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Anticipatory Planning of Sequential Hand and Finger Movements

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ABSTRACT. Hand movements may be anticipatorily planned to reach an immediate target and at the same time facilitate movements to subsequent targets. Researchers have proposed that in anticipatory planning, information about subsequent targets needs to be processed to engage in the planning of the next movement. To test this hypothesis, the authors varied the information 48 participants had about to-be-executed two-step hand and finger movement sequences prior to a choice reaction signal. Movements were initialized faster if participants had advance information about the second target of the sequence than if participants had no advance information at all. The results imply that movement segments to late targets in a movement sequence may be at least partially planned, even if information about earlier targets is not yet available.

Keywords: anticipation, movement sequences, planning

Before accurate goal-directed movements can be performed, they need to be planned. During the planning of a point-to-point hand movement, various movement parameters are determined, such as movement direction and amplitude (Bock & Arnold, 1992; Cisek & Kalaska, 2005; Rosenbaum, 1980), based on the initial body state (Soechting, Buneo, Herrmann, & Flanders, 1995) or the presence of obstacles (Dean & Brüwer, 1994). This has led to several theories about the planning of single hand movements—which emphasize the specification of movement parameters (Erlhagen & Schöner, 2002)—the determination of arm postures and arm trajectories (Rosenbaum, Loukopoulos, Meulenbroek, Vaughan, & Engelbrecht, 1995; Rosenbaum, Meulenbroek, Vaughan, & Jansen, 1999), the determination of neural control signals (Harris & Wolpert, 1998), or the task-dependent preparation of an adaptive neural controller (Butz, Herbort, & Hoffmann, 2007).

However, nearly all simple manual movements are a part of a larger sequence of movements. We do not play single notes on an instrument, but rather, we play entire scores, and we do not execute isolated grasping movements, but rather, we do something with the grasped object. Like simple point-to-point movements, sequential movements need to be at least partially prepared (Henry & Rogers, 1960; Klapp & Erwin, 1976; Rosenbaum, Inhoff, & Gordon, 1984), including sequential arm movements (Glencross, 1973; Lajoie & Franks, 1997; Lavrysen et al., 2003; Smiley-Oyen & Worringham, 2001; Vindras & Viviani, 2005).

Interestingly, the planning of the movement parameters of the individual point-to-point movements that constitute a movement sequence has received less attention. However, the planning of point-to-point movements in a sequence might considerably differ from the planning of isolated point-to-point movements because the parameters of isolated movements and movements that are part of a sequence differ considerably. The term *anticipatory modification* of a movement refers to the observation that parameters of a movement are not determined only by initial conditions and a target, but also by upcoming tasks. Anticipatory modifications have been frequently observed in manual movements, for example, in grasping (Johnson-Frey, McCarty, & Keen, 2004; Mutsaarts, Steenbergen, & Bekkering, 2006; Rosenbaum et al., 1990) and coarticulation in speech production (Fowler & Saltzman, 1993; MacNeilage, 1980). Furthermore, anticipatory modifications have been reported in sequential reaching movements. Parameters of a point-to-point movement depend on a subsequent movement's index of difficulty (Rand & Stelmach, 2000), movement direction (Adam et al., 2000), hand target location (Fischer, Rosenbau, & Vaughan, 1997; Klein Breteler, Hondzinski, & Flanders, 2003), availability of feedback (Lavrysen, Helsen, Elliott, & Adam, 2002), or if there is a second movement at all (Adam et al.; Glencross, 1980). However, it is unclear how such anticipatory modifications emerge. For example, the dependency of movement parameters on the sequential context may be caused by the interference of the control of the ongoing movement and the preparation of the upcoming one (Adam et al.). However, anticipatory modifications in grasping clearly seem to facilitate upcoming movements, for example by optimizing the end-state comfort after replacing a grasped object (Rosenbaum et al., 1990). Likewise, pointing movements end in arm postures that facilitate the execution of the next movement (Klein Breteler et al.; Fischer et al.).

These findings strongly suggest that anticipatory modifications of movements are the result of anticipatory movement planning. In anticipatory movement planning, not only are the initial conditions and the immediate goal of a movement are taken into account to determine movement parameters, but information about upcoming movements is also considered. Fischer et al. (1997) and Herbort and Butz (2007) proposed a model for anticipatory planning of movement end postures. Both accounts assumed that anticipatory planning of the first movement in a movement sequence begins with the planning of a movement to the second target. The plan for a movement to the second target provides constraints in form of a distance metric. The metric thus constrains the plan generation of the first movement segment in accordance to the demands of the second movement segment. According to Fischer et al., this implies selecting an end posture for the first movement that is close to both, the initial posture and

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the desired end posture at the second target. Thus, the first movement is modified by the demands of the second target and results in a reduction of the trajectory length of the entire movement sequence.

