedly pulled away in preceding trials. A *mirror* effect is revealed from the *difference* between the values for a movement parameter in the two kinds of recurring targets. Mirror effects of task history may for example be expected if subjects postponed the use of visual information about the target if it sometimes unexpectedly jumped. In that case, a tendency to start moving straight ahead will increase the IMDirection and the Curvedness for the left recurring target and decrease them for the right ones.

5.3 Statistics

5.3.1 Consistent changes

We first tested how each task history altered hits toward recurring targets (compared to the task history in the Reference session). We averaged the movement parameters for each kind of recurring target, subject and session (15 trials per average). We used paired t-tests to test for congruent- and mirror effects (12 pairs: one for each subject). In each test we compared the influence of a given task history with that in the Reference session. In this way, 48 t-tests were needed (3 task histories, 8 variables, 2 [congruent or mirror] effects).

This is a considerable number of t-tests, so we need to determine whether the number of statistically significant results that we find is above the number that one would expect from chance. As a first approximation, this number follows from the threshold used ($\alpha = .05$). Thus, one expects 5% statistically significant outcomes, even if the task history had no effect whatsoever. However, this is only an approximation because, as we already mentioned, some movement parameters and the related t-tests were dependent. We therefore did the two following controls to estimate the number statistically significant results that we can attribute to chance.

First, we carried out a control experiment in which 12 subjects did the Reference session three times. As the three sessions of this control experiment were of the same type, the number of significant outcomes in the comparison between them is not related to task history. We analysed this experiment 100 times, each time assigning each subject's three control sessions to three arbitrary groups (by this eliminating possible order effects). The same t-tests as described above were carried out between each of the three arbitrary groups of control sessions. From the distribution of the number of significant results in each of the 100 analyses we estimated the 95% limit for the number of chance-based significant results. If the proportion of significant results in our main experiment is larger than this limit, we will consider this as strong evidence for there being an influence of task history.

A second estimate for the limit to the number of chance based statistically significant results was obtained by randomly dividing the sessions from the main experiment into four arbitrary groups in the same manner as we did with the control sessions. We also did this 100 times and computed the 95% limit for the number of significant results that can be attributed to chance.

5.3.2 Inconsistent changes

Apart from the above question of whether the task history had a consistent effect *across subjects*, we also calculated how many *within-subject* changes there were between sessions. This gave us a measure of the variability that was not related to the task history across subjects. For each subject we compared the hits towards recurring targets of each session with those of the same subject's Reference. Unpaired t-tests were used ($\alpha = .05$). For each task history, 168 t-tests were carried out (12 subjects, 7 variables, 2 [congruent or mirror] effects). This measure was not applicable for the VarError, which is not defined for individual trials.

5.3.3 Order related changes

We tried to minimise possible effects related to the order (like learning and fatigue) on our results in two ways. Firstly, the order of performing the kinds of sessions was counterbalanced across the subjects. Secondly, the trials from the first quarter of each experimental session were not analysed. To estimate how much variability was caused by order effects, we estimated the effects of order both within- and between sessions. The kind of session was ignored. For the within session variability we split the 30 analysed trials within each experimental session into the first 15 trials and the last 15 trials. Paired t-tests were performed on the averages of 15 trials. A possible influence of the order of presentation was examined with 56 tests (4 sessions, 7 variables, 2 [congruent or mirror] effects).

To find out whether variability between sessions was caused by systematic differences between earlier and later performed sessions, we used another set of paired t-tests. These tests were calculated on the four sessions by the order in which they were executed (so ignoring the kind of session). There were 6 possible between-session comparisons (8 variables, 2 [congruent or mirror] effects = 96 tests).

5.3.4 Influence of the preceding trial

We examined the effects of using information from previous trials, by testing the influence that the *preceding trial* had on the hitting movements. This was done for sessions Speed, Jump and Force. In each of these sessions we distinguished three groups of preceding targets. In session Speed the three groups were: ‘10 cm/s’, ‘15 cm/s’ and ‘20 cm/s’, in session Jump: ‘no jump’, ‘left jump’ and ‘right jump’ and in session Force: ‘no change’, ‘pull’ and ‘release’. We averaged the movement parameters for each kind of recurring target and each preceding group (6 averages for each subject in each session). The means were calculated from 5 trials on average. This number was variable because the targets appeared in random order.

The subsequent tests that we used were very similar to those used in the analysis of the consistent changes. We used paired t-tests to test for congruent and mirror effects (12 pairs: one for each subject). Each t-test compared the values for two groups of preceding targets. In session Speed, we compared the groups of preceding trials ‘10 cm/s’ and ‘20 cm/s’. In session Jump we compared groups ‘left jump’ and ‘right jump’, and in session Force we compared groups ‘release’ and ‘pull’. In this way, 42 paired t-tests were needed (3 task histories, 7 variables, 2 [congruent or mirror] effects). These were the groups for which we expected the largest effects (based on the literature cited in the Introduction). These were also the comparisons that would cancel out in the test for consistent changes between the sessions.

We estimated the number of chance based statistically significant results in the same manner as before. We repeated the analysis 45 times, with a randomly assigned group number to each of the analysed trials with recurring targets. From the distribution of the number of significant effects we estimated the 95% limit. If the number of significant results in the experiment is larger than this limit, we will consider this as strong evidence for influences of the preceding trial.

5.4 Results

5.4.1 Consistent changes

Figure 5.5 shows the average of and the difference between the values for the two kinds of recurring targets for the eight movement parameters. Only two of the 48 t-tests evaluating the consistency across subjects were statistically significant. We estimated the number of chance-based significant effects from the randomised main experiment and from the randomised control experiment. In both cases, 95% of the randomised tests contained not more than 7.5% significant effects. This means, that the number of statistically significant comparisons in the main experiment would have had to be above 7.5%*48 = 3.6 to attribute any effect to task history. Thus there was no indication of consistent influences of task history across sessions.

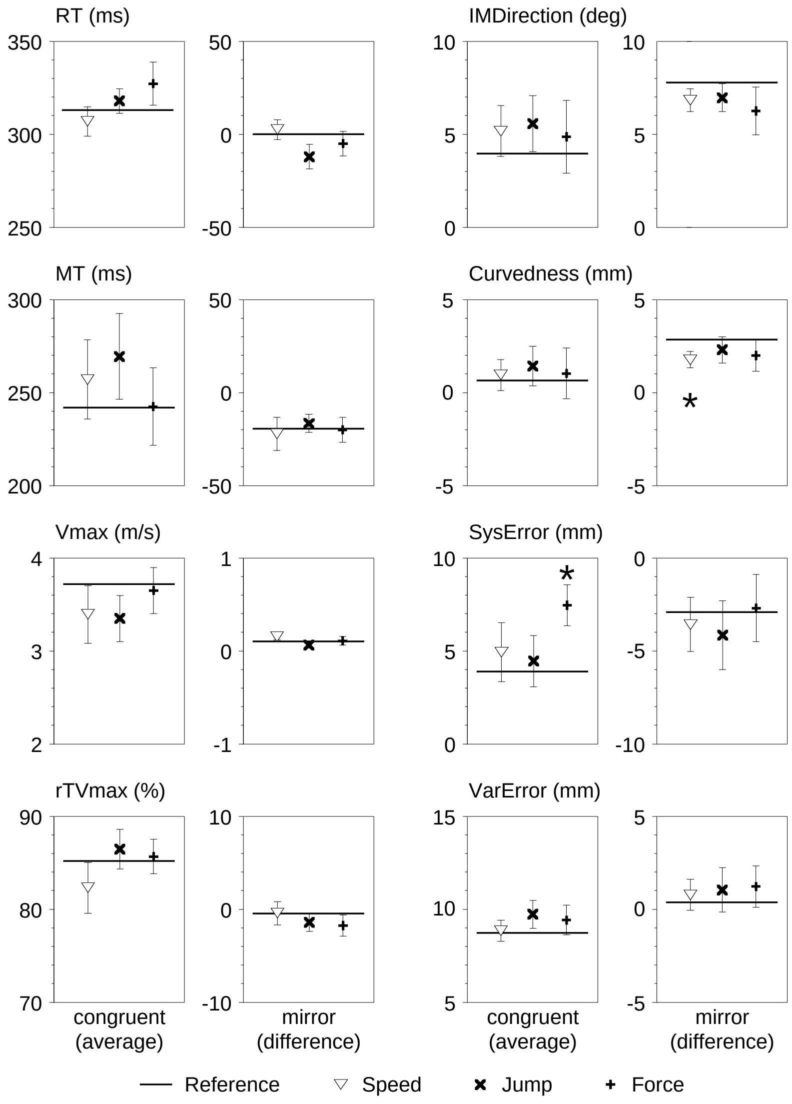

Figure 5.5. Consistent changes: results for the hits towards recurring targets. *Congruent:* Average over the values for the left and right recurring targets. *Mirror:* Difference between the values for the right and left recurring targets. The asterisks (*) indicate values that differ significantly from the Reference (α = .05; paired t-test; significant in Speed: Curvedness and in Force: SysError). Bars are inter-subject standard errors of the difference from the Reference.

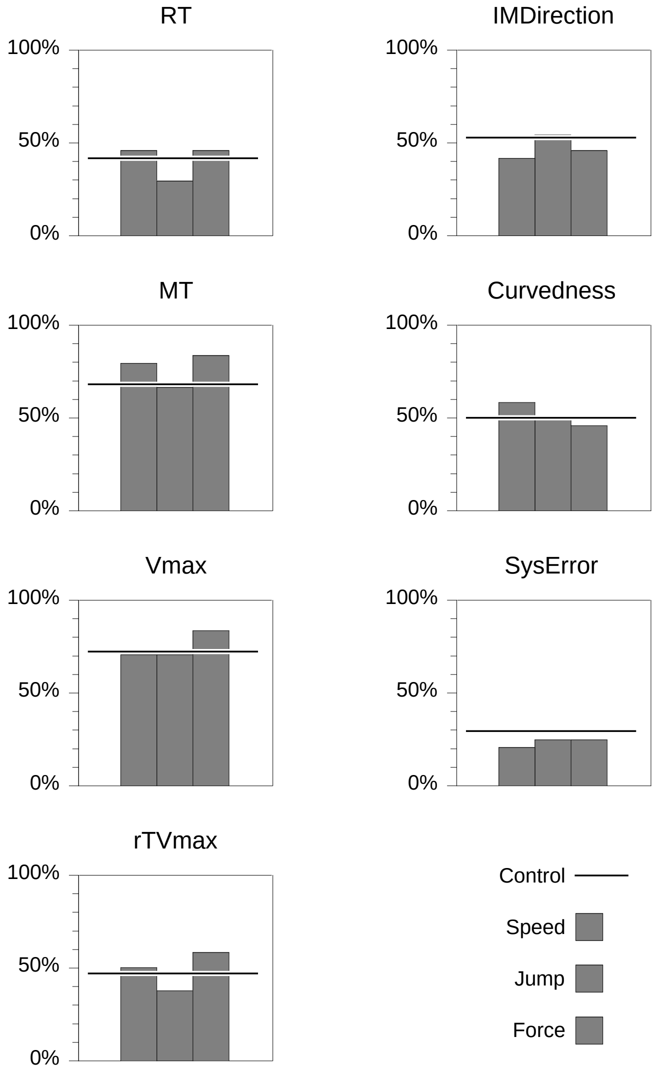

Figure 5.6. Percentage of significant changes between sessions ('inconsistent changes') for individual subjects (unpaired t-tests; $\alpha = .05$). The measure was not applied to the VarError, as it is not defined for individual trials. Bars: comparisons between the Reference session and the three other sessions in the main experiment. Horizontal lines: comparisons between the sessions in the control experiment.

5.4.2 Inconsistent changes

The reason why there was no consistent influence of the task history on the sessions, could be that the subjects did not change their movements between sessions at all. The t-tests evaluating the inconsistent differences between sessions showed that this was not so. In the main experiment, 49% of the tests was statistically significant (51% in the control experiment). Figure 5.6 shows the number of significantly different individual comparisons for the various movement parameters. Figure 5.7 shows the same data averaged over the three sessions and seven parameters, for the 9 subjects that participated in both the main experiment and the control experiment. There are of course differences between the parameters and between the subjects, but a large number of differences between sessions is a consistent feature of all parameters and all subjects in both experiments. The similarity between the number of significant changes for the main experiment and that for the control experiment confirms that the differences are not related to differences in task history.

