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Grasp posture planning during multi-segment object manipulation tasks — Interaction between cognitive and biomechanical factors

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ABSTRACT

The present study examined adaptations in the planning of initial grasp postures during a multi-segment object manipulation task. Participants performed a grasping and placing task that consisted of one, two, or three movement segments. The position of the targets was manipulated such that the degree of object rotation between the home and temporally proximal positions, and between the temporally proximal and distal target positions, varied. Participants selected initial grasp postures based on the specific requirements of the temporally proximal and temporally distal action segments, and adjustments in initial grasp posture depended on the temporal order of target location. In addition, during the initial stages of the experimental session initial grasp postures were influenced to a larger extent by the demands of the temporally proximal segment. However, over time, participants overcame these cognitive limitations and adjusted their initial grasp postures more strongly to the requirements of the temporally distal segment. Taken together, these results indicate that grasp posture planning is influenced by cognitive and biomechanical factors, and that participants learn to anticipate the task demands of temporally distal task demands, which we hypothesize, reduce the burden on the central nervous system.

1. Introduction

Movements performed in daily life rarely occur in isolation, but are most often embedded within a task consisting of multiple actions. For example, when reaching for a coffee carafe the goal is not merely to grasp the handle of the carafe, but also to do something with the carafe once it has been grasped. Although the "something" might differ depending on the situation, research has shown that action goals (e.g., pouring coffee from the carafe into a cup) exert considerable influence over the planning and execution of reach-to-grasp movements (e.g., Ansuini, Giosa, Turella, Altoè, & Castiello, 2008; Ansuini, Santello, Massaccesi, & Castiello, 2006; Armbrüster & Spijkers, 2006; Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987). For example, in Ansuini et al. (2008) participants reached for a bottle filled with water and then either 1) grasped the bottle without any subsequent action, 2) lifted and threw the bottle into a container, 3) lifted and placed the bottle on a target circle slightly larger than the bottle, 4) lifted and poured water from the bottle into a plastic container, or 5) lifted and passed the bottle to the experimenter. Although the initial part of the movement sequence (i.e., reach toward and grasp the bottle) was identical for all conditions, the authors observed that reach duration and the time course of hand shaping (measured at the level of individual finger joints) were influenced by the subsequent action.

The influence of action end-goal has also been shown to influence initial grasp posture planning during manual action sequences (e.g., Herbort & Butz, 2010, 2012; Hughes, Seegelke, & Schack, 2012; Hughes, Seegelke, Spiegel, et al., 2012; Rosenbaum, Vaughan, Barnes, & Jorgensen, 1992; Rosenbaum et al., 1990; Seegelke, Hughes, & Schack, 2011; Zhang & Rosenbaum, 2008). In a study by Zhang and Rosenbaum (2008) participants placed their right hand on top of a round object and slid the object from the start position to one of five final target positions. Their results showed that initial hand orientation varied as a function of the final target position such that participants placed their hands on the object at an angle that was inversely related to the final angle of the hand. Complementing this, Herbort and Butz (2010) had participants grasp a circular knob and turn it 45°, 90°, or 135° in a clockwise or counterclockwise direction. In line with the results of Zhang and Rosenbaum (2008), the authors found that initial forearm angles were inversely related to the final target angles, and that knob rotation direction had a considerably stronger influence (compared to the extent of rotation). Their data also yielded insights about the temporal nature of grasp

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posture formation during object manipulation. Overall, forearm rotations were evident at 25%of the reach-to-grasp phase, and reaction times were shorter when participants were given advance information about the required knob rotation, compared to when no advance information was available. Based on these results the authors argued that grasp postures are selected prior to movement onset, and are strongly influenced by the action goals of the task.

Haggard (1998) was one of the first to investigate planning of initial grasp postures during multi-segment action sequences (but see also Rosenbaum et al., 1990). In that study, participants grasped an octagonal object and subsequently placed it to two, three, or five different targets, depending on condition. Each movement sequence contained a critical target whose position was varied so it was either the first or the last target in the sequence. Haggard found that initial grasp choice differed depending on the specific movements they performed for sequences that consisted of up to three movements. Moreover, adjustments in initial grasp posture were more prominent when the critical target was the first in the sequence as compared to when it was the last. These results provide evidence that the central nervous system is able to integrate multi-segment movement sequences into a single action plan and that participants can better plan for steps that occur early in a movement sequence (i.e., a gradient of advance planning).

Although previous research has provided some insights into the planning of multi-segment actions (Haggard, 1998; Hesse & Deubel, 2010; Seegelke, Hughes, Schütz, & Schack, 2012), they have not assessed variations in grip choice across several repetitions. Accordingly, questions on the stability of initial grasp choice across several replications remain unanswered. Building on this work, the aims of the current study were to examine the influence of target orientation and sequence length on grasp posture planning during a multi-segment object manipulation task, and to ascertain whether initial grasp postures adapt to different task constraints (biomechanical and cognitive) over time. In this task, participants performed a grasping and placing task consisting of one, two, or three movement segments. In the one-segment movement sequence participants grasped a cylindrical object from a home position and lifted it upward 10 cm. In the two-segment movement sequence, participants grasped a cylindrical object from a home position and placed it on a first (temporally proximal) target position. In the three-segment movement sequence participants grasped a cylindrical object from a home position, placed it on a first target position (temporally proximal), and without adjusting their grasp posture placed it on a second target position (temporally distal). We also manipulated the position of the targets such that the degree of object rotation (ranging from 0° to 180°) between the home and temporally proximal target positions and between the temporally proximal target and temporally distal target positions differed.

Based on research indicating that grasp postures are planned prior to movement initiation (e.g., Herbort & Butz, 2010; Hughes, Seegelke, Spiegel, et al., 2012; Rosenbaum et al., 1992), and that participants can plan up to three movements in advance (e.g., Haggard, 1998; Hesse & Deubel, 2010), we hypothesized that initial grasp choice would be influenced by the first (temporally proximal) and second temporally distal targets of the movement. Moreover, given the research demonstrating that holistic grasp planning decreases with the number of action segments (Haggard, 1998), we expected that the temporally proximal target would have a stronger influence on initial grasp postures than the temporally distal target. Further, if participants adapt their movement plans in response to the imposed biomechanical (i.e., target orientation) and cognitive (i.e., target order) task constraints, we expected to observe changes in initial grasp postures over repetitions. Such a finding would be consistent with the hypothesis that grasp posture planning relies on a flexible, rather than a static, constraint hierarchy (Hughes & Franz, 2008; Hughes, Haddad, Franz, Zelaznik, & Ryu, 2011; Wel & Rosenbaum, 2010). Last, given the large corpus of research indicating a proportional relationship between the reaction time and the complexity of an action sequence (e.g., Christina, 1992; Fischman, 1984; Henry & Rogers, 1960; Klapp, 2010; Sternberg, Monsell, Knoll, & Wright, 1978), we hypothesized that movement initiation time (MIT) and approach time (AT) would increase as the number of steps and the required degree of object rotation in the action sequence increase.