However, evidence for the hypothesis that anticipatory planning of a two-step movement sequence requires the planning of a movement to the second of two targets before the initial movement can be planned is scarce. Alternatively, immediate and upcoming targets might be processed in parallel or information about upcoming targets might only be integrated late in the movement planning process or even only during the execution of an ongoing movement. Experiments that report anticipatory modifications of movements are inconclusive in that respect (Fischer et al., 1997; Klein Breteler et al., 2003). Because these experiments mainly report anticipatory modifications late or at the end of a movement, one cannot conclude if these modifications emerge because of anticipatory planning processes before movement initiation as described in the aforementioned models or if these modifications result from the adjustment of ongoing movements. Last, the notion that the planning of a forthcoming movement is based on the plan for a subsequent movement is at odds with the notion that the segments of sequential movements are prepared in the order of their execution (Rosenbaum et al., 1984; Rosenbaum, Hindorff, & Munro, 1987; Ulrich, Giray, & Schaffer, 1990).

The present study was motivated by our desire to determine whether anticipatory modifications of movement parameters result from anticipatory movement planning in two-step hand and finger movement sequences according to the aforementioned models. If this is the case, some information about the second target needs to be processed before the planning of the first segment of the movement sequence can be completed because the demands of the second movement segment need to be integrated into the plan for the first movement segment. Hence, in the present article we test whether it is possible to plan the second movement segment of a two-step movement even before the planning of the first movement segment can be initiated. If this is the case, participants should be able to initiate a sequential movement quicker if they have information about the second target of a movement sequence before a choice reaction signal specifies the first target, than if they have no advance information about the to be executed movement sequences before a choice reaction signal appears.

The results of an experiment designed to analyze the planning of sequential finger-tapping movements (cf. Experiment 2 in Rosenbaum et al., 1984) gives first hints in this direction. In a choice reaction task, participants had to respond to a choice reaction signal with sequential finger-tapping movements. The first part of the sequence was always a tap with the left or right index finger; the second part was always a tap with the left or right middle finger. Before the choice reaction signal determined the specific response sequence, participants knew either which index finger to use, which middle finger to use, or neither knew which index finger, nor which middle finger to use. Reaction times were generally shortest if participants knew the first part of the response. In addition, reaction times were on average somewhat shorter if participants knew the second part of the response than if they knew neither first nor second part of the response. However, this difference was strongly modulated by the complexity of the response rule. If the responses required taps with the index and middle finger of a single hand, reaction times (RT) were numerically shorter if participants knew the second part of the response than if they had no advance information. In contrast, if the responses required taps with the index and middle finger of different hands, RTs were numerically longer if participants knew the second part of the response than if they had no advance information. Thus, it is hard to draw conclusions from Rosenbaum et al.'s experiment for the question that the present article addresses. First, the interaction of the complexity of the response with the advance information condition masked the effect of advance information about the second target on RT. Second, in the experiment responses consisted of a sequence of finger taps with different fingers. However, it is doubtful that single finger taps are modified to facilitate a subsequent tap with another finger (Engel, Flanders, & Soechting, 1997). One reason is that tapping movements are constraint and thus offer little room for modification. Further, there is little dependency between successive finger taps and modifications of the first movement will have little or no effect on the second movement. Hence, participants in Rosenbaum et al.'s experiment might be discouraged from planning anticipatory modifications of movements because it does not improve their performance in the specific experimental setting. Based on these considerations, we adapted the paradigm of Rosenbaum et al.'s Experiment 2 with one central modification which aimed to encourage the participants to engage in anticipatory planning. In the present study, the response sequences had to be executed with a single effector. This assures a high dependency between the movement segments that constitute the first and second part of the response sequence and thus makes anticipatory planning beneficial. Furthermore, this eliminates the influence of the response complexity on RT because all responses are carried out with the same effector.

