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1. Introduction



Characteristics of online movement corrections

We interact with a world that is in motion. When interacting with an object that started moving before we initiate our action towards it, we can use the perceived motion to predict when the object will be where. For example, when you are eating in a conveyor belt sushi restaurant, where the sushi goes around on a track, and you want to grasp a specific plate that you spotted at the other corner, you can use the movement of the plate to predict when it will be within arm's reach. As long as we can predict the position of the plate over time, we can interact with it without processing new information during our movements (Dessing, Oostwoud Wijdenes, Peper, & Beek, 2009; Narain, Mamassian, van Beers, Smeets, & Brenner, 2013). However, sometimes the changes in the surroundings are not in line with our predictions. For example, there might be a technical problem with the belt that makes it suddenly stop moving just when you started to reach for your desired plate. If you would finish your movement as planned, you would not arrive at your desired plate but at a plate adjacent to it. To eat your favorite sushi, you will need to adjust your movement to the new position of the plate. This thesis deals with the type of motor control that is needed to account for unplanned changes of the surroundings when we are in motion. Often, this type of motor control is referred to as online control.

It is unknown how we control our movements. We do not know how the brain uses information to form movement plans and we do not know what these plans look like. Several theories have been proposed to explain how the brain uses information and what the movement plans may look like. For situations in which the surroundings do not change, or if changes in the surroundings are in line with our predictions, motor control may be described by an open-loop control system. For this type of control, the movement is planned before it is executed and then executed as planned. But if the surroundings change unexpectedly during the movement, or if a movement is not exactly executed as planned, an open-loop control system does not correct within the same movement. Humans can adjust their movements extremely rapidly in response to changes in the surroundings (Brenner & Smeets, 1997; Gielen, van den Heuvel, &

Denier van der Gon, 1984; Prablanc & Martin, 1992; Soechting & Lacquaniti, 1983; van Sonderen & Denier van der Gon, 1991) or changes in the perceived position of their own body (Brenner & Smeets, 2003; Sarlegna et al., 2003; Saunders & Knill, 2003). The ability to adjust ongoing movements rapidly is relatively robust against the effects of aging (Farnè et al., 2003; Kadota & Gomi, 2010), and it is preserved in patients suffering from different neurological disorders like cerebral palsy, agenesis of the corpus callosum and Parkinson's disease (Day & Brown, 2001; Desmurget et al., 2004; Van Thiel, Meulenbroek, Smeets, & Hulstijn, 2002). Moreover, the ability is not limited to adjusting pointing movements with one finger, it holds for grasping movements (Paulignan, Jeannerod, MacKenzie, & Marteniuk, 1991; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991; Voudouris, Smeets, & Brenner, in revision) and movements of the limbs during walking (Reynolds & Day, 2005a).

One way in which the problem that arises with open-loop control could be solved is by means of feedback control. This type of control monitors the movement during execution and determines whether the hand will come to a stop at the target. If this mechanism detects that the hand will not stop at the target, it makes sure that the current movement is adjusted. Different variables to specify and monitor the movement have been proposed. Frameworks of motor control for example specify the movement in terms of a desired trajectory in joint angles and resulting net joint torques (Soechting & Lacquaniti, 1981), in terms of a desired equilibrium point that has to be reached (Feldman, 1986) or in terms of one or multiple variables that are optimized (Todorov & Jordan, 2002). Furthermore, different sources of information that monitor the success of the movement have been proposed to be involved in movement corrections. The brain could use afferent information of the executed movement and compare this with the desired movement. To minimize time delays, the brain could also use a prediction of the consequences of the current movement to update the control, i.e. efferent information (von Holst, 1954). Besides, the brain might use knowledge of the internal dynamics of the system to make adjustments (Wolpert, Miall, & Kawato, 1998).

The different frameworks of motor control also describe online movement adjustments in response to changes in the surroundings. For trajectory specification in

terms of minimum jerk it was suggested to either abort the old movement and plan a new movement, or add a second trajectory that moves from the initial target to the new target position and add this trajectory to the initially planned trajectory (Flash & Henis, 1991; Henis & Flash, 1995). The first solution needs efferent information about the kinematic state of the hand at the time of the change, while the second solution is independent of such information. For equilibrium point control, changes of the surroundings involve a shift in the equilibrium point (Flanagan, Ostry, & Feldman, 1993). No online information about the state of the hand or knowledge about the internal dynamics of the hand at the level of the brain is required for this type of control. Optimal control theory describes online corrections as movements resulting from an optimization of energy consumption, endpoint accuracy, endpoint stability and movement speed (Liu & Todorov, 2007). This theory assumes that the brain uses afferent and efferent information as well as an internal model to control movement adjustments. The work in this thesis is not restricted to one of these motor control models for online movement adjustments. Together, they comprise the framework of the movement behavior that I investigated.