2. Experiment 1

2.1. Methods

2.1.1. Participants

20 students from Bielefeld University (mean age = 24.3 years, SD = 4.3, 16 women, 4 men) participated in this experiment. All participants were right-handed (mean score = 96.7, SD = 14.9) as assessed using the Revised Edinburgh Handedness Inventory (Dragovich, 2004) and were paid 5€ for participation. Participants had normal or corrected to normal vision, and did not have any known neuromuscular disorders. The experiment was conducted in accordance with local ethical guidelines, and conformed to the declaration of Helsinki.

2.1.2. Apparatus and stimuli

The experimental apparatus is shown in Fig. 1AB. The set-up was positioned on a height adjustable shelf (200 cm × 60 cm). White paper circles (10.5 cm in diameter, with a 9 cm × 2 cm protrusion) were taped flat to the surface of the shelf and served to indicate the home, center, and outer targets. The home and outer targets were arranged in a semi-circular fashion, each separated by 45°. Viewed from the participant's perspective, the home target was located at 0°, while the outer targets were located at −90°, −45°, 45°, and 90°, as indicated by the protrusions. The center target was located midway between the −90° and 90° outer targets. Protrusions radiated from the left (center target angle −90°) and the right (center target angle 90°) of the white circle and indicated the respective center target orientations. The manipulated object was a gray PVC cylinder (5 cm in height, 10 cm in diameter) that had a protrusion (8.5 cm × 1 cm) which extended from the bottom of the object (Fig. 1 C).

Visual stimuli were presented on a 127 cm flat screen monitor (Panasonic TH-50PF11EK) that was placed behind the shelf. The stimuli consisted of a visual representation of the set-up (bird's eye view) and displayed the required center target and outer target positions (Fig. 1 DEF). Stimulus presentation was controlled via Presentation® (Neurobehavioral Systems).

Kinematic data was recorded using an optical motion capture system (VICON Motion Systems, Oxford, UK) consisting of 10 Bonita cameras with 200 Hz temporal and 1 mm spatial resolution. Three 14 mm diameter retro reflective markers were placed dorsally on the distal end of the third metacarpal (MCP), the styloid process of the ulna (WRP), and the styloid process of the radius (WRT) of the right hand. In addition, two 10 mm diameter markers were attached to the object protrusion (5 cm and 0.5 cm from the tip of the protrusion).

2.1.3. Procedure

After filling out the informed consent form and handedness inventory, participant arm length and hip height were measured, and retro-reflective markers were placed on the right hand. The shelf was set to hip height and the home and target circles were arranged so that the distance from the center target to the home position and each outer target was 60% of participant arm length. The participant stood in front of the shelf so that the right shoulder vertically coincided with the home and center target positions.

At the start of each trial, an experimenter placed the object on the home position. The message “Put your hand to the start position!” (in German) was displayed and the participant placed their hand on the shelf 10 cm to the right of the center target. A fixation cross was then presented for 500 ms, and after a random time interval (500–1500 ms); the stimulus was displayed and remained on the screen until the end of the trial. The participant then grasped the object from

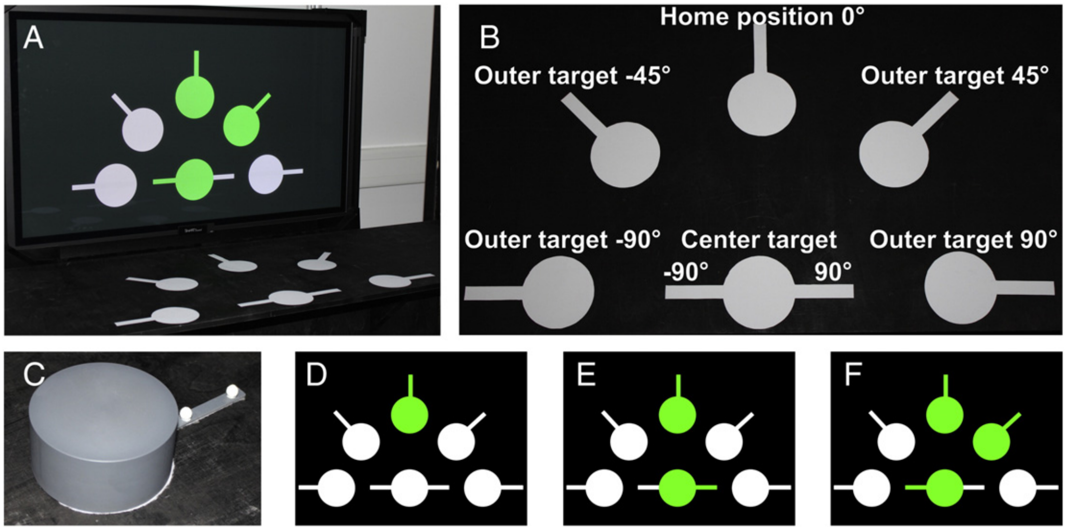

Fig. 1. Experimental setup and stimuli. A Front view of the experimental setup. The stimulus depicts a three-segment movement sequence in which the object is to be grasped from the home position, placed to the −90° center target, and then to the 45° outer target. B Top view of the experimental setup. C Manipulated object. D–F Exemplary stimuli indicating the required center target and outer target object orientations for a: D) one-segment sequence in which the object is to be grasped from the home position, lifted, and set down to the home position, E) two-segment sequence in which the object is to be grasped from the home position, placed to the 90° center target, and F) three-segment sequence in which the object is to be grasped from the home position, placed to the −90° center target, and then to the 45° outer target.

the home position and placed it to the required target(s), as indicated by the stimulus. At the end of the trial, the participant brought their hand back to the start position and waited for the next trial to begin. There were three different tasks. In the one-segment task, the participant grasped the object from the home position, lifted it and set it down to the home position (Fig. 1D). The purpose of the one-segment task was to assess each participant's neutral initial hand angle. In the two-segment task, the participant grasped the object from the home position and placed it to the center target (−90° or 90°, Fig. 1E). In the three-segment task, the participant grasped the object from the home position, then placed it to the center target (−90° or 90°), and subsequently to the outer target (−90°, −45°, 45°, or 90°, Fig. 1F). Participants were told to grasp the object by placing their palm on top of the object and their fingers at the side, and not to change the selected grasp throughout the trial. Furthermore, the instructions emphasized that the task should be performed at a comfortable speed, and movement accuracy was stressed.