According to Rosenbaum et al.'s (1984) Experiment 2, we established three conditions of advance information by requiring our participants to respond to a two-choice reaction signal with a two-step movement sequence. In the uncertain–certain (UC) condition, participants had no information about the first target until a choice reaction signal informed them to execute a movement sequence but were certain about the second target. In the uncertain–uncertain (UU) condition, participants were uncertain of both targets until the choice reaction signal appeared. In the certain–uncertain (CU) condition, participants were certain about the first target and uncertain about the second target until the choice reaction signal appeared. Depending on the condition, participants could thus be sure of the first target in the sequence, the second target, or would not have advance information about either of the two targets.

The critical comparison is between condition UC and UU. In condition UC, participants might be able to plan the second movement before the choice reaction signal, whereas this is impossible in condition UU. Thus, if the second movement segment can be at least partially planned independent of information about the first movement segment, RTs should be shorter in condition UC than in condition UU. As a comparison, we included condition CU, in which participants are able to plan the first movement and are unable to plan the second movement. In addition, to check if the kind of movement influences movement planning, one group of participants had to execute arm movements over larger distances and another group of participants had to perform movements with the index finger over small distances.

Method

Participants had to execute two-step arm or finger movements upon the occurrence of a choice reaction signal. To establish different conditions of advance information, the participants had to execute one of two alternative sequences in each trial of each experimental block. Thus, in each experimental block, only two different sequences had to be executed as response to a choice reaction signal. The two sequences could share the first target (CU condition), the second target (UC condition), or no target at all (UU condition). In addition, we varied the kind of the to-be executed movement (movement type) between two independent groups of participants. Participants in the arm movement group had to move the right hand and arm to press keys with a distance of 20 cm. Participants in the finger movement group had to make sequential movements with the right index finger to press keys with a distance of only 1.2 cm.

Participants

A total of 48 students (24 for each movement type) from the University of Würzburg (37 women, 11 men; age range = 18–41 years; *M* age = 23 years) participated in the experiment, either fulfilling a course requirement or for payment (€6). All participants were unaware of the purpose of the study and had normal or corrected-to-normal vision. According to the handedness scale of the Lateral Preference Inventory (Coren, 1993), 41 participants were right-handed and 7 were left-handed. Regardless of handedness, all participants performed the movements with the right hand. Statistical comparisons of the participants in both groups revealed no significant difference with respect to sex, age, or handedness.

Apparatus and Stimuli

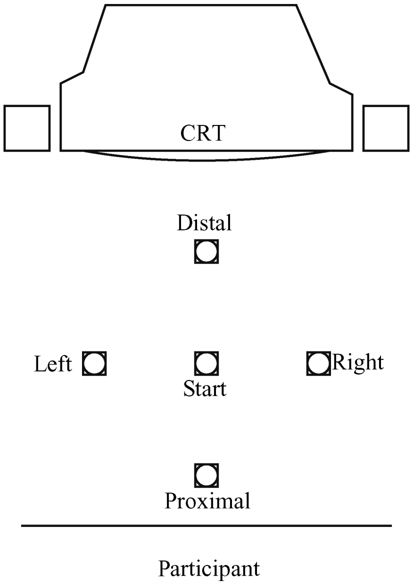

FIGURE 1. The setup of the five response keys in the arm movement condition.

The participants were seated in front of a table, on which five response keys were fixed (see Figure 1). A start key was fixed 25 cm from the border of the table close to the participant and the remaining four keys (left, right, proximal, and distal) were arranged around the start key in the shape of a plus sign. The keys were 1.2 cm × 1.2 cm. For the arm movement group, the distance between the start key and the remaining keys was 20 cm. For the finger movement group, the distance between the start key and the remaining keys was only 1.2 cm. In addition, for the finger movement group a handrest was attached to the table to the right of the keys to enable more comfortable index finger movements. The keys on the sagital axis (proximal, start, and distal) were aligned to the midline of the participant. Stimuli and feedback were provided by a 17-in monitor (display resolution 640 × 480) and two speakers next to it, which both stood 80 cm from the participants. Stimuli were displayed and responses were recorded with the E-Prime software (Psychology Software Tools, Inc., Pittsburgh, PA, USA; Schneider, Eschman, & Zuccolotto, 2002).