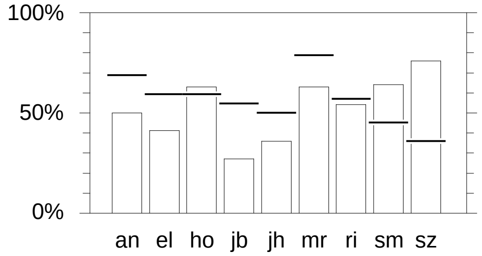

Figure 5.7. Percentage significant changes between sessions ('inconsistent changes') for the nine subjects that participated in both the main experiment and the control experiment (100% = 42 tests). Bars: main experiment. Horizontal lines: control experiment.

5.4.3 Order effects within and between sessions

The order of the sessions was counterbalanced across subjects to prevent order effects (learning, fatigue) from being interpreted as effects of task history. However, possible order effects may have masked the influences of task history. Indeed we did find some order effects, but the proportion of statistically significant tests was small. From the tests on the first and second half of the sessions 8.9% was statistically significant. It is thus possible that there were some within-session order-effects. From the tests comparing earlier and later sessions 6.3% were statistically significant. For the latter test we can use the same estimate for the maximal percentage of chance-based effects as in the test for the consistent changes, i.e. 7.5%. This means that we can conclude that there were no between-session order effects.

5.4.4 Influences of the preceding trial

In the above we did not find any proof of consistent task history related changes between the sessions in fast hitting movements. However, from the literature cited in the Introduction, it is clear that influences from the preceding trial should be present in our data. Table 5.1 summarises the results of this analysis. Out of 42 t-tests, six were statistically significant (14%). We estimated the number of chance-based significant effects from the randomised experimental sessions. A total of 95% of these randomised tests contained 11% or fewer significant effects. We conclude that there were influences of the preceding trial.

Table 5.1. Influences of the preceding trial.

	Speed		Jump		Force	
Variable	difference	P	difference	P	difference	P
RT (ms)	-	-	-	-	-	-
MT (ms)	-	-	-	-	-	-
rTVmax (%)	-	-	-	-	-	-
Vmax (m/s)	-	-	-	-	-	-
IMDirection (deg)	-	-	2.50	0.03	-	-
Curvedness (cm)	0.14	0.04	0.16	0.01	-0.21	0.02
SysError (cm)	-		0.43	0.04	-0.38	0.03

There were only significant congruent effects. The average size of the effect (difference) and the P-values are given for the significant effects. Differences refer to ‘20 cm/s’ – ‘10 cm/s’ (session Speed), ‘right jump’ – ‘left jump’ (session Jump) and ‘pull’ – ‘release’ (session Force), respectively.

5.5 Discussion

We can summarise the results as follows. There were differences between sessions in how subjects moved, but these differences were not related to the differences in task history between the sessions. The only influences of task history that we did find were related to the kind of the preceding target. This means that we only found evidence for the use of information form preceding trials and not for the subjects changing their movement strategy as a result of the task history.

Inherent to our method of looking for influences of the task history in a general way (i.e. without a hypothesis for exactly which effects one expects) it is unlikely to find an influence in the case when there is just one effect. This is even so if this effect would be very large. Figure 5.5 shows however that it is unlikely that there was a single large effect of a consistent influence of task history across sessions in our data. The smaller of the two statistically significant effects was a mirror-effect on the Curvedness in session Speed, while the other was a congruent effect in session Force for the SysError. The magnitude of the first effect hardly differs from the non-significant effects in session Jump and in Session Force, and is therefore unlikely to be more than just statistically significant. The latter effect differs in magnitude clearly from that in session Speed and session Jump, but it is the kind of effect that we expected as a result of the constant pre-load on the hand. It therefore cannot be regarded as an influence of the task history either.

There were many changes in the way the subjects moved in different sessions that were inconsistent across subjects (Figure 5.6). One could argue that two groups of subjects possibly each did change their movement strategy in a consistent way when these two strategies cancelled out each other’s effects. In that case however, one would expect more inconsistent changes in the main experiment than in the control experiment (of which the sessions were the same). The similarity between the number of inconsistent changes between sessions (Figures 6 and 7) shows that this was not the case.

The number of influences from the preceding trial that we found may seem little. The reason for this is that the test for influences of the preceding trial had less power than the test for consistent changes between the sessions, for two reasons. Firstly, the means that were used in the latter test, were calculated from fewer trials (5 instead of 15) and this number varied due to the random order of the trials within a session. In addition, the influences of the preceding trials may last a little longer than just the preceding trial (Kowler et al, 1984), which introduces additional variability. This means that the test for the preceding trial may have underestimated the number of effects. This strengthens our conclusion that there were only influences from the preceding trial, which are not related to changes in movement strategy but only to the use of preceding information.

In contrast to the possible underestimation of the effects from the preceding trial, there is no reason to believe that the number of effects in the comparison for consistent changes between the session types was underestimated. Individual subjects did have many inconsistent changes between the sessions. In addition, we did not find order effects between sessions that could have masked effects of the task history. Therefore, if part of these many changes had been related to consistent influences of the task history, they should have resulted in effects in the test for consistent between-session changes.

What is new in our study is that we were able to distinguish within the same experiment between changes that were related to changes in movement strategy and changes that were due to the use of information from preceding trials. The effects that we found were related to the use of information from the preceding trials. However, the influence of task history in the reaction time study by Miller (1991) showed that task history can affect subjects' movement strategy. The effect that Miller found on the RT was 11 ms. This is about the same as the effect in the RT in session Force (compare Figure 5.5), but here it was not significant. Van Donkelaar et al. (1992) and Brouwer et al. (2000) both did experiments in which targets of different speed had to be intercepted. In both studies these targets were presented either in random order (unpredictable condition) or in clusters in which all targets were of the same speed (predictable condition). In Van Donkelaar et al. the RT was significantly longer in the predictable condition whereas in Brouwer et al., it was not. This discrepancy points in the same direction that our study does: that effects of task history that can be related to differences in movement strategy are very small if present at all. This is in contrast with influences of the preceding trial.

Acknowledgements

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6

Relative damping improves linear mass-spring models of goal-directed movements[10]

Abstract

A limitation of a simple linear mass-spring model in describing goal directed movements is that it generates rather slow movements when the parameters are kept within a realistic range. Does this mean that the control of fast movements cannot be approximated by a linear system? In servo-control theory, it has been proposed that an optimal controller should control movement velocity in addition to position. Instead of explicitly controlling the velocity, we propose to modify a simple linear mass-spring model. We replaced the damping relative to the environment (absolute damping) with damping with respect to the velocity of the equilibrium point (relative damping). This gives the limb a tendency to move as fast as the equilibrium point. We show that such extremely simple models can generate rapid single-joint movements. The resulting maximal movement velocities were almost equal to those of the equilibrium point, which provides a simple mechanism for the control of movement speed. We further show that peculiar experimental results, such as a “N-shaped” equilibrium trajectory and the difficulties to measure damping in dynamic conditions, may result from fitting a model with absolute damping where one with relative damping would be more appropriate. Finally, we show that the model with relative damping can be used to model subtle differences between multi-joint interceptions. The model with relative damping fits the data much better than a version of the model with absolute damping.

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[10] This chapter was submitted to Human Movement Science

6.1 Introduction

The hypothesis of equilibrium point control of posture and movement (Feldman, 1966) proposes that the commands that the brain produces to generate a limb movement do not encode the forces that are needed, but rather task related parameters such as positions or postures of the limb. This feature makes the hypothesis attractive, for it suggests that the brain does not need to perform complex inverse-dynamical computations to generate a movement. The dynamics of the movement arise automatically from the interaction of the mechanics of the limb with the set equilibrium position: the position to which one wants to move.

An important prediction of the hypothesis of equilibrium point control is that the limb's final position is insensitive to perturbations of the limb during the movement. Indeed, the endpoint of a reach with a monkey's unseen arm was insensitive to perturbations that it could not feel because the monkey was deafferented (Bizzi, Accornero, Chapple & Hogan, 1984). Comparable findings have been reported for perturbed movements of healthy human subjects (when they were asked not to intervene voluntarily with the perturbation; Gottlieb, 1994; Shadmehr, Mussa-Ivaldi & Bizzi, 1993; Gribble & Ostry, 2000). When one moves the hand while sitting in a slowly rotating room, coriolis forces act on the arm during the movement, but not during rest (before and after the movement). The equilibrium point hypothesis therefore predicts that unexpected coriolis forces will affect the shape of the movement path but not the end position. When subjects made reaching movement towards remembered targets in a dark, rotating room, the path was perturbed. Nevertheless, at the end of the movement, the final error was negligible as long as subjects did not touch the table surface. In an experiment in which subjects did touch the table surface, the target was missed (Lackner & DiZio, 1994). In the latter case the movements may have been stopped by the table surface before the equilibrium position was reached. This interpretation of the latter experiment is not generally accepted (Lackner & DiZio, 1994; Feldman, Ostry, Levin, Gribble & Mitnitsky, 1998), but it explains why the influence of unexpected coriolis forces can appear to be inconsistent with the equilibrium point hypothesis. Although the equilibrium hypothesis is an elegant description for many movements, there are tasks, such as jumping, exerting a specific force, or adapting to moving in a new kind of force field for which other kinds of models for motor control might be more appropriate.

At present there are a number of equilibrium point models, which all have in common that the moving limb is attracted towards an equilibrium position or posture (e.g. Latash & Gottlieb, 1991; Shadmehr et al., 1993; McIntyre & Bizzi, 1993; St-Onge, Adamovich & Feldman, 1997; Gribble, Ostry, Sanguineti & Laboissière, 1998; Barto, Fagg, Sitkoff & Houk, 1999). The models differ considerably in how they damp the movement. The purpose of damping is to stop the movement without endless oscillations around the equilibrium point.

The damping parameters affect the shape of the movement path and of the velocity profile. Strong damping is needed to limit the extent to which the limb overshoots the target. However, in order to be able to move rapidly, the movement should not be too heavily damped.

In the models mentioned above, this conflict between the damping requirements is solved by making the parameters in the model time- or speed dependent (apart from Flash, 1987, who only modelled slow movements). This was done either by pulse-step control (Barto et al., 1999), by letting stiffness and damping change during the movement (St-Onge et al., 1997), by introducing non-linear muscle properties (Gribble et al., 1998), or by introducing a non-monotonic shift of the equilibrium point (Latash & Gottlieb, 1991). Unfortunately, much of the attractiveness of equilibrium point models is lost by this, because the brain will have to compute some sort of complex inverse dynamics after all (DiZio & Lackner, 1995; Gottlieb, 1998).

In the field of servo control, *velocity feedback* is well known and commonly applied to regulate the speed of movement or to stabilise a system against perturbations. The idea to control velocity in addition to position was also proposed for the control of arm movements (McIntyre & Bizzi, 1993). Schouten, de Vlugt, van der Helm and Brouwn (2001) showed that active velocity feedback plays indeed an important role in the control of posture in the human arm. This solution has been used to model an optimal controller in a model for motor learning (Shadmehr & Mussa-Ivaldi, 1994), but has not had any impact on equilibrium-point models (apart from McIntyre & Bizzi, 1993). Neither were its advantages discussed by critics of equilibrium point control. In the present paper we chose to apply velocity-feedback in the simplest kind of equilibrium-point model, a linear mass-spring model. The advantages of such a very simple model are the few parameters and the comprehensibility of its behaviour. We will show that such models can gain greatly from a modified concept of damping without any extra parameters.

As we saw above, the damping in the existing equilibrium-point models usually counteracts the limb's (or joint's) velocity, as if the limb moves through a basin of water or oil. Indeed, muscles do have velocity-dependent properties (Hill, 1938). However, two underlying concepts of the equilibrium-point hypothesis are that reflexes contribute significantly to the mechanical behaviour of the motor system, and that reflexes function relative to the desired movement (Feldman, 1966, 1986). Modelling damping relative to the *environment* (joint) is inconsistent with this concept. An alternative is a damping term that acts on the hand's movement with respect to the *desired movement velocity* (the velocity of the equilibrium point). We will call the first (conventional) kind *absolute damping* and the latter *relative damping*. This relative damping gives the limb a tendency to move at the same velocity as the equilibrium point, and can be understood as damping with respect to the equilibrium point. Both kinds of damping are the same when the equilibrium point is stationary, but they differ when the equilibrium point moves.