The one-segment task consisted of one condition; the two-segment task consisted of two conditions (center targets −90° and 90°). For the three-segment task, there were 8 conditions comprised of the factors center target (−90°, 90°) and outer target (−90°, −45°, 45°, 90°). There were two blocks, within which each condition was repeated five times in a randomized order. This yielded a total of 110 trials. The entire testing session lasted approximately 45 min.

2.1.4. Data analysis

The 3D coordinates of the retro-reflective markers were reconstructed and labeled. Any missing data (less than 10 frames) were interpolated using a cubic spline and filtering using a Woltring filter (Woltring, 1986) with a predicted mean square error value of 5 mm^2 (Vicon Nexus 1.7). Kinematic variables were calculated using a custom written MatLab program (The MathWorks, Version R2010a). The wrist joint center (WJC) was calculated as the midpoint between WRT and WRP. In addition, two direction vectors were calculated, one pointing distally from the WJC to MCP ($V1 = MCP - WJC$), and a second one passing through the wrist ($V2 = WRP - WRT$). The hand center (HC) was defined on a plane normal to $V1 \times (V2 \times V1)$, positioned palmar from MCP at a distance of (hand thickness + marker diameter) / 2 in a way that (HC–WJC) and (HC–MCP) formed a right angle. The hand angle was calculated as the projection of the vector pointing distally from the WJC to the HC on the shelf plane (Fig. 2). Thus, hand orientations with the fingers pointing up (12 o'clock position), left (9 o'clock position), right (3 o'clock position), and down (6 o'clock position) would result in hand angles of 0°, −90°, 90°, and 180°, respectively. Movement initiation time (MIT) was defined as the time period between stimulus onset and the time when the hand left the start position (movement onset). Approach time (AT) was defined as the time period between movement onset and the time the object was grasped (movement offset). Movement onset was determined as the time of the sample in which resultant velocity of WJC exceeded 5% of peak velocity. Movement offset was determined as the time of the sample in which the resultant velocity dropped below 5% of peak velocity.

Trials performed in the non-instructed manner (moving prior to stimulus presentation, placing the object to a wrong target, changing the grasp during a trial) were counted as errors and were not included in analysis. Error trials comprised less than 6.8% of the data, and were approximately equally distributed across condition and participants.

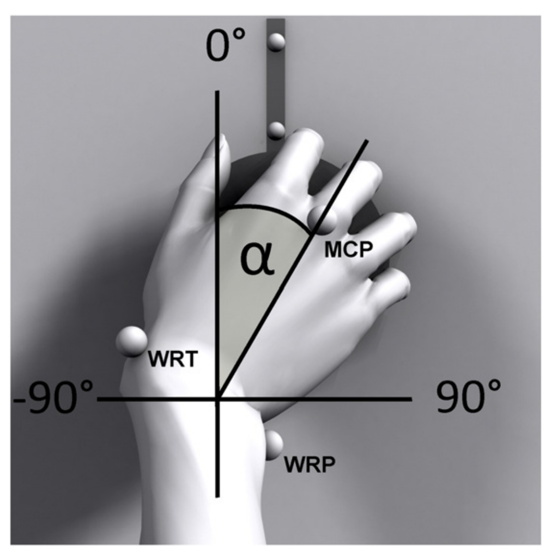

Fig. 2. Calculation of hand orientation angle α.

2.2. Results

2.2.1. Movement initiation time

MIT data are shown in Fig. 3A and C. A block(block 1, block 2) × sequence length (one segment, two segment, three segment) repeated measures analysis of variance (RM ANOVA) revealed that average MITs were shorter during the second block compared to the first block, $F(1,19) = 18.760$, $p < 0.001$, $\eta^2_p = 0.497$. MIT values increased with the number of segments in the action sequence, $F(2,38) = 9.287$, $p = 0.005$, $\eta^2_p = 0.328$. Post hoc tests (Bonferroni corrected) showed that MITs were significantly longer for the three-segment sequence (806 ± 99 ms), compared to both the one-segment (647 ± 67 ms, $p = 0.022$) and the two-segment sequence (669 ± 70 ms, $p = 0.011$). The difference between the one-segment and the two-segment sequence was not significant ($p = 0.628$, Fig. 3A).

To investigate the influence of target orientation on MIT during the three-segment sequence condition, a block (block 1, block 2) × center target (−90°, 90°) × outer target (−90°, −45°, 45°, 90°) RM ANOVA was conducted. The main effect of center target [$F(1,19) = 6.444$, $p = 0.020$, $\eta^2_p = 0.253$] and the interaction between center target and outer target was significant, $F(3,57) = 5.366$, $p = 0.027$, $\eta^2_p = 0.220$. For sequences involving the −90°center target, MIT values were smallest for the −90° outer target, and increased for the −45°, 45°, and 90° outer target conditions. Post hoc tests (Bonferroni corrected) indicated that MIT values were smaller for the −90° outer target compared to the −45° and 45° outer targets ($p = 0.040$ and 0.044 respectively). In contrast, for sequences involving the 90° center target the opposite pattern was found. Here, MIT values were smallest for the 90°outer target and increased for the 45°, −45°, and −90° outer target conditions. However, post hoc tests (Bonferroni corrected) did not reveal any significant differences (Fig. 3C). In addition, there was a significant main effect of a block, with shorter average MITs during the second block compared to the first block, $F(1,19) = 9.690$, $p = 0.006$, $\eta^2_p = 0.338$.

2.2.2. Approach time

AT data are shown in Fig. 3B and D. As with MIT, average AT values were smaller during the second block compared to the first block, $F(1,19) = 5.700$, $p = 0.028$, $\eta^2_p = 0.231$. AT increased with the number of segments in the action sequence, $F(2,38) = 40.289$, $p < 0.001$, $\eta^2_p = 0.680$. Post hoc tests (Bonferroni corrected) revealed that mean AT was longer for the three-segment action sequence (1110 ± 47 ms), compared to both the one-segment (965 ± 42 ms) and two-segment action sequence (1058 ± 44 ms), both p values < 0.01. Additionally, mean AT values were significantly longer for the two-segment, compared to the one-segment, action sequence ($p < 0.001$).