Procedure and Design

A trial began when the participant pressed and held down the start key. After the presentation of a black screen for 1,000 ms, a white square (6.5° × 6.5°) was displayed for another 1,000 ms and a tone was played for 100 ms (440 hz). After a variable interstimulus interval (ISI) of 500 ms, 750 ms, or 1,000 ms, a letter (S, T, O, or X, subtending 1.8° × 1.8°) indicated the to be executed movement. The association between letter and movement sequence was held constant throughout each experimental session but was balanced between participants. Which letter referred to which sequence was displayed throughout the experiment on a printed instruction, which was placed on the table. The participant had to respond to the letter by releasing the start key and then pressing two keys in a specific sequence. Participants in the arm movement group were instructed to move with the arm and to press the keys with the flat hand. Participants in the finger-movement group were instructed to keep the hand on the handrest and press the keys with the index finger. After the correct execution of the movement sequence, the word *richtig* (German word for *correct*) was displayed in green letters, accompanied by a low-pitch tone (256 Hz, 200 ms). If the response was erroneous the word *falsch* (German word for *wrong*) was displayed in red letters and a high-pitch tone was played (1,056 Hz, 200 ms). The feedback remained visible until the participant pressed the start key again and thus initiated the next trial. If the participant released the start key before the choice reaction signal was displayed, the trial was repeated from start.

During the experiment, four different movement sequences had to be executed. Each started from the start key, the first key in a sequence was always either the distal or proximal key, the second key was always either the left or the right key. Thus, there were four possible sequences: distal–left, distal–right, proximal–left, and proximal–right. In each block of the experiment only two different sequences had to be executed. This resulted in six different pairings of sequences, which were tested in six consecutive blocks. In the CU condition blocks, required responses alternated randomly between two sequences that shared the first target (e.g., distal–right and distal–left). In the UC condition blocks, required responses alternated randomly between two sequences that shared the second target (e.g., distal–right and proximal–right). Last, in the UU condition blocks, required responses alternated randomly between two sequences that shared neither the first nor the second target (e.g., distal–right and proximal–left). The different blocks were presented in a participant-wise randomized order, which assured that each advance information condition was presented once in the first three blocks and once in the last three blocks of the session of each participant.

Each experimental block consisted of 6 training trials and 72 test trials (2 Sequences × 3 ISIs × 12 Repetitions) presented in randomized order. Before the training and before the test trials, participants were informed about the sequences that would have to be performed in the block and were asked to react as fast and correct as possible. To encourage the participants to faster responses, the average time to initiate and execute a sequence and the percentage of errors made were displayed at the end of each block.

Dependent Variables

For the data analysis, four dependent measures were recorded. As the variable of main interest, the RT is defined as the time from the onset of the choice reaction signal to the release of the start key. The *movement time of the first movement* (MT1) is defined as the time between the release of the start key to the pressing of the first target, the *dwell time* (DT) is the time from pressing the first target key to its release, and the *movement time of the second movement* (MT2) is the time from releasing the first target key to pressing the second target key. In addition, we recorded the percentage of errors (PE) of each block.

Results

We only evaluated data from the test trials. Trials in which the sequence was carried out incorrectly were excluded from the analysis (2.7%). From the remaining trials, we removed those in which RT or the overall movement time (MT1 + DT + MT2) deviated more than two standard deviations from the participant's average for the respective combination of advance information, ISI, and sequence (8.8%). We first averaged RT, MT1, DT, MT2, and PE for each participant and advance information condition (see Table 1). The data was statistically evaluated with split-plot ANOVAs with advance information condition (CU, UC, UU) as within-subject factors and movement type (arm, finger) as between-subject factors.

We wanted to test the hypothesis that participants benefit from advance information of the second target in a movement sequence, even if they do not yet know the first target. For

TABLE 1. Means and Standard Deviations of Reaction Time (RT), Movement Time of the First Movement Segment (MT1), Dwell Time on the First Target (DT), Movement Time of the Second Movement Segment (MT2, in ms), and Percent Errors (PE, in%) by Movement Type and Advance Information Condition.

	RT		MT1		DT		MT2		PE	
Variable	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*	*M*	*SD*
Arm movements										
Certain–uncertain	347	70	200	34	70	18	226	35	1.47	1.28
Uncertain-certain	392	64	218	33	72	20	330	35	1.80	1.37
Uncertain–uncertain	400	69	222	38	74	23	232	33	2.14	1.37
Finger movements										
Certain–uncertain	336	63	107	26	104	18	118	26	3.47	2.85
Uncertain–certain	379	63	116	23	104	15	116	22	3.59	2.75
Uncertain–uncertain	390	67	116	24	104	17	113	22	3.73	3.14