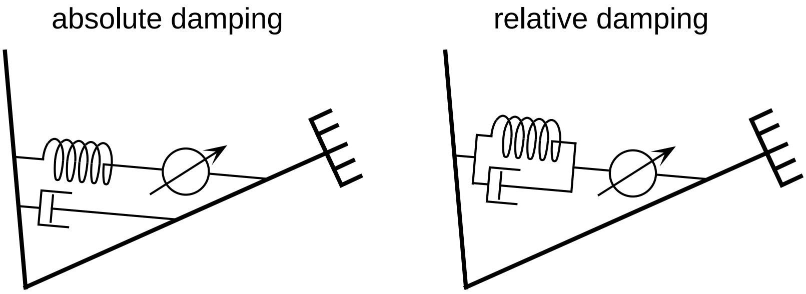

Figure 6.1. Illustration of a simple elbow model with the two kinds of damping. Drawn are an upper arm and a forearm with hand. Each model contains linear stiffness (the spring), linear viscous damping (the dash pot) and is powered through moving the equilibrium point (the circle with arrow).

We will evaluate the performance of models with absolute and relative damping by modelling the movement of a single-joint human arm (Figure 6.1). This kind of movement has frequently been used to test mass-spring models. Beside being used to model whole movements, linear models can also be applied to a limited range of a non-linear system (Bennett, Hollerbach, Xu & Hunter, 1992). As a second test, we will therefore model differences between rapid multi-joint interceptive movements. For this test we use Smeets and Brenner's (1995a) model to compare the effect of absolute and relative damping in these movements.

6.2 Models with absolute and with relative damping

We will now derive the equations for the mass spring models. Let $\underline{q(t)}$ be the equilibrium position and *x(t)* be the hand's position (with either metric or angular units). Their time derivatives, velocity and acceleration, will be represented with one or two dots over the variable. The differential equation of a linear mass spring system with viscous damping and parameters mass (*M*), damping (*B*) and stiffness (*K*) is for absolute damping

$$M\ddot{x} + B\ \dot{x} + K\ (x - q) = 0. \tag{6.1}$$

and for relative damping

$$M\ddot{x} + B\ (\dot{x} - \dot{q}) + K\ (x - q) = 0. \tag{6.2}$$

We are only interested in systems with an *attracting* equilibrium point, so $K > 0$ (and $M > 0$). The number of constant parameters is redundant, which means that each of the equations can be written as a function of just two constant parameters. This can be achieved by dividing all parameters by *M* and defining new constants, *b* and *k* (respectively with units s^{-1} and s^{-2}). This yields for absolute damping

$$\ddot{x} + b\ \dot{x} + k\ (x - q) = 0 \tag{6.3}$$

and for relative damping

$$\ddot{x} + b\ (\dot{x} - \dot{q}) + k\ (x - q) = 0 \tag{6.4}$$

We need the solution for (6.3) and (6.4) for an equilibrium that moves at a constant velocity $q(t) = q_0 + \dot{q}t$. This solution can be found in many textbooks on mathematics or physics. With boundary conditions $x(0) = x_0$ and $\dot{x}(0) = \dot{x}_0$, the solution can be written for the *underdamped* case (i.e. $k > b^2/4$) as

$$x = \dot{q}t + \hat{q} - \mathrm{e}^{-t/\tau}\left((\hat{q} - x_0)\cos(\omega t) + \left(\frac{\dot{q} - \dot{x}_0}{\omega} + \frac{\hat{q} - x_0}{\omega\tau}\right)\sin(\omega t)\right) \tag{6.5a}$$

where $\tau = 2/b$ and $\omega = \sqrt{k - \frac{1}{4}b^2}$, and for the *overdamped* case (i.e. $k < b^2/4$) as

$$\begin{aligned} x = \dot{q}t + \hat{q} - &\frac{\tau_1}{\tau_1 - \tau_2}\ \left((\dot{q} - \dot{x}_0)\tau_2 + \hat{q} - x_0\right)\ \mathrm{e}^{-t/\tau_1} \\ &+ \frac{\tau_1}{\tau_1 - \tau_2}\ \left((\dot{q} - \dot{x}_0)\tau_1 + \hat{q} - x_0\right)\ \mathrm{e}^{-t/\tau_2} \end{aligned} \tag{6.5b}$$

where $1/\tau_1 = \frac{1}{2}b + \sqrt{\frac{1}{4}b^2 - k}$ and $1/\tau_2 = \frac{1}{2}b - \sqrt{\frac{1}{4}b^2 - k}$.

Note that (6.5) is valid for both absolute and relative damping. For absolute damping, $\hat{q} = q_0 - \frac{b}{k}\dot{q}$, whereas for relative damping $\hat{q} = q_0$. Equation (6.5a) is the equation for a gradually damping out oscillation, and (6.5b) contains the sum of two exponential functions that both approach zero (though at different rates). It may appear strange that (6.5) for absolute damping contains equilibrium velocity ($\dot{q}$), whereas (6.1) does not. The reason for this is that q in (6.1) is not a constant, but changes at a rate $\dot{q}$.

6.3 Modelling a single joint movement

The modelling of a single joint elbow movement was aimed to demonstrate that relative damping makes it possible to generate fast movements with a linear mass-spring model. We compared the models with absolute and relative damping for a range of values of *b* and *k*. Apart from this we modelled “typical examples” of movements. For these predictions we used reasonable estimates for *b* and *k*. The elbow stiffness has been estimated by Bennett et al. (1992) for rhythmic single-joint elbow movements, and by Gomi and Kawato (1997) for discrete two-joint (shoulder and elbow) movements. Assuming a lower arm length of 0.4 m, we estimated the average value of *k* in the elbow to have been about 20 s^{-2} in both studies. For the typical examples of movements that we simulated with our mass-spring model we therefore used $k = 20\ \mathrm{s}^{-2}$. For these examples we used a value for b that resulted in about 10% overshoot of the target. This was $b = 5\ \mathrm{s}^{-1}$ for absolute damping, and $b = 10\ \mathrm{s}^{-1}$ for relative damping. Note that the first results in an underdamped system, whereas the latter results in a slightly overdamped system.

We assume the simplest velocity profile of the equilibrium point: the equilibrium point moves at a constant velocity from the start to the target, where it stays. The movement time (MT) is defined as the time between the beginning of the movement and the moment at which 90% of the distance to the target is covered. This measure also yields interpretable results for overdamped movements that undershoot the target. For underdamped movements the overshoot is defined as the maximal elbow angle beyond the target, expressed as a percentage of target angle.

6.3.1 Results

Examples of the elbow movements predicted with absolute and relative damping are shown in Figure 6.2B. The movement is much faster with relative damping than with absolute damping. The difference in movement time between the movements predicted with absolute and with relative damping exists for a large range of the equilibrium point MTs (Figure 6.2C). This is even so when the equilibrium point moves instantaneously (i.e. as the equilibrium point MT approaches 0). Using the above-mentioned values for b and k, the fastest movement with absolute damping is 0.5 s, whereas with relative damping it is less than 0.2 s (Figure 6.2C). The latter MT is representative of a rapid human movement (Figure 6.2A). In the model with relative damping, the elbow’s movement time is almost the same as that of the equilibrium point (Figure 6.2C).

Figure 6.2D shows that for the model with relative damping the peak velocity of the movement is almost equal to the equilibrium velocity over a large range of equilibrium velocities. In contrast, for the model with absolute damping the peak velocity only increases with the equilibrium velocity for slow movements.

In the above example, the difference between the lowest possible movement times with absolute and with relative damping is considerable (Figure 6.2C). The contour plots in Figure 6.3 (upper panels) show that this is the case for a range of values of b and k. For both kinds of damping, shorter movement times are obtained by increasing the stiffness. However, the effect of increasing the damping differs between the two kinds: increasing *absolute damping* increases the movement time, while increasing *relative damping* decreases the movement time.

The lower panels of Figure 6.3 show that the amount of overshoot also depends on b and k. The overshoot is generally smaller with absolute damping than with relative damping. Increasing the amount of *absolute damping* decreases the overshoot and increases the movement time. In contrast, increasing the amount of *relative damping* decreases both the overshoot and the movement time, which is of course a favourable situation. Note that with absolute damping there is no overshoot in the overdamped range, whereas with relative damping there is always overshoot. This can be shown mathematically (Appendix).

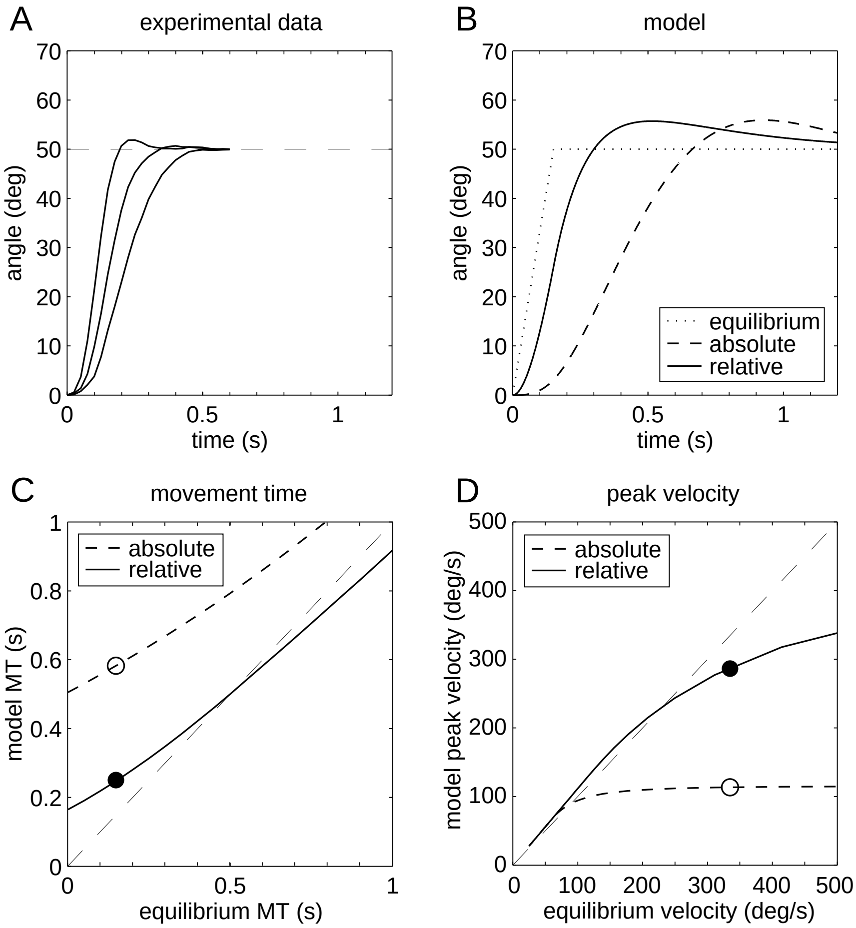

Figure 6.2. Panel A: Fast elbow flexions towards targets at 50° eccentricity with a width of 3°, 6° and 12° (data from Gottlieb, Corcos & Agarwal, 1989: Figure 6.4). **Panel B:** Examples of predicted single-joint elbow movements. Equilibrium MT = 0.15 s; $k = 20\ \mathrm{s}^{-2}$; absolute $b = 5\ \mathrm{s}^{-1}$; relative $b = 10\ \mathrm{s}^{-1}$. **Panels C and D:** The predicted relation between the movement of the equilibrium point and that of the elbow. The values for b and k and target distance are as in panel B. The movements have an overshoot of about 10%, irrespective of the speed of the equilibrium point. Open and filled dots indicate the movements of panel B.

6.3.2 Discussion

Damping of the elbow from a stationary position has often been measured without problems in a posture control task (e.g. Flash, 1987). However, attempts to measure damping of the elbow during active arm movements have not been very successful (Gomi & Kawato, 1997: Gomi, personal communication;

Bennett et al., 1992). One reason for this could be that such studies used a model with absolute damping. If the subject does not intend to move, the equilibrium point will remain stationary, so there is no difference between absolute and relative damping. During a movement, however, fitting a model with absolute damping to a system with mostly relative damping will result in a strong velocity dependency of the damping parameter. Indeed, Bennett et al. (1992) found a velocity dependency of the absolute damping parameter.