A block (block 1, block 2) × center target (−90°, 90°) × outer target (−90°, −45°, 45°, 90°) RM ANOVA conducted for the three-segment movement sequence revealed a significant main effect of center target [$F(1,19) = 42.175$, $p < 0.001$, $\eta^2_p = 0.689$], outer target [$F(3,57) = 4.145$, $p = 0.010$, $\eta^2_p = 0.179$], and a significant interaction between center target and outer target, $F(3,57) = 5.183$, $p = 0.013$, $\eta^2_p = 0.214$. For sequences containing the −90° center target, AT values were higher for the 90° outer target, compared to the −90°, −45°, and 45°outer target conditions. Post hoc tests (Bonferroni corrected) indicated significant differences between the −90° and 90° outer targets ($p = 0.017$). In contrast, for sequences containing the 90° center target, AT values were higher for the −90° outer target condition compared to the −45°, 45°, and 90°outer target conditions. However, post hoc analysis (Bonferroni corrected) did not reveal any significant differences (Fig. 3D). Thus, similar to the MIT data, three-segment movement sequences AT values were higher for conditions that required a larger degree of object rotation between the center and outer targets.

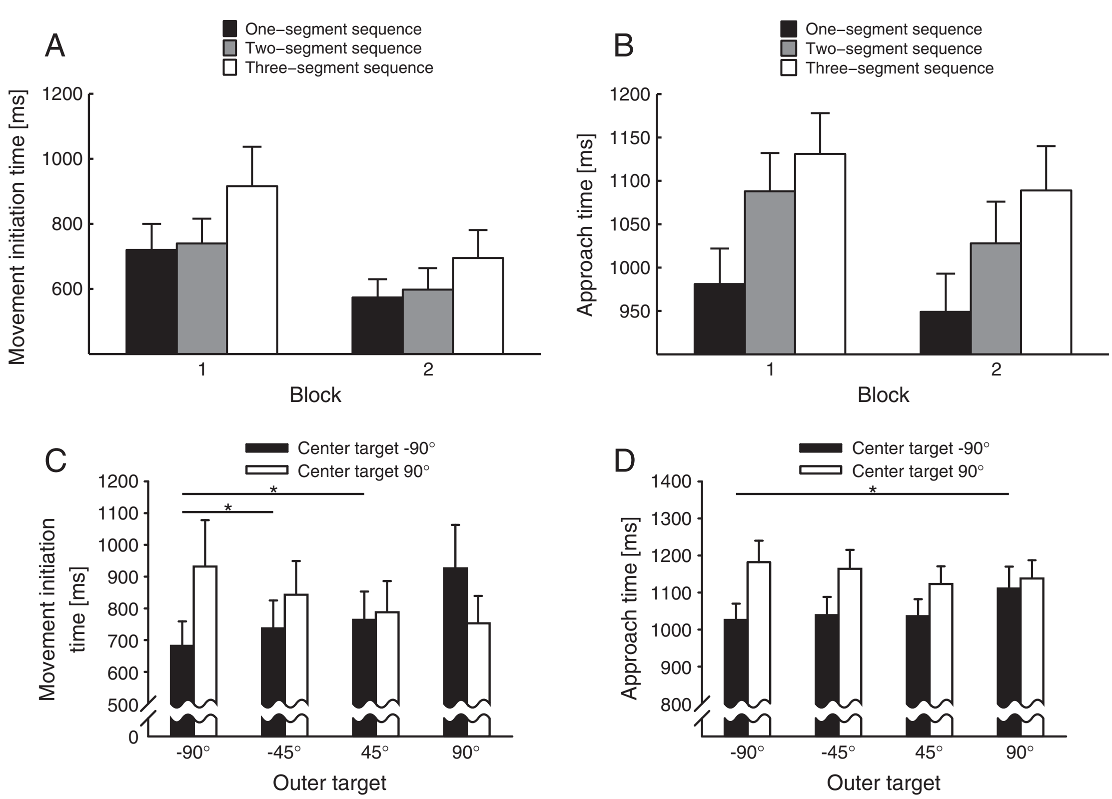

Fig. 3. Average movement initiation times (MITs) and approach times (ATs) as a function of sequence length and block in Experiment 1(panels A and B), as a function of center and outer targets during the three-segment sequences in Experiment 1 (panels C and D), and as a function of center and outer targets during the three-segment sequences in Experiment 2 (panels E and F). Error bars represent standard errors between subjects. Asterisks indicate significant differences (***$p < 0.001$, **$p < 0.01$, *$p < 0.05$).

In summary, the MIT and AT data indicate that participants planned the entire action sequence in advance and that the time to plan an action sequence depends on the number of steps in that sequence and the required degree of object rotation between the center and outer targets.

2.2.3. Grasp postures

To analyze the influence of the center target on initial hand angles during the two-segment sequences, we conducted a block (block 1, block 2) × sequence (one-segment, two segment −90° center target, two-segment 90° center target) RM ANOVA. Mean hand angle during the one-segment movement sequence was −1.1 (±1.9). During the two-segment movement sequences, initial hand angles were influenced by the center target [center target −90° = 13.7 ± 2.5°; center target 90° = −36.2 ± 3.2°, $F(2,38) = 114.738$, $p < 0.001$, $\eta^2_p = 0.858$]. The interaction between block and sequence was significant, $F(2,38) = 8.177$, $p = 0.007$, $\eta^2_p = 0.301$. For the one-segment trials and trials involving the −90° center target, mean initial hand angles increased from block 1 to block 2 ($p = 0.010$ and $p < 0.001$, respectively). In contrast, initial hand angles were similar in block 1 compared to block 2 for trials with the 90° center target ($p = 0.113$).

To examine the influence of the center and outer targets on initial grasp postures during the three-segment movement sequences (see Fig. 4), we performed a block (block 1, block 2) × center target (−90°, 90°) × outer target (−90°, −45°, 45°, 90°) RM ANOVA. On average, initial hand angles were inversely related to both the center and outer targets [main effect of center target: $F(1,19) = 149.204$, $p < 0.001$, $\eta^2_p = 0.887$; main effect of outer target: $F(3,57) = 7.484$, $p = 0.005$, $\eta^2_p = 0.283$]. However, these effects were modulated by a significant center target × outer target interaction, $F(3,57) = 3.575$, $p = 0.038$, $\eta^2_p = 0.158$. For sequences containing the −90° center target, post hoc tests (Bonferroni corrected) indicated significant differences between the −90° outer target and the −45° and 45° outer targets ($p = 0.028$ and $p = 0.031$, respectively). For sequences containing the 90° center target, post hoc tests (Bonferroni corrected) revealed significant differences between the 90° outer target and the −45° and 45° outer targets ($p = 0.023$ and $p = 0.004$, respectively).