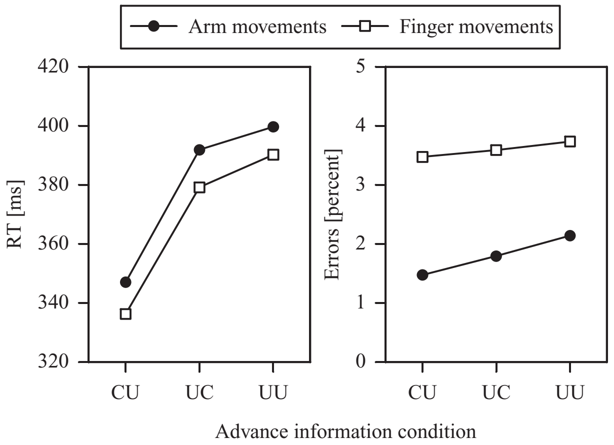

FIGURE 2. RTs and percentage errors for arm and finger movements dependent on advance information condition. CU = certain–uncertain, UC = uncertain–certain, UU = uncertain–uncertain.

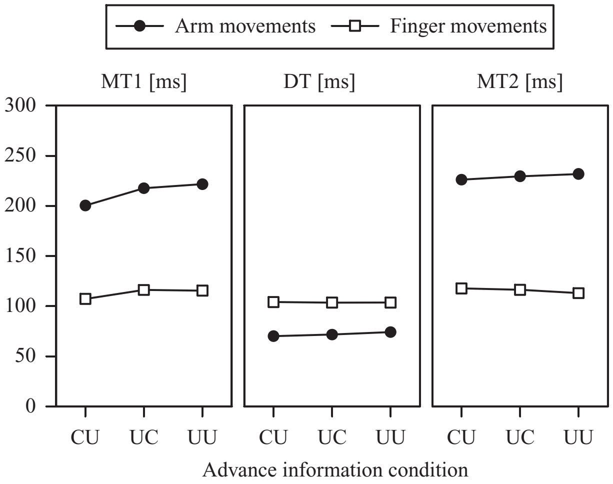

FIGURE 3. Duration of the movement from the start key to the first target (MT1), the dwell time (DT), and the duration of the movement from the first to the second target for arm and finger movements dependent on advance information condition. CU = certain–uncertain, UC = uncertain–certain, UU = uncertain–uncertain.

both movement types, RTs were shorter if participants had advance information about the second target but not the first than if participants knew neither the first nor the second target. Advance information about the first target resulted in the most pronounced decrease of RTs. Figure 2 shows that in general, RTs were approximately 53 ms shorter in the CU condition and still approximately 9 ms shorter in the UC condition compared with the UU condition, $F(2, 92) = 124.44$, $p < .001$. A contrast analysis confirmed that RTs in the CU condition were significantly shorter than in the UU condition, $F(1, 46) = 183.57$, $p < .001$. According to our hypothesis, RTs were also significantly shorter in the UC condition than in the UU condition, $F(1, 46) = 8.42$, $p < .01$. Interestingly, RT was not affected by movement type, $F(1, 46) = 0.346$, $p = .56$. There was no interaction between advance information and movement type, $F(2, 46) = 0.10$, $p = .90$. To summarize, our results demonstrate that advance information about upcoming movement targets may be processed even if the immediate target is yet unspecified.

Percentage of Errors

The right panel of Figure 2 shows PE. More errors were made in the finger movement experiment than in the arm movement experiment, $F(1, 46) = 10.10$, $p < .01$. Like RT, PE was lowest in the CU condition, higher in the UC condition, and highest in the UU condition, but the differences were not significant, $F(2, 92) = 1.28$, $p = .28$. Thus, a speed–accuracy trade-off can be ruled out to explain the RT differences between the advance information conditions.

Movement Times and Dwell Time

Next, we analyzed the movement and dwell times of the executed movements. Not surprising, finger movements over short distances were much faster than arm movements over longer distances (see Figure 3). However, the time the hand or finger rests on the first target was shorter for arm movements than for finger movements. In addition, if the first target was known, movement times to the first target were reduced stronger in arm movements than in finger movements, compared with condition UU.

MT1 was 100 ms shorter for finger movements than for arm movements, $F(1, 46) = 148.09$, $p < .001$. The advance information condition had a significant influence on MT1, $F(2, 92) = 23.38$, $p < .001$, and interacted with movement type, $F(2, 92) = 3.84$, $p < .05$. A contrast analysis showed that MT1 was shorter in the CU condition than in the UU condition, $F(1, 46) = 32.91$, $p < .001$ and that this difference was more pronounced in arm movements than in finger movements, $F(1, 46) = 6.32$, $p < .05$.