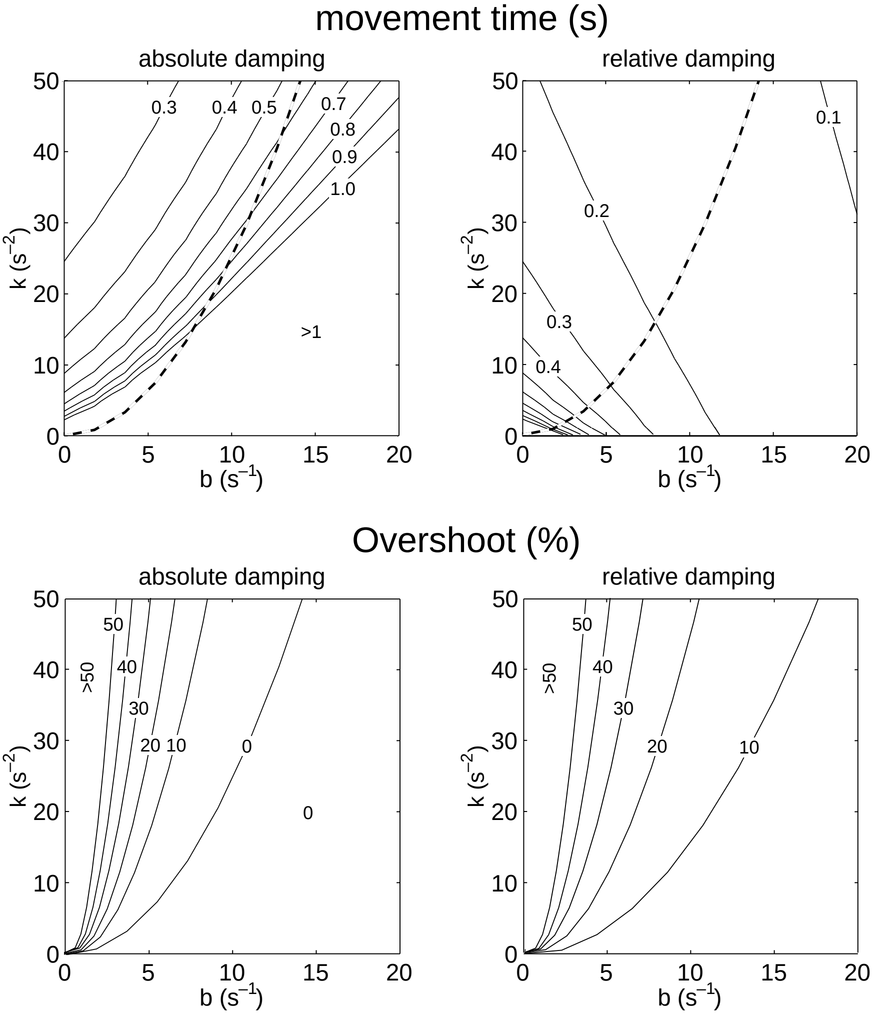

Figure 6.3: Predicted shortest possible movement times (equilibrium point MT approaches 0) for a range of values of *b* and *k*. **Left panels:** absolute damping; **Right panels:** relative damping. **Upper panels:** Continuous lines are contours of equal movement time. Dashed lines show the range of critical damping; to the left of these lines are overdamped movements and to the right underdamped movements. **Lower panels:** Predicted overshoot for the same conditions. Continuous lines are contours of equal overshoot. Note that the 0% line in the left panel (absolute damping) is the range of critical damping.

The model with relative damping not only is a simple way to generate fast movements, it can also help to interpret some peculiar experimental findings. Latash and Gottlieb (1991) reconstructed the time-course of the equilibrium-position, by fitting a linear model without damping to perturbed elbow movements. For fast movements, they found that the equilibrium point moves forth, back and forth again, two times changing its direction (they termed it an "N-shaped virtual trajectory"). Our proposal of relative damping gives an alternative interpretation for Latash and Gottlieb's (1991) results. In our view, the "N"-shape of the equilibrium trajectory originates from fitting an inappropriate model. If one fits a model without damping to a system with non-negligible damping, the damping forces will be attributed to shifts in the equilibrium point's position. An example is given in Figure 6.4. We generated a movement with our model with relative damping (b = 10 s^{-1}). Subsequently we determined at each time the equilibrium position assuming that b = 0 (following the method of Latash & Gottlieb, 1991). Figure 6.4 shows that our model with relative damping predicts that the method of Latash and Gottlieb (1991) yields a "N-shaped virtual trajectory" in rapid movements.

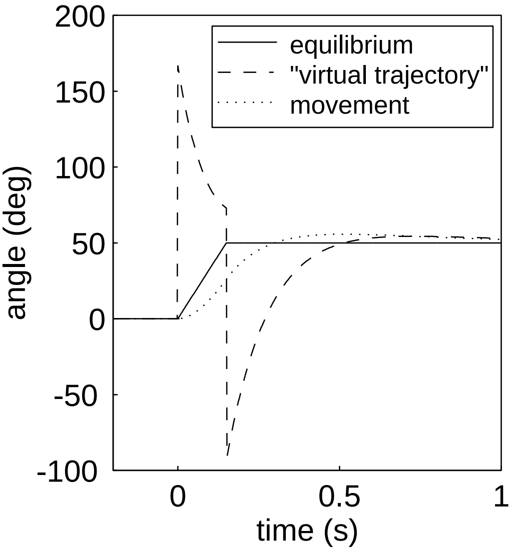

Figure 6.4. An N-shaped "virtual trajectory" (dashed line) is found when applying the method of Latash and Gottlieb (1991) to a movement generated with our model (dotted line), using a ramp-shaped equilibrium trajectory (solid line). Equilibrium MT = 0.15 s; k = 20 s^{-2}; relative b = 10 s^{-1}.

The results of Bellomo & Inbar (1997) can be interpreted as evidence that the damping in elbow movements is indeed relative damping. They used a "lambda-equilibrium model" (Feldman, 1986), which is a non-linear model in which the threshold activity of the muscles is controlled. This threshold depends not only on the equilibrium position, but also on the movement velocity (absolute damping). Bellomo & Inbar (1997) used EMG activity as a measure of muscle activity. They measured how the model parameters changed during elbow movement with different loads. For an equilibrium point that moves with a continuous velocity to the target, the “absolute damping” depended on the difference between the hand’s velocity and the virtual velocity. This is the same as a *constant relative damping*. This shows that relative damping not only improves a simple linear model model, but also improves a non-linear model such as the lambda model.

In one aspect, the final slowing down phase, the mass-spring movements do not look very realistic (compare Figure 6.2A and B). There is a rather large overshoot of the target followed by a slow return, irrespective of the kind of damping. We could undoubtedly improve this for instance by introducing a smoother movement of the equilibrium point. However, we will not do so because a simple model is valuable for providing insight into the general pattern of behaviour, rather than for giving an exact fit of the observed behaviour.

6.4 Modelling the effect of moving targets in a fast interception

A linear mass-spring model can also be used to model small variations in a non-linear system. To investigate whether relative damping also improves the model’s performance in such applications, we used the data from experiment 3 in Smeets and Brenner (1995a). Subjects had to hit static and moving spiders on a screen in front of them (Figure 6.5A) in a rapid, unrestrained 3-D movement. The mass-spring model is used to describe the control of the hand’s movements in the same component that the targets moved in (from left to right).

Kinematic data of the 3-D hand movements were averaged over subjects for each condition. These averages were calculated (in the left-right direction) over points in the paths that were at the same distance from the screen. To obtain the responses to the targets’ positions and velocities, the average path towards the stationary target at 0 cm was subtracted from each path (Figure 6.5B). The movements started on average 38 cm from the screen. The movement component towards the screen approximated a constant acceleration. Consequently, at half the MT the hand had moved one quarter of the distance towards the hitting screen, so that it was 28.5 cm from the screen. In all conditions, a position 28.5 cm from the screen was reached (on average) within 5 ms of half of the MT.

6.4.1 The models

We used the model as a linear approximation of the non-linear behaviour of the arm. To do so, we only modelled the differences between the responses to the targets, i.e. the differences in the lateral (left-right) component of the hand’s movements. Note that the lateral component was much smaller than the forward component (Figure 6.5B), but that it is the only direction in which the positions and velocities of the spiders differed (Figure 6.5A). We chose the stationary 0-cm target as a reference, i.e. we only modelled the differences with respect to the paths made in this condition. The modelled paths are therefore directly comparable to the experimental ones when displayed as in Figure 6.5B.

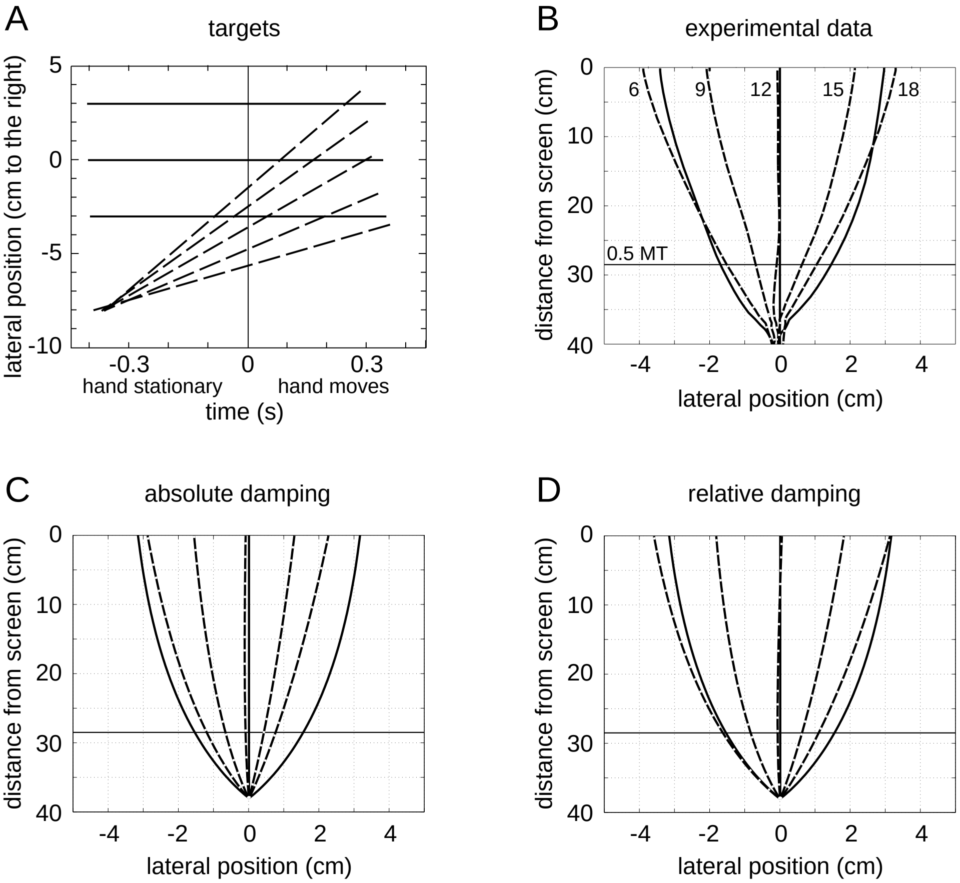

Figure 6.5, panel A: Lateral (left-right) positions of stationary (solid lines) and moving (dashed lines) targets that were presented in random order (Smeets & Brenner, 1995a). The stationary ones appeared at –3, 0 or 3 cm with respect to the hand's current lateral position. The moving ones appeared at –8 cm, moving at a velocity of 6, 9, 12, 15 or 18 cm/s to the right. Time = 0 is when the hand started to move. The start and end of each line indicate the average times at which the target appeared and at which the screen was reached. **Panel B:** Experimental paths, averaged over 12 subjects. The path towards the target at 0 cm was subtracted from the others (data from Smeets & Brenner, 1995a). Numbers near the dashed lines indicate the target's velocity (cm/s). **Panels C and D:** Model fits of the lateral movement component. The forward component was modelled as a continuous acceleration.

Fast interceptive movements are not ballistic, which means that information about the target continuously influences the hand's movement (Prablanc, Pélisson & Goodale, 1986; Smeets & Brenner, 1995b). Figure 6.5B shows that moving and static spiders were not hit in the same way: the trajectories towards the 6 cm/s targets and the 18 cm/s targets are less curved than the paths towards stationary spiders. A possible explanation for this is that the subjects did not use the spider's velocity to predict where it will be hit (Smeets & Brenner, 1995a), but instead used an expected velocity (this may be the preceding spider's velocity: de Lussanet, Smeets & Brenner, 2001). Smeets and Brenner (1995a) proposed that the subjects continuously predicted how far ahead of the spider's current position they would hit it.