To examine the magnitude of influence that the center and outer targets exerted on initial grasp postures across the experimental session, we conducted linear multiple regressions for the initial hand angles on the center and outer targets separately for each block and participant. The slopes of these regressions provide an estimate of the contribution of the center and the outer target positions on initial hand angles and are shown in Fig. 5. A block (block 1, block 2) × target (center target, outer target) RM ANOVA indicated that the slopes for the best-fitting straight lines were significantly steeper for the center target (mean slope = −0.266), compared to the outer target (mean slope = −0.036), $F(1,19) = 150.421$, $p < 0.001$, $\eta^2_p = 0.888$. In contrast, slopes were similar during the second block (mean slope = −0.162) compared to the first block (mean slope = −0.140), $F(1,19) = 3.874$, $p = 0.064$. These results indicate that the center target had a stronger influence on initial grasp postures than the outer target, but there was no evidence that the influence of the center target and the outer target increased over the experimental session.

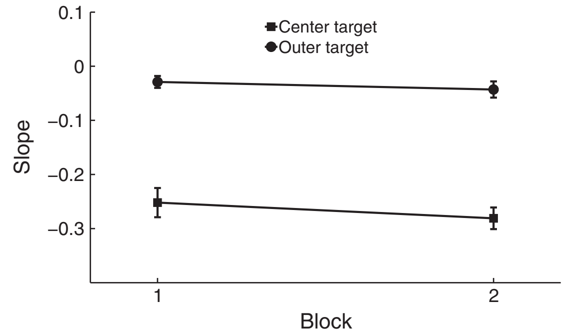

Fig. 5. Slope values of the best-fitting straight lines for the center target (circles) and outer target (squares) as a function of block in Experiment 1. Error bars represent standard errors between subjects.

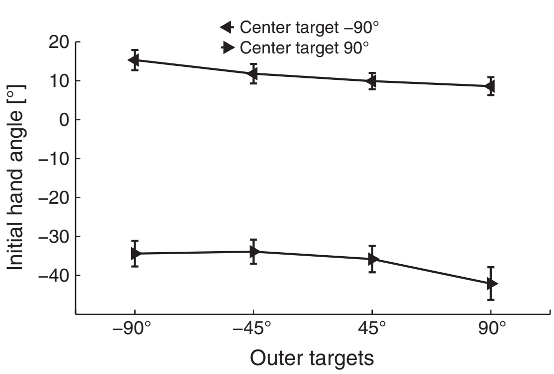

Fig. 4. Initial hand orientation angles as a function of center and outer targets for the three-segment sequences for Experiment 1. The −90°center target is represented by leftward facing triangles, while the 90°center target is represented by rightward facing triangles. Error bars represent standard errors between subjects.

2.3. Discussion

In line with previous work (e.g. Fischman, 1984; Klapp, 1995, 2010; Sternberg et al., 1978), the results of Experiment 1 demonstrate that the time to plan a manual action sequence increased with the number of segments in the movement. MIT and AT values were significantly larger during the three-segment movement sequences compared to the one-segment and two-segment sequences. Moreover, MIT, AT, and initial grasp postures were influenced by both the center and the outer targets during the three-segment movement sequences. Specifically, MIT and AT increased with the required degree of object rotation between the first and second targets, and initial grasp posture orientation angles were inversely related to hand orientation angle at the center and outer targets. These observations are consistent with Rosenbaum et al. (1990) and Zhang & Rosenbaum (2008) who showed that participants select initial grasp postures that allow the limbs to be at, or close to, midrange positions (rather than at extreme positions) at the end of the movement. According to Rosenbaum, van Heugten, & Caldwell (1996) end postures that afford midrange limb positions ensure more control during object manipulation. Accordingly, the results of the present study suggest that participants selected initial grasp postures that allowed them to optimize control not only at the temporally proximal target (i.e., center target), but also at the temporally distal target (i.e., outer target) in an action sequence. Together, these data demonstrate that manual action sequences are planned holistically in advance, that each segment was considered when planning their initial grasp postures, and that task demands that occur earlier in a sequence exhibit a stronger influence on initial grasp postures (i.e., a planning gradient, e.g. Haggard, 1998).

Evidence that grasp planning improved across the experimental session was only manifest in the timing variables. In general, MIT and AT values decreased from block 1 to block 2, indicating that less time was required to plan the movement. In contrast, there was no evidence for adaptations in initial grasp posture across the experimental session.

However, the center and outer targets differed in spatial position, which may have placed unequal biomechanical constraints on arm configuration. As such, it is possible that the unequal biomechanical constraints between the center and outer target positions may have influenced initial grasp posture planning. Given that the results of Experiment 1 may have arisen because of biomechanical factors associated with spatial features of the target positions or by cognitive limitations in advance planning, we conducted a second experiment to dissociate between these two possibilities.

3. Experiment 2

In Experiment 2 we investigated whether the results from Experiment 1arose from cognitive limitations in planning multi-segment actions or biomechanical factors related to the position of the targets. To distinguish between these two possibilities, we reversed the temporal order of the center and outer targets during the three-segment movement sequence. If the results of Experiment 1 are due to biomechanical factors, then we would expect to obtain results similar to Experiment 1. That is, the center targets would have a stronger influence on initial grasp postures than the outer targets. However, if the results of Experiment 1 are due to cognitive factors (i.e., the planning gradient hypothesis), we would expect that the outer targets would have a strong influence on initial grasp postures, and that the center targets would have a weaker effect on initial grasp postures. Last, these two hypotheses are not mutually exclusive, and as such there exists the possibility that both cognitive and biomechanical factors contributed to the results of Experiment 1.

3.1. Methods

3.1.1. Participants

22 students from Bielefeld University (mean age = 25.2 years, SD = 4.5, 16 women, 6 men) participated in this experiment. None of the participants participated in Experiment 1. All participants were right-handed (mean score = 99.1, SD = 4.3) as assessed using the Revised Edinburgh Handedness Inventory (Dragovich, 2004) and were paid 5€ for participation. Participants had normal or corrected to normal vision, and did not have any known neuromuscular disorders. The experiment was conducted in accordance with local ethical guidelines, and conformed to the declaration of Helsinki.