DT was approximately 30 ms shorter for arm movements than for finger movements, $F(1, 46) = 42.49$, $p < .001$. There was no main effect of advance information condition, $F(2, 92) = .38$, $p = .69$, and no interaction, $F(2, 92) = .58$, $p = .56$.

MT2 was 113 ms shorter for finger movements than for arm movements, $F(1, 46) = 189.74$, $p < .001$. There was no main effect of advance information condition, $F(2, 92) = .14$, $p = .87$. However, movement type and advance information condition interacted, $F(2, 92) = 4.06$, $p < .05$. A post hoc test showed that the interaction resulted because the difference between MT2 of arm and finger movements was smaller in condition CU than in condition UU, $F(1, 46) = 8.52$, $p < .01$. To summarize, arm movements were generally slower than finger movements. However, the dwell time was significantly shorter for arm movements. Additionally, arm movement times benefited more from advance information about the first target than finger movements. Finally, the movement execution in the UC condition did not differ from the UU condition.

Discussion

The aim of the present experiment was to investigate if the second segment of a two-step movement can be at least partially prepared independently of the first movement segment. Hence, we asked our participants to perform two-step arm or finger movements, and we manipulated the information the participants had about the upcoming movement sequence. Movements were initiated faster if participants already knew the second target of the movement sequence but not the first target, as compared with a condition in which participants had no advance information about either target. Furthermore, this effect was not modulated by the effector used to execute the movement. Thus, we concluded that participants could use the information about the second target to start with the movement planning processes before the choice reaction signal specifies the entire movement sequence and thus information about the first movement segment is available. This supports models according to which anticipatory modifications of sequential movements result, at least partially, from anticipatory movement planning (Fischer et al., 1997; Herbort & Butz, 2007).

For the present study, we adapted Rosenbaum et al.'s (1984) procedure for their Experiment 2 for mainly three reasons. First, in each advance information condition the participants had to select between two possible movement sequences. Hence, the decision which response to initiate is as complex in the UU condition as in the CU and UC conditions, and hence, confound between advance information condition and response complexity is avoided (Hick, 1952). Second, different movement sequences might result in different RTs because of specific properties of the movement (Munro, Plumb, Wilson, Williams, & Mon-Williams, 2007). However, each participant executed each movement sequence the same number of times in all three advance information conditions, balancing the to-be-executed movements over the advance information conditions. Thus, RT differences between advance information conditions cannot be attributed to the kinematics or other features of the required movements. Third, the choice reaction signals were letters and had no spatial features that would make the discrimination of the stimuli easier dependent on the advance information condition. Furthermore, the letters were balanced over the participants, thus eliminating the impact of possible perceptual or semantic stimulus-response compatibilities. Thus, the RT differences between advance information conditions cannot be attributed to the perceptual processing of the choice reaction signal.

Theories of Anticipatory Movement Planning

Different computational models of anticipatory movement planning have been proposed. Based on experimental data, Fischer et al. (1997) proposed an account within the framework of the posture-based motion planning theory (Rosenbaum et al., 1995). According to the posture-based motion planning theory, during movement planning a desired end posture among many possible end postures of a movement is selected, based on various constraints. Fischer et al. proposed that the desired end posture at the first target of a two-target sequence is determined by a two-stage process. First, a movement from the initial arm posture to the second target is planned, resulting in a desired posture at the second target that is comparably close to the initial arm posture. After that, a desired arm posture at the first target location is selected that minimizes the movement costs of the first and second movement segment. Thus, the selection of the end posture of the first of two movement segments is aligned to the demands of the second movement segment.

A related account is offered in the SURE REACH framework (Butz et al., 2007; Herbort & Butz, 2007). This neural network model assumes that a movement plan is prepared that provides for each possible arm posture motor commands that drive the arm toward a manifold of potential end postures. The neural movement plan implicitly encodes the distance to the target from each possible arm posture. Similar to Fischer et al.'s (1997) account, given a two-target sequence, first a movement plan for a movement to the second of two targets is prepared. The implicit distance metric provided by this movement plan can be neurally overlaid with a representation of acceptable arm postures at the first target. This effectively discounts those potential end postures in the goal representation of the first movement segment that are distant from acceptable end postures at the end of the second movement segment. On the basis of such a weighted representation of the first goal, a movement plan can be prepared that biases the first movement to terminate at a posture that is close to the second goal.