Let s, x and q be the lateral positions of respectively the spider, the hand and the equilibrium point. With a stationary spider, we assume that the equilibrium position is simply the spider's position: $q = s$. The position of the equilibrium point (q) at a given instant is the sum of the spider's actual position (s) and the subject's prediction for how much further the spider will move (in the remainder of the movement time). The spider's position changes at its actual velocity ($\dot{s}$), whereas the prediction is made with the expected velocity (v), so that q in (6.3), (6.4) and (6.5) is substituted with:

$$q = s_{-\mathrm{RT}} + \dot{s}\ \left(RT + t\right) + v\ \left(MT - t\right) \tag{6.6}$$

where the time $t = 0$ is when the hand starts to move, and $t = RT$ is when the spider appears.

The model with *absolute damping* is given in (6.3) with q according to (6.6). In the model with *relative damping* (6.4), not only (6.6) is substituted but also the velocity of the equilibrium point ($\dot{q} = \dot{s} - v$). This is the velocity at which the subject's prediction of where the target will be hit (the equilibrium point), moves. This means that the target's final *position* is continuously updated on the basis of the expected velocity, and relative damping drives the hand in the direction of the difference between the target's velocity and the expected velocity. In de Lussanet, Smeets and Brenner (2001), we presented evidence that this expected velocity is equal to the preceding target's velocity (which on average is the average velocity of all the targets in a randomised experiment).

For modelling the differences in the lateral component of the interceptions, the speed of the target dictates the movement of the equilibrium point. Stationary spiders appeared at their position well before the hand started to move, so the equilibrium point was stationary during the hand's movement. This implies that the models with absolute and relative damping do not yield different results for stationary targets.

6.4.2 Fitting procedure

The root of the mean squared difference (RMS error) between the model and the measured paths was minimised. We first fitted the model to the two eccentric stationary targets (thick paths in Figure 6.5B) to obtain b and k. Therefore the RMS error was minimised at 28.5 and 0 cm from the screen (corresponding with half and the end of the MT). This resulted in $b = 7.96\ \mathrm{s}^{-1}$ and $k = 61.0\ \mathrm{s}^{-2}$ (RMS error = 0.18 cm). These values of b and k were used to fit the expected velocity v in each model to the conditions with moving targets.

6.4.3 Results and discussion

Figures 5C and D show the results. The paths for the stationary targets are the same in both panels and show the best fit of b and k to the conditions with stationary targets (see fitting procedure). For v we expect a value that is close to the average velocity of the (preceding) spiders, which was 10.125 cm/s (in the experiment there were additional conditions that we do not treat here). The best fit for the model with absolute damping was obtained with $v = 10.6$ cm/s (RMS error = 0.49 cm[11]). The best fit for the model with relative damping was $v = 9.5$ cm/s (RMS error = 0.19 cm). So both models yielded a value for v that was close to the expected value. The model with relative damping describes the data better than does the model with absolute damping. This can be seen when comparing the dashed lines (for the moving targets) in Figure 6.5C and D with those in panel B. Moreover, the model with relative damping describes the paths towards the moving targets as well as those to the static targets (the RMS errors are almost the same). However, for the static conditions, two parameters were fitted, whereas just one parameter was fitted for the moving ones. This means that the model with relative damping describes the moving target conditions very well, compared to the fit of the static conditions.

6.5 General Discussion

With a realistic value of stiffness and damping, a simple linear mass-spring model with absolute damping generates rather slow movements (Figure 6.3). To obtain rapid movements, one has to assume that stiffness is higher than what is measured experimentally (Bennett et al. 1992; Gomi & Kawato, 1997). Previously, it has been proposed to “solve” this problem by introducing non-linearities (such as a non-monotonic movement of the equilibrium-point) and extra parameters in the model. Apart from not being very elegant, such solutions suggest that the human motor system behaves non-linearly. An argument against such non-linearity is that people can easily scale-up their characteristic movement trajectories without changing the shape of the movements (Merton, 1972). This would be difficult with a non-linear motor control system. A solution from servo control is to control the desired velocity of the movement in addition to the desired position (or trajectory). For human movements, this solution has been used for models with an optimal controller in the learning of goal-directed arm movements (Shadmehr & Mussa-Ivaldi, 1994), for interception in a model using a dynamic systems approach (Zaal, Bootsma & van Wieringen, 1999) and for equilibrium point models of goal-directed movements (McIntyre & Bizzi, 1993).

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[11] The model with absolute damping fit the same data worse than it did in Smeets and Brenner (1995a). The reason for this is that differences in reaction time and movement between the conditions (Figure 6.5A) were ignored when making the original fit. The good result of that original fit is therefore probably a coincidence.

The stiffness value that we obtained for the fast interception (section 4: k = 49.6 s^{-2}) was higher than the one that we used to model the single joint movement (section 3: k = 20 s^{-2}). The latter value was based on the literature (Bennett et al., 1992; Gomi & Kawato, 1997). Does that mean that the k obtained by fitting the model to interceptive movements is unrealistic? No, because the first value is the endpoint stiffness of a complete arm whereas the latter is the isolated elbow stiffness. Gomi & Kawato (1997) also measured the endpoint stiffness for an arm flexion towards the shoulder, opposite in direction from the hitting movement in Smeets and Brenner's experiment. From movement start to peak velocity, the lateral endpoint stiffness measured by Gomi & Kawato was fairly constant and remained within a range of 40-60 N/m (two subjects). Assuming similar stiffness values when moving in the opposite direction and assuming an effective mass of about 1 kg, this range of stiffness is equal to k = 40-60 s^{-2}. Thus, the value that we estimated for k for the fast interception is within a realistic range.

The linear mass-spring model is a course simplification for a system that consists of both muscles and reflexes. As we mentioned in the introduction, the muscles have (non-linear) *absolute damping* properties that we neglected. In addition, we neglected the delays of the reflex system. In neglecting these properties we certainly introduced errors. However, by keeping the model we gained much insight in its behaviour. Moreover, the muscle reflex-system has such a complex structure, that merely introducing reflex delays and a realistic muscle force-velocity relationship would not make the model appreciably more biologically realistic. On the other hand, a truly realistic model would be almost as incomprehensible as the muscle-reflex system itself.

Single joint movements have been modelled very often, because in such movements there are no interactive (coriolis) forces between the limb segments. The present paper gives evidence that relative damping provides a very simple alternative explanation that can account for results that previously appeared to indicate that motor control is complex. It would be interesting and useful to reanalyse earlier data by Bellomo and Inbar (1997), Bennett et al. (1992), Gomi and Kawato (1997) and Latash and Gottlieb (1991) using models with relative damping. Given the present results, this may result in reliable estimates of the damping during the movement and may free Latash's version of the lambda model from the N-shaped equilibrium trajectory.

From the viewpoint of optimal control it does make sense that the muscle-reflex system forms a unit that behaves as a singular linear system. For example, the non-linear stretch reflex and non-linear stiffness were shown to provide a more linear muscle stiffness (Nichols & Houk 1976). In addition, muscles without reflexes only behave spring-like for a limited duration, whereas reflexes act after a brief delay. The combination of the two time scales of muscle and reflex properties could potentially result in approximately linear behaviour over both time scales. The good results of the simple model with relative damping to predict the effects of differences in target velocity provides support for this view.

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6.7 Appendix: Relative damping always gives overshoot

The model with relative damping for a single joint movement predicts that the target will be overshot even in the overdamped case (Figure 6.3). Here we show mathematically that this is the case for all equilibrium MTs. We will regard positive damping and stiffness parameters.

The model is linear, so the target's distance does not change the shape of the trajectory (it only scales the trajectory). For simplicity we set the target distance at 1. Let the equilibrium MT be t_q, so while the equilibrium point moves, $\dot{q} = 1/t_q$. The initial values are $x_0 = \dot{x}_0 = q_0 = 0$. From (6.5b) it follows that at time t_q, when the equilibrium point reaches the target, the hand's position and velocity are

$$x\left(t_q\right) = 1 - \frac{\tau_1 \ \tau_2}{\tau_1 - \tau_2} \ \frac{1}{t_q} \ \left(e^{-t_q/\tau_1} - e^{-t_q/\tau_2}\right) \qquad (6.7a)$$

$$\dot{x}\left(t_q\right)=\frac{1}{t_q}+\frac{1}{\tau_1-\tau_2}\;\frac{1}{t_q}\;\left(\tau_2\;\mathrm{e}^{-t_q/\tau_1}-\tau_1\;\mathrm{e}^{-t_q/\tau_2}\right) \tag{6.7b}$$

By their definition $0 < \tau_1 < \tau_2 < \infty$ when $b > 0$. This means that $0 < x(t_q) < 1$, in other words, the hand never reaches the target before the equilibrium point does.

After the equilibrium point reaches the target, it remains there. The hand will then either slowly approach the target (but never reach it), or the hand will shoot past the target and return slowly. If there is always overshoot, the time t_{target} –when the hand reaches the target– must be within the range ($t_q < t_{target} < \infty$), regardless the values of b, k and t_q. After time t_q, the equilibrium point $q = 1$ and $\dot{q} = 0$, so

$$x\left(t_{target}\right)=q=1 \tag{6.8}$$

so (5b) becomes

$$\begin{aligned}1-\frac{\tau_1}{\tau_1-\tau_2}\;\left(-\dot{x}_q\,\tau_2+1-x_q\right)\;\mathrm{e}^{-\frac{t_{target}-t_q}{\tau_1}}&\\+\frac{\tau_2}{\tau_1-\tau_2}\;\left(-\dot{x}_q\,\tau_1+1-x_q\right)\;\mathrm{e}^{-\frac{t_{target}-t_q}{\tau_2}}&=1\end{aligned} \tag{6.9}$$

which can be rewritten as,

$$\mathrm{e}^{\left(t_{target}-t_q\right)\left(\frac{1}{\tau_1}-\frac{1}{\tau_2}\right)}=\frac{\tau_1}{\tau_2}\;\frac{\dot{x}_q\,\tau_2-1+x_q}{\dot{x}_q\,\tau_1-1+x_q} \tag{6.10}$$

When we substitute $x_q=x\left(t_q\right)$ and $\dot{x}_q=\dot{x}\left(t_q\right)$ as given in (6.7), we get

$$\mathrm{e}^{\left(t_{target}-t_q\right)\left(\frac{1}{\tau_1}-\frac{1}{\tau_2}\right)}=\frac{1-\mathrm{e}^{-t_q/\tau_1}}{1-\mathrm{e}^{-t_q/\tau_2}} \tag{6.11}$$

so

$$t_{target}=t_q+\frac{\ln\left(1-\mathrm{e}^{-t_q/\tau_1}\right)-\ln\left(1-\mathrm{e}^{-t_q/\tau_2}\right)}{1/\tau_1-1/\tau_2} \tag{6.12}$$

From (6.12) we can calculate t_{target} for positive damping ($b > 0$) to range from $t_{target}=\dfrac{\ln\left(\tau_1/\tau_2\right)}{1/\tau_1-1/\tau_2}$ for $\lim\limits_{t_q\downarrow 0}$, to $t_{target} = t_q$ for $\lim\limits_{t_q\to\infty}$. This means that for any $0 < \tau_1 < \tau_2 < \infty$, there is a time $t_q < t_{target} < \infty$ when $x(t_{target}) = 0$. Thus there will be overshoot for all movements with positive relative damping.

7

A test for the new mass-spring model

Abstract

A linear mass-spring model is tested, in which damping works with respect to the target (the equilibrium point) instead of with respect to the limb. In an experiment subjects had to hit virtual targets moving to the right. Target velocity was varied, and some targets changed velocity after 250 ms. An electric servomotor applied a constant rightward force to the hand. In some trials the force started to change as a ramp. The hand made 3-D movements, of which the main component was forwards. The model was fitted to the differences in the left-right component of the hand's movement towards targets that appeared at different positions. The fitted model predicted such differences well for targets of different velocities, and rather well for targets that changed speed. This confirms the findings of chapter 6 that a simple linear mechanical model can predict difference in the hand's lateral moves in rapid interceptive movements towards targets of various velocities and positions. The model failed to predict the effect of the force perturbations, which is consistent with the findings of chapter 2 (using a different linear model). We conclude that our *mechanical* model is quite suitable for describing (equilibrium point) control, but –paradoxically– not for describing the limb's *mechanical* behaviour.