3.1.2. Apparatus, procedure, and data analysis

The apparatus and the stimuli were nearly identical to that used in Experiment 1. The only difference was that participants only performed the three-segment sequences, and the order of events was reversed such that participants grasped the object from the home position, placed it to an outer target (−90°, −45°, 45° or 90°), and subsequently to a center target (−90° or 90°).

The experiment consisted of 8 conditions, comprised of the factors the center target (−90°, 90°) and outer target (−90°, −45°, 45°, 90°). There were two blocks, within which each condition was repeated five times in a randomized order. This yielded a total of 80 trials. The entire testing session lasted approximately 30 min.

Trials performed in a non-instructed manner (moving prior to stimulus presentation, placing the object to a wrong target, changing the grasp during a trial) were counted as errors and were not included in analysis. Error trials comprised less than 2% of the data, and were approximately equally distributed across condition and participants. The data were analyzed using RM ANOVAs with the factors block (block 1, block 2), center target (−90°, 90°), and outer target (−90°, −45°, 45°, 90°).

3.2. Results

3.2.1. Movement initiation time

MIT data are shown in Fig. 6A. There was a significant main effect of outer target [$F(3,63) = 7.531$, $p < 0.001$, $\eta^2_p = 0.264$] and a center target × outer target interaction, $F(3,63) = 10.099$, $p = 0.002$, $\eta^2_p = 0.325$. For sequences involving the −90° center target, MIT values were smallest for the −90° outer target, and increased for the −45°, 45°, and 90° outer target conditions. Post hoc test (Bonferroni corrected) indicated that MIT values were significantly larger for the 90° outer target compared to all other outer targets (all p values < 0.01). In contrast, for sequences involving the 90° center target, MIT values were smallest for the 90° outer target and increased for the 45°, −45°, and −90° outer target conditions. Post hoc tests (Bonferroni corrected) revealed that MIT values were significantly larger for the −90° outer target compared to all other outer targets (all p values < 0.05).

3.2.2. Approach time

AT data are shown in Fig. 6B. The main effect of center target [$F(1,21) = 10.211$, $p = 0.004$, $\eta^2_p = 0.327$], the main effect of outer target [$F(3,63) = 5.908$, $p = 0.001$, $\eta^2_p = 0.219$] and the center target × outer target interaction was significant, $F(3,63) = 19.007$, $p < 0.001$, $\eta^2_p = 0.475$. AT values were smallest for the −90° outer target, and increased for the −45°, 45°, and 90° outer target conditions for sequences containing the −90° center target. Post hoc test (Bonferroni corrected) indicated that all comparisons were significant (all p values < 0.05), with the exception of the comparison between the −90° and −45° outer targets. In contrast, AT values for sequences containing the 90° center target were smallest for the 90° outer target and increased for the 45°, −45°, and −90° outer targets. Post hoc analysis (Bonferroni corrected) revealed that MIT values were significantly larger for the −90° outer target compared to the 45° and 90° outer targets (p = 0.042 and p = 0.017).

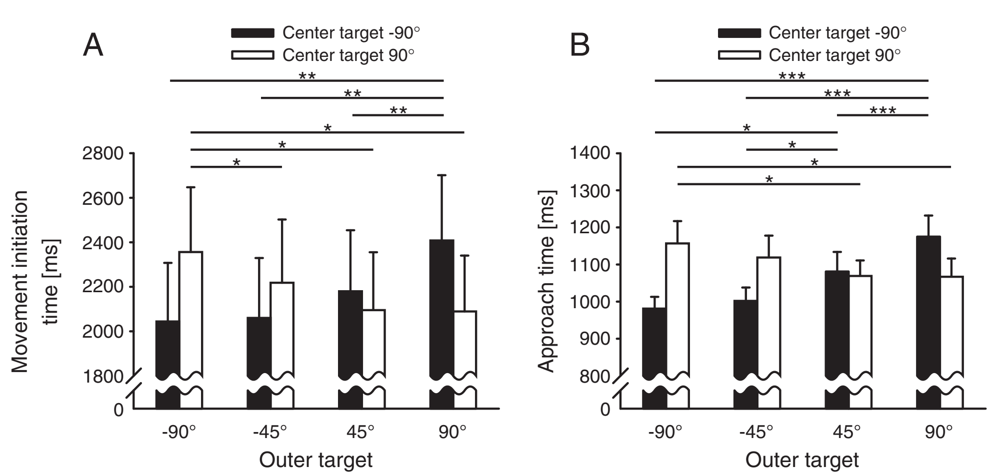

Fig. 6. Average movement initiation times (MITs) and approach times (ATs) as a function of center and outer targets during the three-segment sequences in Experiment 2. Error bars represent standard errors between subjects. Asterisks indicate significant differences (***p < 0.001, **p < 0.01, *p < 0.05).

3.2.3. Grasp posture

Initial hand postures were, on average, inversely related to both the center and the outer targets [main effect of center target: $F(1,21) = 31.938$, $p < 0.001$, $\eta^2_p = 0.603$; main effect of outer target: $F(3,63) = 44.810$, $p < 0.001$, $\eta^2_p = 0.681$]. These effects were modulated by the center target × outer target interaction [$F(3,63) = 7.848$, $p = 0.001$, $\eta^2_p = 0.272$], such that the difference in initial hand angle between the −90° and 90° center targets was more pronounced for the −90° and −45° outer targets, compared to the 45° and 90° outer targets (see Fig. 7). For sequences containing the −90° center target, post hoc test (Bonferroni corrected) indicated significant differences between all outer targets (all p values < 0.05). For sequences containing the 90° center target, all comparisons except between the −90° and −45° outer targets were significant (all p values < 0.05).