To summarize, both models assume that the planning of the first segment of a two-step movement requires that a movement to the second goal has to some extent, already been planned. Hence, according to the models, the second segment of a movement is planned before the first movement segment is planned, and thus independently of the characteristics of the first movement segment. Thus, one prediction that could be derived from these models is that information of the second target in a two-step movement can be partially processed, even if no information about the first target is available. This notion is supported by our experiments because RTs are smaller when only information of the second target is available (UC) to the participant than when neither information of the first nor the second target is available (UU). Participants seem to be able to process the information about the location of the second target to some extent before the choice reaction signal appears and thus are able to initiate a movement more quickly in condition UC than in condition UU.

The result that RTs are generally shortest if the first target is known prior to the choice reaction signal is not necessarily at odds with both accounts, considering the participants' response strategies and the complexity of movement planning. First, participants are not bound to engage in anticipatory movement planning but may do so or not dependent on task requirements (Short & Cauraugh, 1999). In our experiment anticipatory movement planning might facilitate the execution of the two-step movement but is not crucial to follow the instructions. Thus, in the CU condition, participants might plan the first movement prior to the choice reaction signal, independent of the sequential context. This strategy may be beneficial for two reasons. On the one side, participants have more time to plan the first movement segment in condition CU than in condition UC or UU because they are informed about the first target before the onset of the choice reaction signal. Thus they can initiate planning without time pressure. The prolonged time to plan may be used to generate more elaborate movement plans for the first movement segments in condition CU than in the other conditions, which also results in significantly shorter movement times for the first movement segment in condition CU than for the first movement segment in conditions UC and UU. Hence, in condition CU, the benefits from planning the first movement segment independent of the sequential context might outweigh the benefits for integrating the sequential context into the movement plan and thus discourage participants from anticipatory planning. Alternatively, if participants plan the first movement independently of the second movement, RT in condition CU can be further reduced by postponing the preparation of the second movement segment until the execution of the first movement segment starts. Such a strategy may be feasible because MT1 is usually approximately 200 ms in arm movements and thus offers enough time to finish the preparation of the second segment movement during the execution of the first one.

Second, both models surely do not account for every aspect of movement planning but focus on the explicit or implicit selection of end postures at the end of point-to-point movements. However, motor control is generally considered as a process that requires multiple representations and coordinate transformations (Cisek, 2005; Haruno, Wolpert, & Kawato, 2003; Hoffmann, Butz, Herbort, Kiesel, & Lenhard, 2007; Jordan & Wolpert, 1999). Hence the results of the planning process that are described in both models are likely to be not used directly for motor control but require additional computations. Both models describe how the end posture of the first movement may be computed by the brain's motor system, given the desired hand target and the sequential context (solving the inverse kinematics problem). However, once the desired end posture is determined, still other aspects of the movement may have to be planned. For example, the motor system also has to plan a sequence of motor commands that transports the arm from the current posture to the desired end posture (solving the inverse dynamics problem; Harris & Wolpert, 1998; Jordan & Wolpert; Todorov, 2000). This additional planning process may take additional time and may only be initiated once a desired end posture is determined. Hence, the RT benefits from planning a movement to the second target before the appearance of the choice reaction signal in condition UC may be much smaller than the RT benefits for preparing the first movement in condition CU. In the first case, only some aspects of the kinematic features (e.g., end postures) of the movements may be planned in advance. In contrast, in the latter case, not only the movement kinematics but also the movement dynamics (e.g., motor commands) may be fully planned. Thus, in experimental conditions in which the first movement is known prior to the choice reaction signal, participants may prefer to prepare all parameters of the movement over the alternative to only start anticipatory planning and then having to finish planning as soon as the choice reaction signal appears.