Investigating the characteristics

The work described in this thesis tries to unravel the online control of movement by describing how the corrections are fulfilled. Knowledge about the characteristics of online corrections can serve the development of motor control models within the different frameworks of motor control. By going through the timeline of a movement adjustment backwards, I will describe these characteristics. Thus, I will start with the action of the movement adjustment and discuss how, in terms of behavior, the online control mechanism makes sure that the movement is adjusted when the surroundings change. Then I will discuss what online information is monitored to determine whether the hand will end at the target and what serves as input for the forthcoming adjustment. Finally, I will go beyond the within-movement level and determine whether previous movement adjustments affect future movements.

The characteristics of movement adjustments are discussed on the basis of four different behavioral parameters: response latency, response intensity, movement

duration and endpoint accuracy. Response latency refers to the amount of time that passes from the moment that a change in the surroundings occurs to the moment that one starts to correct for this change. In order to precisely determine the response latency, we need to know exactly when the change in the surroundings occurred and when the hand deviated from its planned path. In an experiment, the changes in the surroundings are controlled and registered by the experimenter with a reliability that is limited by the accuracy and precision of the image projection equipment. The reliability of the identification of when the hand exactly starts to deviate from its planned path is of course limited by the reliability of the movement registration equipment, but depends also strongly on the method that is used to determine the deviation. Chapter 2 describes a modeling study to systematically examine which method determines the moment that the hand starts to deviate from its originally planned movement most reliably. Since this moment is unknown for real movement adjustments, I simulated movements and movement adjustments with a known latency. The performance of three different methods that are commonly used in the field are compared with the true latency of the simulated movement adjustments.

The second parameter, response intensity, refers to how vigorously the movement is adjusted. It is influenced by both the size and the duration of the adjustment: large adjustments are more intense than small adjustments with the same duration, and adjustments that last shorter are more intense than similar sized adjustments that last longer. Movement duration refers to the time that elapses from movement onset to movement end. Endpoint accuracy refers to how close to the target the movement ended.

Changing the surroundings

To evoke the rapid corrections described in Chapters 3, 4, 5 and 6, a double-step paradigm was used (Georgopoulos, Kalaska, & Massey, 1981; Pélisson, Prablanc, Goodale, & Jeannerod, 1986; Soechting & Lacquaniti, 1983). In this paradigm an initial target is presented to the subject and the subject is instructed to move to this target. At some time during the trial, the initial target disappears and at the same time a second

target appears at another location. This results in a so-called target 'jump'. Thus the changes in the surroundings that are used in this thesis are changes in the position of the target.

Executing the adjustment

Different combinations of response latency, intensity and movement duration can result in a successful correction. For example, one could postpone the initiation of a correction as long as possible to gather as much information as possible, and execute the correction vigorously as late as possible. However, one could also end at the new target position by initiating a correction as fast as possible with a vigorousness of execution that depends on the time left to correct with regard to the end of the movement. Besides these two examples many other combinations of latency, intensity and duration could result in successful corrections. Chapter 3 examines how the online control mechanism ensures that the movement is adjusted when the position of the target changes. Is there a single strategy that people use to adjust their movements and what is this strategy? I tried to answer this question by varying the timing of the occurrence of target jumps and the number of jumps and examining the resulting movement adjustments.

Planning the adjustment

The surroundings can change in infinitely many ways. Not all changes of the target require adjustments of our movements. For example, if the shading of the sushi plate changes because the waiter dimmed the light there is no need to adjust the movement. One aspect of the target that is considered important is the target position. For the planning of a movement, it is suggested that the target position is considered in terms of direction and distance (Ghez et al., 1997; Gordon, Ghilardi, & Ghez, 1994; Krakauer, Pine, Ghilardi, & Ghez, 2000; Rosenbaum, 1980). Chapter 4 examines whether this also holds for online movement adjustments and whether the same strategy is used to correct for changes in target distance and direction. Another aspect of the target that is considered important is its velocity (Brenner, Smeets, & de Lussanet, 1998; Smeets & Brenner, 1995). When a target instantaneously changes its position it appears to

move from the one location to the other (Wertheimer, 1912; Zeeman & Roelofs, 1953). Chapter 5 examines whether this apparent motion influences the online adjustment by comparing the response latency and intensity in conditions with apparent motion to conditions with less apparent motion.

Movement history

Chapters 3-5 study online movement adjustments that occur if changes in the surroundings are not in accordance with our predictions. What happens in this case with our predictions? Do online corrections result in an update of our predictions for movements in the future? This was studied in Chapter 6. Subjects were presented with a simple sequence of target jump trials: the size of the target jump alternated between two possibilities for consecutive trials. I measured the extent to which subjects updated their predictions to anticipate the target jumps.

Epilogue

The last chapter summarizes the main findings of the studies presented in this thesis. Furthermore, the findings of the different studies are related in view of the examined behavioral parameters. The application of the method to determine the response latency is considered. Also, the findings are discussed in relation to other perturbations that affect the control of movements and motor control frameworks. The epilogue closes with a brief conclusion.