Again, we conducted a block (block 1, block 2) × target (center target, outer target) RM ANOVA on the slopes. The negative correlation between initial hand orientation angle and center target and between initial hand orientation angle and outer target, respectively, was significant in each block (all p values < 0.01). The block × target interaction was significant, $F(1,21) = 4.891$, $p = 0.038$, $\eta^2_p = 0.189$. Slopes were initially (block 1) steeper for the outer target (mean slope = −0.156), compared to the center target (mean slope = −0.098, p = 0.043). However, this difference was abolished in block 2 as slope steepness decreased from block 1 to block 2 for the outer target (mean slope = -0.116), while it increased for the center target (mean slope = −0.135, p = 0.496). A Bonferroni corrected post hoc test on the difference scores (block 2 − block 1) revealed that the steepness of the slopes decreased for the outer target (mean slope difference = 0.040) while it increased for the center target (mean slope difference = −0.037), p = 0.038 (see Fig. 8). This finding indicates that grasp postures were influenced by the outer target, more than the center target, during the initial phase of the experimental session. However, as the experimental session progressed, the influence of the center target increased, while the influence of the outer target decreased.

3.2.4. Cross-experiment analysis

To directly compare initial grasp posture selection between Experiments 1 and 2, we conducted a mixed-effects ANOVA on the slopes, using block (block 1, block 2) and target (temporally proximal, temporally distal) as within-subject factors, and experiment (Experiment 1, Experiment 2) as the between-subject factor. Averaged across experiments, the temporally proximal target (mean slope = −0.201) yielded a stronger influence on initial grasp postures than the temporally distal target [mean slope = −0.076, $F(1,40) = 76.107$, $p < 0.001$, $\eta^2_p = 0.655$]. However, this effect was modulated by the significant target × experiment interaction, $F(1,40) = 54.585$, $p < 0.001$, $\eta^2_p = 0.577$.

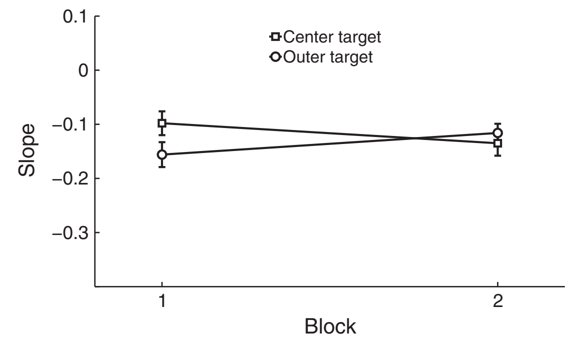

Fig. 8. Slope values of the best-fitting straight lines for the center target (circles) and outer target (squares) as a function of block in Experiment 2. Error bars represent standard errors between subjects.

Post hoc tests indicated that the influence of the temporally proximal target was stronger in Experiment 1 (center target mean slope = −0.266) compared to Experiment 2 (outer target mean slope = −0.136, p < 0.001). In contrast, the influence of the temporally distal target was stronger in Experiment 2 (center target mean slope = −0.117) compared to Experiment 1 (outer target slope = −0.036, p = 0.002, see Fig. 9).

3.3. Discussion

As in Experiment 1, MIT, AT, and initial grasp postures were influenced by both the center target and the outer target indicating that participants planned the movement sequence holistically in advance. However, averaged across both experiments, the temporally proximal target had a considerably stronger influence on initial grasp postures. The stronger influence of targets that occurred proximally in an action sequence (Experiment 1: center targets, Experiment 2: outer targets) supports the planning gradient hypothesis, indicating that limitations in multi-segment grasp posture planning are driven by cognitive limitations (e.g., working memory capacity). However, cognitive limitations associated with advance planning alone do not fully account for the results of Experiment 2. Specifically, the center target (temporally distal target) also had a moderate influence on initial grasp postures that was greater than the influence of the temporally distal target (outer target) in Experiment 1. Moreover, the findings indicate that biomechanical factors of the motor system were considered to a stronger degree (cognitive limitations could be overcome) in later repetitions, as evidenced by the increased influence of the center target and decreased influence of the outer target over repetitions. Taken together,

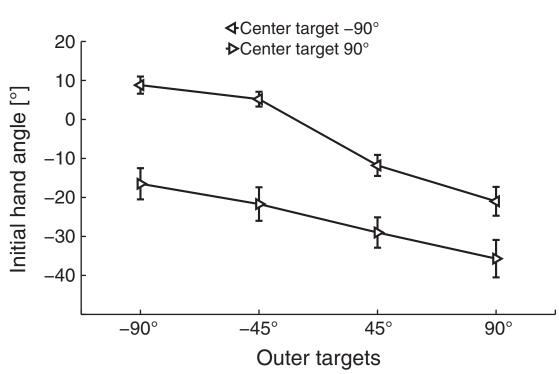

Fig. 7. Initial hand orientation angles as a function of center and outer targets for Experiment 2. The −90°center target is represented by leftward facing triangles, while the 90°center target is represented by rightward facing triangles. Error bars represent standard errors between subjects.

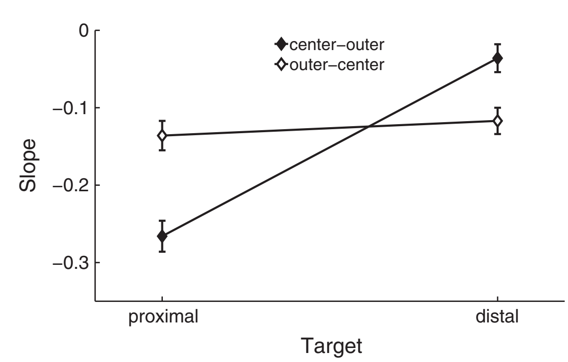

Fig. 9. Slope values of the best-fitting straight lines as a function of target order (temporally proximal target, temporally distal target). Black diamonds represent slopes from Experiment 1 (i.e., center target to outer target sequences), white diamonds represent slopes from Experiment 2 (i.e., outer target to center target sequences). Error bars represent standard errors between subjects.

these results demonstrate that both biomechanical factors and cognitive limitations contributed to the planning of initial grasp postures during the multi-segment movement sequences. They, however, do not provide information about the precise magnitude of the influence of each factor. Further research is needed to specify the relative contributions of these factors.

4. General discussion

The present study examined adaptations in initial grasp posture planning during a multi-segment object manipulation task. In line with previous work (Haggard, 1998; Hesse & Deubel, 2010), we found that initial grasp postures were influenced by the specific requirements of the temporally proximal and distal targets during three-segment sequences. Replicating and extending previous work (Zhang & Rosenbaum, 2008), initial hand angles in the present study were not only inversely related to the temporally proximal, but also to the temporally distal target orientation, suggesting that participants generated movement plans that allowed them to adopt postures that optimize control at both the temporally proximal and distal segments in the action sequence.