Order of the Preparation of Sequential Movements

The current experiment complements findings of previous studies on the preparation of sequential movements. We replicated Rosenbaum et al.'s (1984) Experiment 2 by showing clear RT benefits for those conditions, in which the first target is known before the onset of the choice reaction signal (CU) in contrast to conditions, in which neither first nor second target are known in advance (UU). Interestingly, in Rosenbaum et al.'s Experiment 2 and in the present study, RTs were shorter (approximately 9 ms in both experiments) in conditions in which only the second target is known in advance (UC) as compared with conditions in which neither first nor second target are known in advance (UU). The main difference between Rosenbaum et al.'s experiment and the present study is that in the former the responses consisted of sequential taps with different fingers (index and middle finger), whereas in the present study responses had to be carried out by a single effector (arm or finger movements). This distinction is critical because the RT difference between condition UC and UU was numerically strongly modulated depending on whether the response required taps with the fingers of only one hand or both hands in Rosenbaum et al.'s Experiment 2. This makes their data hard to interpret regarding the question of the present study. As our experiment uses a protocol in which the response had to be executed with a single effector (finger or arm) and thus a possible modulation of our response as in the original experiment was eliminated, we were able to complement the previous findings. The current data provides evidence that it is possible to process information related to the second of two targets independent of information about the first target. Because the results of our experiments do not depend on whether the response is performed with the index finger or the arm, it could be speculated that the small average RT difference between conditions UC and UU Rosenbaum et al. found could be attributed to advance preparation of the second tap, independent of the first tap.

Rosenbaum et al.'s (1984) experiment is part of a line of experiments that resulted in the prominent Hierarchical Editor Model for movement preparation (c.f. Rosenbaum et al., 1987). The Hierarchical Editor Model, according to which the individual segments of a sequential movement are planned in order of their execution, seems to be incompatible with models of anticipatory movement planning (Fischer et al., 1997; Herbort & Butz, 2007), which state that individual segments of a sequential movement are planned in reverse order. However, when comparing both seemingly contradictory approaches, one needs to consider two aspects. First, whereas models of anticipatory movement planning account for sequential arm movements, for which individual movement segments are strongly interdependent, the hierarchical editor model accounts for finger tapping movements, which exhibit less dependency between the individual movement segments. Hence, both models have been devised to account for rather different types of sequential movements. Second, even though our findings in the present experiment and the discussion of Rosenbaum et al.'s (1984) findings suggested that also in comparatively simple finger movements, late movements in a sequence might be planned partially before earlier movements, this does not necessarily contradict models that assume that the segments of sequential movements are planned in the order of their execution. In contrast, both models might account for different partially overlapping stages of movement planning. Consider that planning a two-step movement requires multiple computational processes, such as the planning of the movement kinematics and dynamics (Butz et al., 2007; Flash & Sejnowski, 2001). When participants engage in anticipatory planning, they might start by processing information about the second target. However, the planning of the second movement may not result in a full movement plan but may only determine some aspects of the movement such as the arm kinematics at the end of the second movement segment. Based on this preliminary planning, participants then prepare a complete movement plan of the kinematics and dynamics of both segments of the sequential movement. The preparation of the fully specified movement plan is likely to be organized in an order fashion (Rosenbaum et al., 1984, 1987). To conclude, models of anticipatory movement preparation may account for processes that provide preliminary constraints for optimizing a fully specified movement plan. Once these constraints are provided, the complete movement plan might be prepared in an ordered fashion.

Other evidence for the hypothesis that the segments of sequential reaching movements have to be prepared in order of their execution comes from experiments in which participants have been informed about the direction of the first (i.e., to the left or right) or second segment (i.e., away or toward the participant) of a two-step movement (Ulrich et al., 1990). We can only speculate why participants could not make use of information about the direction of the second movement segment in this earlier experiment but could use information about the location of the second target in the present study to partially plan movements. Current models for anticipatory movement planning offer one possible explanation (Fischer et al., 1997; Herbort & Butz, 2007). If participants know the exact location of the second target of a two-step movement, they can already determine a desired end posture for the second target and use this information for planning the first movement segment. Alternatively, if only the direction of the second movement segment is known, the to-be-executed movement sequence might terminate in either of two target locations. Hence, the final target location remains uncertain and participants cannot determine the end posture of the second movement in advance. However, besides the spatial layout of the target sequences, Ulrich et al.'s experiment differed from the present study in several other ways. Thus, further research is needed to pinpoint the crucial differences between Ulrich et al.'s and the present experiment.

Conclusion

By now, anticipatory modifications of movements have been reported in numerous manual tasks. However, the process that underlies these modifications, that is anticipatory movement planning, has received less attention. The present study demonstrates that for the planning of sequential reaching movements, information about upcoming targets may be processed even if the participant does not yet know the initial movement segment. These results support current theories of the anticipatory planning of movements (Fischer et al., 1997; Herbort & Butz, 2007), which claim that information about late targets in a movement sequence can be processed independent of information about the initial movement segment. However, further research is needed to unravel the details of anticipatory movement planning.

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