7.1 Introduction

In chapter 2, we described an experiment to test a mass-spring model for equilibrium-point control. The test involved comparing the influence of visual and mechanical perturbations. We had to conclude that the model could not describe the influence of either kind of perturbation. In the subsequent chapters we developed our understanding of how people use velocity information for the direction in which they aim. In chapter 6 we proposed a new mass-spring model, with relative damping, that could describe the data of an interception task with targets of various velocities (Smeets & Brenner, 1995). In the present chapter, we discuss the results of an experiment equivalent to that in chapter 2, with which we test this model. As in chapter 2 and in section 6.4, we model only the left-right (lateral) component of an interceptive movement of which the major component is forward.

The present experiment resembles that in chapter 2, with some improvements and some additional conditions. Some targets of constant velocity differed in position only, other targets changed to a different velocity, whereas in other trials a force ramp occurred. To predict the reaction to targets that change velocity, assumptions have to be made about how subjects deal with the delay between the occurrence of the velocity change and the hand's first possible reaction to it. This problem does of course not exist with targets of a constant velocity. We therefore additionally presented targets of constant higher or lower velocity, that reached the position that the perturbed targets reached at the time when their velocity changed.

The model will be fitted to the responses to targets that differ in position only. This fitted model will be used to predict the responses to targets that differ in velocity but that (almost) have the same position at the time when the subject's hand starts to move. For the targets that change velocity, we will follow an assumption analogous to that in chapter 2 (Fig. 2.7). This is: after the target changes velocity, the hand will continue to move as if the target did not change its velocity, until the new current position and velocity are fully processed. After this, the target's current position and velocity are assumed to fully influence the hand's movement.

The results of the mechanical perturbations in chapter 2 indicated that the stiffness changed during the perturbation. This could have been caused by the stiffness being non-linear (Feldman, 1966). However, during the interception, the arm's posture changed from almost completely flexed to almost completely extended. As a result of this, the effective mass of the "hand" (and thus the stiffness and damping parameters) could have changed considerably. In addition, during an interception the hand had an almost constant acceleration towards the hitting screen (Fig. 2.3; Brenner et al., 1998). Therefore, early and late in the movement, the arm's muscles are in a very different dynamic state. In the present experiment we therefore administered the force ramp at different times after the target's appearance. If the arm's stiffness and damping are time or posture dependent, the influence of the early and late force initiation should be different.

7.2 Model

The model was explained in chapter 6 (see equation (6.2) and section 6.4.1). In the presence of a lateral force on the hand (6.2) becomes

$$M\ddot{x} + B\ (\dot{x} - \dot{q}) + K\ (x - q) = F(t), \tag{7.1}$$

where x is the hand's position, q that of the equilibrium point and F the perturbing force (the number of dots on x and q denote the order of time-derivative). In most trials the force was of the same, constant magnitude. Since we only study the differences between the hand's trajectories, a possible influence of this constant force will not influence the results. The equilibrium point's position changes when the target (a spider with position s) has a different velocity than the subject expects (see section 6.4.1). If the target has a position $s_0 = 0$ at time = 0 (when the hand starts to move) and the velocity expected by the subject is v, we can write equation (7.1) as:

$$M\ddot{x} + B\ (\dot{x} - \dot{s} + v) + K\ (x - \dot{s}t + vt) = F(t). \tag{7.2}$$

In chapter 2 the mechanical and visual perturbations were designed such that the model (of section 2.3) predicted that the hand would follow the same trajectories. In chapter 2 this prediction did not hold because there was a delay in when the change in target velocity started to influence the hand's movements. In the present experiment we avoided this problem by presenting targets of constant velocity (see above). The present model predicts that the hand will follow the same trajectories with a perturbing force that follows from (7.2):

$$F(t) = B\ (\dot{s} - v) + K\ (\dot{s}t - vt), \tag{7.3}$$

which means that the force should change as a step-ramp. The problem with such a perturbation is that it will be clearly noticeable for the subjects, and they will be likely to change their strategy. Instead we chose to only apply a ramp force (as in chapter 2), starting at different times after the target appeared. Note that, contrary to chapter 2, the model predicts different trajectories for the visual and mechanical perturbations.

7.3 Method

Figure 7.1 shows the 11 conditions that were presented in the experiment. The experimental set-up was as in chapters 3-5. The perturbations in chapter 2 were too small and too gradual for the subjects to notice (they only noticed the force returning to its base level after the trial had been completed). We nevertheless improved the set-up with respect to chapter 2. We used a much lighter lever on the axle of the electric servomotor, and placed the force transducer close to the lever (instead of close to the hand). By doing so, we got rid of small 50 Hz oscillations that were present in the previous experiment (Fig. 2.3). In addition, the lever could accelerate much faster than in the original experiment so the force on the hand remained almost constant even when the hand moved rapidly to intercept the target. As in chapter 2, subjects reported (when asked) only to have noticed a force change after they hit the screen.

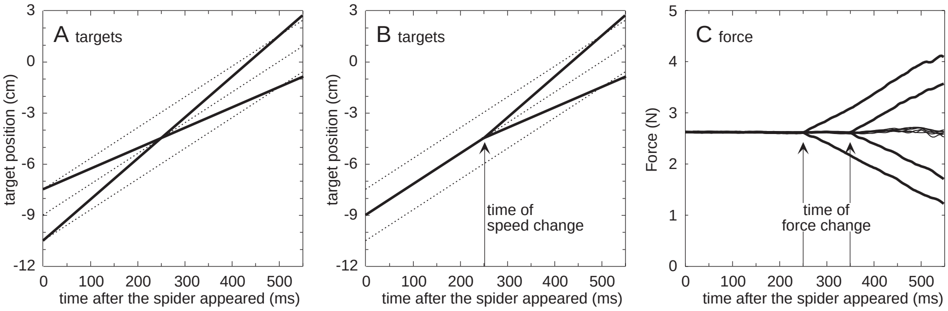

Figure 7.1 There were 11 conditions, each of which occurred 10 times in random order. In 7 conditions, the lateral force on the hand remained constant. 18 cm/s targets appeared at –7.5, –9.0 or –10.5 cm (dotted lines). 0 cm is the hand's lateral position when the target appeared. **A:** 12 cm/s targets appeared at –7.5 cm, 24 cm/s targets appeared at –10.5 cm (thick lines). **B:** In two conditions (thick lines), a 18 cm/s target (that appeared at –9.0 cm), changed to 12 or 24 cm/s respectively after 250 ms. **C:** In four conditions (thick lines), the lateral force on the hand was not constant. An 18 cm/s target appeared at –9.0 cm; after 250 or 350 ms a force ramp of –5 or 5 N/s started.

In chapter 2 we tried to minimise the variation in the timing between the subject's reaction time and the initiation of the perturbation, by predicting the reaction time from that in the preceding trials. This strategy did not work well. In the present experiment the perturbations were timed with respect to the target's appearance (so the subjects' variability in reaction time did not introduce variability in the timing of the perturbations). In addition, we only presented relatively fast targets because the reaction time is more variable for stationary targets, and velocity dependent for slow ones (van den Berg & van de Grind, 1989).

7.4 Analysis

The trajectories of the hand's left-right position were averaged per condition, over subjects. We use our model to predict the *differences* between conditions. In chapter 3 we showed that people expect targets to move at the same velocity as the preceding ones, so the expected velocity (equation 7.2) is 18 cm/s, the average velocity. We therefore subtracted the average trajectory to the 18 cm/s target that appeared at –9.0 cm (thin line in Fig. 7.1A), from all trajectories, to obtain the deviations for which we can make predictions using the model.

In the mechanically perturbed trials, the hand will only deviate as a result of the force ramp, because the target moves exactly the same as the reference. We therefore defined the *model onset time* (t = 0 in equations 7.1-7.3) as the start of the force ramp, 250 or 350 ms after the target appeared. For the conditions with a constant force, the model onset time needs some explanation. There is reason to believe that the moment when the hand starts to move need not be the same as the moment when the target's velocity and position begin to influence the direction in which the hand actually moves (chapter 4). Therefore we defined the model onset time (with a constant external force) as the moment when the hand's deviation velocity exceeded 1 cm/s. In chapter 2 we saw that it takes some time before the first reaction to a change in the target's velocity becomes visible, and in chapter 4 we showed that the reaction time in the left-right direction (the direction of the target's movement) is later for fast targets. We therefore determined one reaction time for the 18 cm/s targets, one for the 12 cm/s target and one for the 24 cm/s target. A fourth reaction time was determined for the targets that changed velocity.

The variability between the trajectories was too large (probably as a result of the high velocity of the movements) to estimate reliable model onset times or to fit the model for individual subjects, so we used the average trajectories. We fitted the model (with expected velocity v = 18 cm/s) to the trajectories towards the left and the right 18 cm/s targets, using equation (6.5). From this fit we obtained $b = B/M$ and $k = K/M$ (as explained in section 6.2). To obtain two independent parameters, the model needs to be fitted to at least two moments in the trajectory. For the fitting we minimised the sum of the squared differences between the model and the experimental trajectories at 375 and 500 ms after the target appeared. We used the same parameters to predict the trajectories in the other conditions.

For the conditions with a ramp force, we had to estimate an additional parameter (the mass M) to predict the trajectories. The mass parameter M was fitted at 375 ms from the conditions with an early ramp.

7.5 Results

The model onset time was 310 ms for both the 12 and 18 cm/s targets. For the 24 cm/s target, the model onset time was 360 ms (50 ms longer), and for the conditions with a change in velocity it was 415 ms (165 ms after the target's speed changed). On average the targets were hit after 563 ms (± 44 ms, 14 subjects). The time that the hand's velocity *towards the screen* exceeded 0.1 m/s was 291 ± 30 ms (on average 7 ms longer for 12 cm/s and 3 ms shorter for 24 cm/s targets). Although the model was fitted to just four points in the trajectories towards two of the 18 cm/s targets, the model trajectories described the entire trajectories well (Fig. 7.2A). The parameters were $b = 8.7\ \mathrm{s}^{-1}$ and $k = 72.2\ \mathrm{s}^{-2}$.

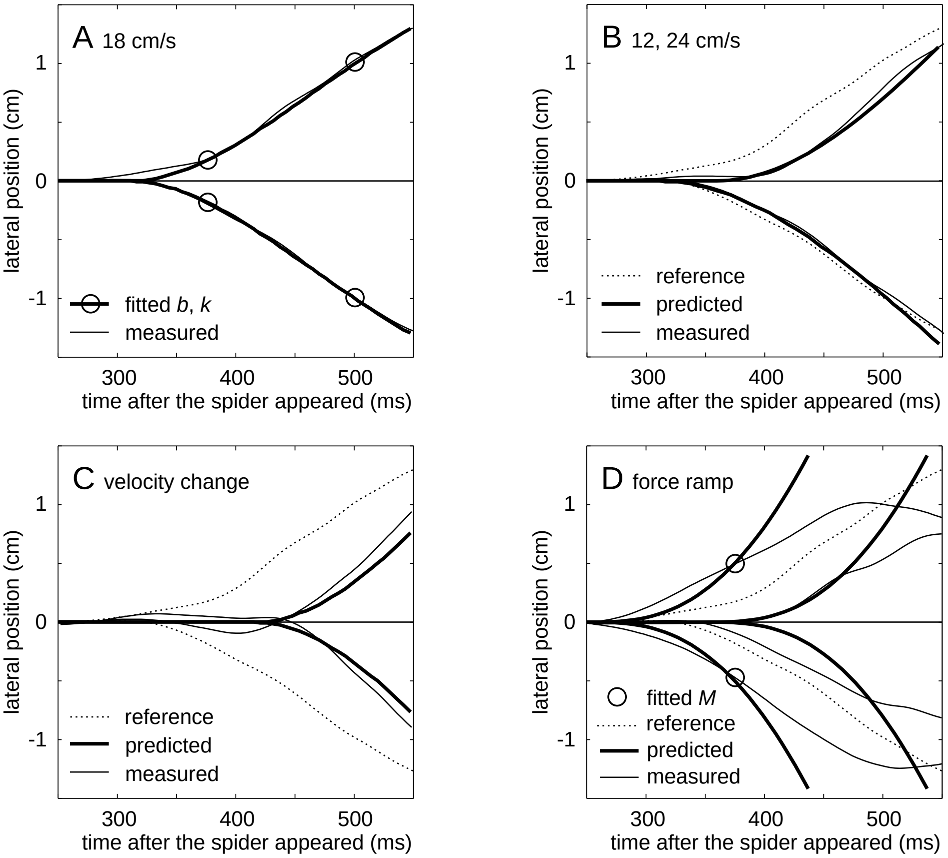

Figure 7.2 The hand's average lateral position (10 trials per condition, 14 subjects) between 250 and 550 ms after the target appeared. The hand's position is shown with respect to the trajectory to the 18 cm/s target that appeared at –9 cm. **A:** The fit of the model (thick curves) to the hand's trajectories (thin curves) towards the left and right 18 cm/s targets. The RMS error at 375 and 500 ms after the target appeared (circles) was minimised. The measured trajectories towards 18 cm/s targets are also shown in the other three panels, for comparison (dotted lines). **B:** Measured and predicted trajectories for the conditions with the 12 and 24 cm/s targets. **C:** Measured and predicted trajectories for the conditions with the targets that changed velocity after 250 ms. **D:** Measured and predicted trajectories for the conditions with a ramp torque after 250 or 350 ms. To scale the paths, the mass was fitted at time = 375 ms.