Interestingly, initial grasp postures were differently adjusted to the requirements of the center and outer target positions, and also changed differently over the experimental session, depending on the temporal order of the targets. Averaged across both experiments, the temporally proximal target exhibited a significantly stronger influence on initial hand angle than the temporally distal target. More specifically, in Experiment 1, the center targets (temporally proximal) had a much stronger influence on initial grasp postures compared to the outer targets (temporally distal), indicating that participants prioritized control at the center target location, over control at the outer target location. In contrast, Experiment 2 revealed that the outer targets (temporally proximal) had (initially) a stronger influence on initial grasp posture compared to the center target (temporally distal). The reversal of the temporal order of target location in Experiment 2 demonstrates that initial grasp postures were adjusted more to the temporally proximal, than the temporally distal, action segment. These finding support the planning gradient hypothesis (Haggard, 1998). Theoretically, improved planning for temporally proximal action segments might be one way that the CNS copes with cognitive demands associated with multi-segment action sequences.

Although limitations in planning for multiple action segments prior to movement initiation certainly influenced grasp posture planning, they cannot fully account for the results. The influence of the temporally proximal (i.e., center) target on initial grasp postures in Experiment 1 was much stronger than the influence of the temporally proximal (i.e., outer) target in Experiment 2, whereas the influence of the temporally distal target was stronger in Experiment 2 (i.e., center target) than in Experiment 1 (i.e., outer target). It is possible that differences in the number of possible target orientations between the center and outer targets contributed to our findings. This interpretation is further supported by the MIT and AT data. Specifically, average MIT values were much larger during Experiment 2 (2181 ms) compared to Experiment 1 (767 ms). It has been shown that the response latency increases as the amount of possible choice alternatives increases (Hick, 1952; Hyman, 1953). Recall that there were two different center target orientations, but four outer target orientations. Thus, the greater number of target orientations at the first target orientation in Experiment 2 may have increased the cognitive costs associated with the planning of initial grasp postures.

However, it is also possible that biomechanical costs associated with the spatial position of the targets account for stronger influence of the center target. Consequently, we postulate that both biomechanical and cognitive factors are considered during grasp posture planning. Support for an interaction between biomechanical factors and cognitive limitations can be derived from the changes in initial grasp postures across the experimental session. In Experiment 1, the steepness of the slopes was similar between block 1 and block 2 for both the temporally proximal (center) and the temporally distal (outer) targets, indicating no adjustment of initial grasp postures to the target positions. The planning gradient hypothesis would have predicted a similar pattern for Experiment 2. This was not the case, however. During the first block of the experimental session the influence of the temporally proximal (outer) target on initial grasp postures was larger than the influence of the temporally distal (center) target. In contrast, during the second block, this difference was abolished as the influence of the temporally distal (center) target increased whereas the influence of the temporally proximal (outer) target decreased.

We speculate that the absence of adaptation in initial grasp postures in Experiment 1 results from the different weighting of the biomechanical costs associated with the spatial position and cognitive limitations in advance planning. It is likely that the biomechanical costs are considerably higher at the center target position compared to the outer target position because the range of optimal control is much smaller at the center target position. Due to a planning gradient, initial grasp postures are primarily adjusted to the center target when the center target is the temporally proximal target (Experiment 1). Nevertheless, grasp postures at the outer target might still be tolerable given the larger range of optimal control at these positions. Consequently, participants did not change their grasp posture planning across several repetitions. In contrast, in Experiment 2, grasp postures are initially primarily adjusted to the outer target (temporally proximal) position. However, this resulted in grasp postures at the center target that were outside the tolerable range. Consequently, participants changed their grasp posture plans over the experimental session to better incorporate the task demands of the center target. These results suggest that there are limitations in the ability of the CNS to consider temporally distal action segments during the early stages of a task. However, over time participants learn to integrate the task demands of temporally distal steps into their movement plan, which reduces the burden on the CNS.

Together, these findings demonstrate that planning of initial grasp postures during multi-segment movement sequences is influenced by both cognitive and biomechanical factors, and that the relative influence of these constraints relies on a flexible hierarchy (see Hughes & Franz, 2008; van der Wel & Rosenbaum, 2010 for similar arguments based on experiments on bimanual grasp posture planning) that allows for adaptations in grasp posture planning over time.

Finally, it is noteworthy that action sequence length and the required degree of object rotation also affected the time to select an initial grasp posture. In line with previous work (see Christina, 1992; Fischman, Christina, & Anson, 2008; Klapp, 2010 for reviews), we found that movement initiation time and approach time were influenced by the number of steps in the action sequence, such that MIT and AT values were larger for three-segment movement sequences, compared to both one- and two-segment movement sequences. MITs and ATs also increased with the required degree of object rotation between the first and the second targets. We hypothesize that anticipatory movement planning was, in part, influenced by motor imagery (e.g. Jeannerod, 1997). Similar to visual imagery (e.g. Shepard & Cooper, 1982; Shepard & Metzler, 1971), motor imagery involves mentally simulating a forthcoming action. However, in contrast to visual imagery, motor imagery is sensitive to both cognitive and biomechanical constraints (Johnson, 2000). For example, Johnson (2000) had participants reach out and grasp a dowel oriented in different ways in real space or verbally judge how they would grasp the presented dowel. The results showed that reaction time was larger for awkward hand postures, and that reaction time increased as a function of the angular distance between the initial posture and the posture chosen to grasp the dowel for both the grip condition and the judge condition. In line with this research, we postulate that participants mentally simulated the forthcoming actions when planning their initial grasp postures. Consequently the costs associated with multi-segment action planning increase with the number of action steps and the required degree of rotation between the first and second targets, thus making it harder for participants to use motor imagery for grasp posture planning.

In sum, the results of the present study provide further evidence that multi-segment manual action sequences are planned holistically in advance. Overall, participants selected initial grasp postures based on the specific requirements of the temporally proximal and temporally distal targets, indicating that each element was considered when planning an action sequence. Interestingly, initial grasp postures were differently adjusted to the requirements of the targets depending on the temporal order in which in object was to be placed to these targets, suggesting that both biomechanical and cognitive factors influence the planning of initial grasp postures during multi-segment movement sequences. Further, the planning of initial grasp postures was influenced to a larger extent by the temporally proximal target demands during the initial stages of the experimental session. This finding suggests that cognitive limitations influence the ability of the CNS to plan for temporally distal task demands. However, with several repetitions, participants could overcome these cognitive limitations and consequently adjusted their initial grasp postures more strongly to the requirements of the temporally distal target.

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