Figure 7.2 B and C show the trajectories predicted for the conditions with the 12 and 24 cm/s targets and for those with targets that changed velocity. The model predicted these trajectories well, although the model slightly underestimated the reaction to the change in velocity.

The effects of the unloading and the loading perturbations were approximately symmetrical (Fig. 7.2D). The shape of the hand's trajectories to the early and the late force ramps were very similar, although the trajectory for the late positive force ramp started to deviate relatively long after the force ramp, compared to the other three trajectories. The mass parameter of the model was fitted $M = 0.24$ kg. As the early and late force ramps were of the same magnitude, the predicted trajectories had the same shape. However, the real trajectories were very different from the experimental ones. In the beginning, when the perturbing force was still very small (Fig. 7.1 B), the hand was drawn away much more than predicted by the model, whereas later, when the perturbing force was larger, the hand's trajectory was perturbed much less than predicted.

7.6 Discussion

7.6.1 Status of the model

The model worked well for targets of different velocities (confirming the result in section 6.4). In the experiment that is described in section 6.4 (Smeets & Brenner, 1995), the moving targets all appeared at the same position, so that their positions differed considerably by the time that the hand started to move. Due to this, the model with absolute damping (equation 6.1) could predict the trajectories for moving targets relatively well. In the present experiment, the 12 and 24 cm/s targets reached the same position after 250 ms. For such targets, that have about the same position but a different velocity when the hand starts to move, the model with absolute damping predicts very large undershoots (as in Fig. 2.6; ahead of slow targets and behind fast ones). The present results show that the model with relative damping that we test here works well for such targets.

As in chapter 4, the velocity of the fastest targets did not influence the hand's *initial* movement direction. In section 4.8.1, we suggested that velocity the of fast targets may be used later in the movement. This suggestion is supported by the results of the present experiment, in that the model did predict the movements towards the 24 cm/s target well, while the model does use velocity information.

The model even appeared to predict the responses to a change in target velocity well. This could be a coincidence. Using a similar experiment, Brenner and Smeets (1997) provided evidence that people react to motion onset with a maximal response, irrespective the size of the change. They let subjects hit targets that jumped or started to move as soon as the subject's hand started to move. The subjects' response (the acceleration profile of the hand's left-right movement) was the same when the target jumped or started to move. Neither did it depend on the size of the jump (2 or 4 cm) or the velocity change (12 or 24 cm/s). Note however, that people may respond differently a change in velocity than they do to motion onset.

The results of the perturbing force ramp confirm chapter 2 in that our simple mass spring model –which is basically a mechanical model– cannot describe the influence of a perturbing force. The shape of the mechanically perturbed experimental trajectories is very similar to those in chapter 2. This is not surprising because the perturbation was the same ramp-force. The models used in chapter 2 (equation 2.1) and in the present chapter (equation 7.1) both predict the same trajectories for the mechanical perturbations (because the equilibrium position is stationary). One could argue that posture changes of the arm change the effect of the ramp force. However, despite the extreme change in posture and velocity, the influence of the perturbing force ramp was not related to the time (and thus posture) when the perturbation started (Fig. 7.2D), so the changes in the arm’s posture and dynamics cannot account for the poor prediction.

The influence of the loading and unloading perturbing load were symmetric. One would expect such behaviour for a linear system like our model, but the influence of the perturbing force ramps was clearly non-linear. A likely explanation is that the reaction to the perturbing force depends on the hand’s distance from the desired position, in other words, that the stiffness is non-linear. Feldman and co-workers (e.g. Feldman & Levin, 1995) hypothesise a non-linear stiffness curve, that is approximately symmetric around the equilibrium. Such a symmetric, non-linear curve requires that the hand is not far from the equilibrium position at any time during the movement to obtain symmetric mechanical perturbations. In Feldman’s model, however, (as in many other equilibrium point models) the equilibrium point is far ahead of the real movement. This means that such models cannot account for our finding of symmetrical effects of loading and unloading perturbations. Our finding of a non-linear stiffness also implies that a linear approximation does not hold for the effects of the mechanical perturbations, even though they were very small and were not noticed by the subjects.

As the model works very well for variations in the visual input, but not for mechanical perturbations, we must conclude that our mechanical model describes control, but not the mechanical behaviour.

7.6.2 The model onset time

The model onset time was longer than in the forward direction. This justifies our choice for using the former, because it means that at least some subjects always started to move in the same direction when they detected a target, irrespective of its position and velocity. This observation confirms the idea that the initiation of the movement and the direction of moving are controlled separately (chapter 4; Brenner & Smeets, 1996; van Donkelaar et al., 1992).

The results indicate that we may have to weaken a conclusion of chapter 4 a little. We there concluded that the velocity of targets of 12 cm/s and faster does not influence the hand’s initial movement direction. If this were the case, the trajectory to the 12 cm/s target should have started in the same direction as the one towards the middle 18 cm/s target did. However, the movements towards the left 18 cm/s target and to the 12 cm/s target clearly started in the same direction (compare in Fig. 7.2B the lower dotted curve with the thin continuous curve).

The model onset time was about 50 ms longer for the condition with the 24 cm/s target than for the 12 cm/s target. The model predicted the responses to both very well, which is evidence that for both velocities velocity information was used from the beginning of the model onset time (note that at that time the targets' *positions* did not differ much from the reference). In chapter 4 we showed that velocity information of fast targets does not influence the *initial* movement direction. The model onset time did not differ for the targets that changed velocity (Fig. 7.2C). This suggests that the difference in model onset time between 12 and 24 cm/s may have been caused by the fact that it takes longer to accurately pursue a fast target than a slower one (Carl & Gellman, 1987).

For the conditions with a change in target velocity, the model onset time was just 165 ms after the speed change. This is considerably less than the 200 ms that we found for the first influence of a change in target speed on the hand's acceleration towards the screen (Brenner et al., 1998). In Brenner et al, the change in speed was only 3 cm/s, half the change of the targets in the present experiment, which could explain the difference.

7.7 References

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8

Summary and conclusions

In this thesis we addressed the strategies that normal human subjects employ to make rapid interceptive movements. In the planning and continuous control of such movements, sensory information of very different modalities has to be integrated rapidly and accurately, and has to be translated into useful movements of the hand. We addressed the problem both with and without a model. With the mass-spring model we wanted to test whether such a model gives a valid description for both manipulations of the equilibrium point and of the endpoint (**chapters 2, 6 and 7**; cf. Fig. 1.1). In using a mass-spring model, we supposed that subjects used one single strategy for the sensory-motor control throughout an experiment (stable control). In **chapter 5** we tested the validity of this assumption of stable control. Finally we specifically addressed the question whether –and if so, how– people use velocity information (rather than only position information) to guide their action (**chapters 3, 4 and 6**).

A new test of linear mass-spring models (chapter 2)

In **chapter 2** we carried out a new test for the hypothesis of equilibrium-point control (equilibrium hypothesis) (Feldman & Levin, 1995). This hypothesis proposes that signals that the brain sends to the muscle-reflex systems of a limb, do not encode the muscle forces that are needed (including the complex dynamical interactive forces). Instead, the equilibrium hypothesis states that every muscle is commanded as if it is a spring. The brain only commands the desired length for all the muscles and a few additional parameters (such as co-contraction of antagonists). The resting length of a spring can be changed not only by setting the spring, but also by exerting a mechanical force on the end of the spring. Our test was to compare the effects of both ways to change the limb’s resting position in an experiment with human interceptive movements. The movement was a fast hit of a virtual target that ran to the right on a screen in front of the subject. Of this 3-D movement the model only described the left-right (lateral) component. The first way to change the resting position was to change the hand’s lateral equilibrium position in reaction to an unexpected change in the target’s speed, the second way was to exert a force on the subject’s hand.

The first result was that the model could not explain the effect of the visual perturbations (the change in the target’s velocity). Our explanation was that the model did not take into account delays that occur between a visual event and a motor action. We proposed that the motor system overcomes this problem by continuously predicting the target’s present position on the basis of the latest information (Smeets, Brenner & de Lussanet, 1998). However, the implementation of this solution worsened the model’s predictions. This gave rise to the experiments described in **chapters 3 and 4**.

The second result was that the mass-spring model badly predicted the effects of the mechanical perturbations. We concluded, that there probably is no linear mass-spring model that could predict the subject’s responses. This conclusion however, gave rise to **chapters 6 and 7**.

The use of velocity for interception (chapters 3 and 4)

We showed before that the target’s velocity continuously influences the hand’s velocity (Brenner, Smeets & de Lussanet, 1998), but some results suggested that the target’s velocity does not influence the direction in which the hand moves (Smeets & Brenner, 1995a). There is some consistency in this result: velocity information could be used to control the hand’s speed, whereas position information could be used for the formation of the trajectory to the target (Brenner & Smeets, 1996). However, the results of **chapter 2** encouraged us to look deeper into the influence of the target’s velocity on the hand’s trajectory.

In the experiments of **chapter 4** we varied both the velocity and the position of the moving targets systematically. These experiments revealed that not only the target’s position, but also its velocity influences the direction in which the hand starts to move. However, this was only when the target was not very fast (less than 12 cm/s which is about 12°/s). For faster targets the influence of the velocity on the initial direction of the hand’s movement was strongly reduced. In contrast, the preceding target's velocity influenced the direction in which the hand moved, and this was especially evident for fast targets (**chapter 3**: de Lussanet et al., 2001).

The influence of task history (chapter 5)

In **chapter 5** we asked whether people adapt their strategy of movement control in an interception task if sequential targets differ strongly. If the set of preceding trials would influence how subjects move towards a specific target, it could mean that they changed their control strategy. We found influences of the kind of target in the directly preceding trial (such as in **chapter 4**), but no influences that can be explained by an adapted movement strategy. This means that the subjects acted in a stable way rather than in a flexible way, i.e. they used the available information in a consistent way to guide the hand to the target (and not each time differently).

Damping in mass-spring models (chapter 6)

The results of **chapter 4** show that people do use velocity information to control the direction in which their hand goes (i.e. the lateral movements). On the basis of this new insights, we proposed a new mass-spring model for the left-right component of the hand's movements (**chapter 6**). In the new model, damping with respect to the target (*relative damping*) was incorporated, which gives the hand a tendency to move as fast as the target (in contrast to the more often used absolute damping which gives the limb a tendency to slow down). This means that it matches better with the equilibrium point hypothesis than absolute damping does. We showed that linear models with relative damping generate faster movements with the same stiffness and damping, than do models with absolute damping. Moreover, we showed that fitting a linear model with absolute damping to a trajectory that is generated by a linear model with relative damping will yield a recursive ("N-shaped") equilibrium trajectory (as was indeed reconstructed by Latash & Gottlieb, 1991, and Gomi & Kawato, 1997). This means that the reconstruction of a recursive equilibrium trajectory using a model without relative damping, cannot be used as a valid argument against the general idea of equilibrium point control. A final result was that introducing relative damping to the model of Smeets and Brenner (1995) much improved its prediction of their results. As the Smeets and Brenner model was the basis for **chapter 2**, we decided to redesign the experiment and specifically test a mass-spring model with relative damping (**chapter 7**).

A test for the new mass-spring model (chapter 7)

In **chapter 7** we adapted the experiment of **chapter 2** to test the relative damping-model (**chapter 6**). The model was fitted for the hand's movement in the left-right direction towards targets that differed only in the position where they appeared. The model predicted the hand's trajectory towards faster and slower targets well, as well as those towards targets that changed their velocity. However, the model failed in predicting the effect of force perturbations. As the effects of early and late force perturbations were very similar, the result cannot be explained by the major change in the arm's posture and velocity. Instead, the most probable reason why the model did not predict the effect of the force is that the stiffness was non-linear. We conclude that paradoxically our –mechanical– mass-spring model gives a good description of the planning and control process but not of the limb’s mechanical behaviour.

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Samenvatting en conclusies

Dit proefschrift gaat over de strategieën die gezonde menselijke proefpersonen gebruiken voor het maken van snelle onderscheppende bewegingen. Tijdens het plannen en uitvoeren van dergelijke bewegingen moet sensorische informatie van verschillende modaliteiten (bv. gezicht, spiersensoren) snel en nauwkeurig worden geïntegreerd en vertaald naar zinvolle handbewegingen. Dit probleem hebben we zowel modelmatig als experimenteel benaderd. Voor de eerste benadering gebruikten we een zgn. massa-veer model. We wilden testen of een dergelijk model manipulaties van de doel positie ("equilibrium" positie) en van de handpositie beiden goed kan beschrijven (**hoofdstukken 2, 6 en 7**; vgl. Fig. 1.1). Een onderliggende aanname bij het gebruiken van het model, was dat de proefpersonen gedurende het experiment niet van steeds dezelfde strategie voor sensorisch-motorische motorsturing gebruikten (dwz, de model parameters waren constant). De validiteit van deze aanname werd getest in **hoofdstuk 5**. De **hoofdstukken 3, 4 en 6** gaan over de vraag of, en zo ja hoe, mensen snelheidsinformatie gebruiken (in combinatie met positie-informatie) als het doel beweegt.

Een nieuwe test voor massa-veer modellen (hoofdstuk 2)

Hoofdstuk 2 beschrijft de resultaten van een nieuwe test voor de hypothese voor equilibrium-punt controle (“equilibrium hypothese”) (Feldman & Levin, 1995). Deze hypothese stelt dat de signalen die het brein naar het spier-reflexsysteem stuurt coderen voor spierlengte en niet voor spierkracht. Dit impliceert dat het brein geen rekening hoeft te houden met complexe interactieve dynamische krachten die optreden tijdens snelle armbewegingen. In plaats daarvan stelt de equilibrium hypothese dat een spier wordt aangestuurd alsof het een mechanische veer is. De rustlengte van een dergelijke veer kan veranderen door middel van een commando uit het brein, maar ook door middel van een mechanische belasting. Onze test was de effecten van beide manieren om de rustlengte te veranderen te vergelijken in een experiment met menselijke onderscheppende bewegingen. De beweging was een snelle slag naar een naar rechts lopend virtueel doel, een spinnetje (om het experiment aantrekkelijk te maken voor de proefpersonen). Van deze driedimensionale handbeweging beschreef het massa-veer model alleen de links-rechts (zijwaartse) component. De eerste methode om de rustpositie te verstoren was om de equilibrium positie van de hand te laten veranderen in reactie op een onverwachte verandering van de doelsnelheid. De tweede methode was de hand weg te trekken met een zijwaartse, geleidelijk veranderende, kracht.

Het eerste resultaat van dit experiment was dat het model niet het effect van de visuele verstoring (de veranderde doelsnelheid) kon verklaren. Onze verklaring hiervoor was dat het model geen rekening hield met de vertraging tussen een visueel waargenomen gebeurtenis en de reactie van de hand daarop. Wij stelden voor dat het motor controle systeem dat probleem deels ondervangt door continu de huidige positie van het doel te “voorspellen”, op basis van de laatste verwerkte visuele informatie (Smeets, Brenner & de Lussanet, 1998). Echter, de implementatie hiervan in het model verslechterde de voorspellingen van het model. Dit gaf aanleiding tot de experimenten die beschreven zijn in de **hoofdstukken 3 en 4**.

Het tweede resultaat was dat de modelvoorspellingen voor het effect van de mechanische verstoringen erg slecht waren. Aan de hand van simulaties concludeerden we dat er waarschijnlijk geen lineair massa-veer model is dat het effect van de verstoringen kan verklaren. Deze conclusie gaf echter aanleiding tot de **hoofdstukken 6 en 7.**

Het gebruik van snelheidsinformatie voor het slaan van een bewegend doel (hoofdstukken 3 en 4)

In het verleden hebben we laten zien dat de doelsnelheid de snelheid van de hand continu beïnvloedt (Brenner, Smeets & de Lussanet, 1998). De resultaten van vergelijkbare experimenten suggereerden echter dat de snelheid van een naar rechts bewegend doel de *richting* waarin de hand beweegt *niet* beïnvloedt (Smeets & Brenner, 1995a). Er is enige consistentie in dit resultaat: proefpersonen zouden snelheidsinformatie kunnen gebruiken om de snelheid van de hand te sturen en positie-informatie om het pad van de hand te sturen (Brenner &

Smeets, 1996). Echter, de resultaten van **hoofdstuk 2** moedigden ons aan om dieper in te gaan op de invloed van doelsnelheid op het pad van de hand.

In de experimenten van **hoofdstuk 4** varieerden we de snelheid en positie van de doelen systematisch. Hieruit bleek dat niet alleen de doelpositie, maar ook de doelsnelheid de richting waarin de hand vertrekt beïnvloedt. Echter, dit gold alleen voor tamelijk trage doelen (trager dan 12 cm/s, ongeveer 12°/s). Bij snellere doelen was de invloed op de startrichting van de hand sterk gereduceerd. daarentegen was er een invloed van de snelheid van het doel in de *voorgaande* onderschepping op de richting waarin de hand vertrok, in het bijzonder als het *huidige* doel snel was (**chapter 3**: de Lussanet et al., 2001).

De invloed van taakgeschiedenis (hoofdstuk 5)

In **hoofdstuk 5** vroegen we ons af of mensen hun bewegingsstrategie aanpassen als de opeenvolgende doelen die ze moeten slaan sterk verschillen. Als de set van eerder geslagen doelen beïnvloedt hoe proefpersonen naar een bepaald type doel bewegen, kan dat betekenen dat set van eerdere doelen de bewegingsstrategie heeft beïnvloedt. Net als in **hoofdstuk 3** vonden we invloeden van het voorgaande doel, maar geen invloeden die duiden op een aangepaste bewegingsstrategie. dat betekent dat de proefpersonen eerder stabiel waren dan flexibel, dwz. dat ze de beschikbare informatie op een consistente manier gebruikten en niet steeds op een andere manier.

Demping in massa-veer modellen (hoofdstuk 6)

De resultaten van **hoofdstuk 4** laten zien dat mensen snelheidsinformatie gebruiken om de richting waarin de hand beweegt (de zijwaartse bewegingen) te sturen. Op grond van dit nieuwe inzicht definieerden we in **hoofdstuk 6** een nieuw massa-veer model voor de zijwaartse bewegingen van de hand. In het nieuwe model was de dempingsterm gedefinieerd ten opzichte van het doel (*relatieve demping*). In tegenstelling tot bij conventionele demping (die elke beweging uitdooft), heeft de hand de neiging om even snel te bewegen als het equilibrium punt. Verrassend genoeg is relatieve demping daardoor beter in overeenstemming met de equilibrium hypothese. We lieten zien dat modellen met relatieve demping bij dezelfde stijfheid en demping snellere bewegingen voorspellen dan modellen met absolute demping. Bovendien lieten we zien dat het fitten van een lineair model met absolute demping aan een traject dat is gegenereerd met een relatieve demping-model, leidt tot een recursief (N-vormig) equilibrium traject (zoals inderdaad werd gereconstrueerd door Latash & Gottlieb, 1991, en Gomi & Kawato, 1997). Het betekent dat de reconstructie van een recursief equilibrium traject op basis van een model zonder relatieve demping, niet kan worden gebruikt als een geldig argument tegen de algemene idee van equilibrium punt sturing. Een laatste resultaat was dat relatieve demping in het model van Smeets en Brenner (1995a) de voorspelling door het model sterk verbeterde. aangezien het model van Smeets en Brenner de basis was van **hoofdstuk 2**, besloten we het experiment van dat hoofdstuk in een verbeterde vorm te herhalen, als een test voor een model met relatieve demping (**hoofdstuk 7**).

Een test voor het nieuwe massa-veer model (hoofdstuk 7)

In **hoofdstuk 7** bespreken we de resultaten van een verbeterde versie van het experiment uit **hoofdstuk 2**, om het model met relatieve demping te testen (**hoofdstuk 6**). Het model werd gefit aan de zijwaartse component van de snelle onderscheppende bewegingen van de hand, voor doelen die alleen verschilden in de plaats van verschijnen. Het gefitte model voorspelde de zijwaartse bewegingen van de hand uitstekend, net als e bewegingen naar doelen die van snelheid veranderden. Het model kon echter niet de bewegingen als gevolg van de kracht verstoringen voorspellen net als in **hoofdstuk 2**). Aangezien de effecten van vroege en late verstoringen vrijwel gelijk waren, kan dit resultaat niet worden verklaard door de (grote) veranderingen in houding en snelheid van de arm. De meest waarschijnlijke verklaring waarom het model de invloed van de verstorende kracht is dat de stijfheid sterk niet-lineair is. We concluderen dat ons –mechanische– massa-veer model de plan en sturingsprocessen goed beschrijft, maar paradoxaal genoeg niet het mechanische gedrag van de arm.

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Marc de Lussanet

Levensloop

Na mijn geboorte op 8 december 1968 te Rijswijk, groeide ik op in Woudenberg. In mei 1987 slaagde ik voor mijn examen VWO (Voorbereidend Wetenschappelijk Onderwijs, met exact vakkenpakket) aan Scholengemeenschap "De Amersfoortse Berg" (Amersfoort). Hoewel ik al enige jaren biologie wilde studeren, ging ik eerst een jaar naar Finland, waar ik met veel plezier de wintercursus "kunstzinnige vorming" aan de Volkshogeschool Åland deed. In september 1988 begon mijn studie Biologie, oriëntatie organisme aan de Landbouw Universiteit Wageningen. Ik volgde een zeer breed pakket van vakken, waaronder drie afstudeeronderwerpen. Het eerste over de relatie tussen het gedrag van bladluizen en hun efficiëntie als overbrengers van virussen op planten. Het tweede en belangrijkste onderwerp was biomechanica: een studie naar de optimale lengtes van beweeglijke (been- en pees-) elementen in de kop van zeepaardjes en aanverwanten (*Syngnathidae*) en andere vissen. Tenslotte deed ik een onderzoekje naar de invloed van grootte en verdeling van gastheren op de optimale tijd- en energiebesteding van een parasitaire sluipwesp *Asobara tabida* (*Braconidea*). November 1994 studeerde ik af.

Februari – juli 1995 werkte ik met een VSB-beurs bij R.McN. Alexander in Leeds (UK) aan een wiskundig model voor optimale moment-armen en coördinatie van spieren over twee gewrichten (biartikulaire spieren zoals de biceps). In oktober-december van dat jaar verbleef ik bij D.A. Rosenbaum (Pennsylvania, USA) om mee te werken aan zijn model voor motor sturing. Tot september 1996 werkte ik aan publicaties (de Lussanet & Alexander, 1997; de Lussanet & Muller 1997) en aan de uitwerking van een model voor de optimale lengte van de snuit van zeepaardjes en de uitwerking van data van mijn hoofdafstudeeronderwerp. In september 1996 begin ik met het promotieonderzoek waarvan dit proefschrift het resultaat is. Inmiddels (november 2001) ben ik begonnen aan een onderzoek bij Markus Lappe, Psychologie, Münster. Dit onderzoek gaat over het waarnemen en herkennen van "biologische" beweging, bijvoorbeeld hoe je uit zeer summiere en verstoorde informatie al een niet-rigide bewegend figuur (zoals een mens of dier) kan herkennen.

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