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RESEARCH ARTICLE

The influence of reducing intermediate target constraints on grasp posture planning during a three-segment object manipulation task

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Abstract The present experiment examined the influence of final target position on grasp posture planning during a three-segment object manipulation task in which the required object orientation at the first target position was unconstrained. Participants grasped a cylindrical object from a home position, placed it at an intermediate position in a freely chosen orientation, and subsequently placed it at one of four final target positions. Considerable inter-individual differences in initial grasp selection were observed which also led to differences in final grasp postures. Whereas some participants strongly adjusted their initial grasp postures to the final target orientation, and thus showed a preference for end-state comfort, other participants showed virtually no adjustment in initial grasp postures, hence satisfying initial-state comfort. Interestingly, as intermediate grasp postures were similar regardless of initial grasp adjustment, intermediate-state comfort was prioritized by all participants. These results provide further evidence for the interaction of multiple action selection constraints in grasp posture planning during multi-segment object manipulation tasks. Whereas some constraints may take strict precedence in a given task, other constraints may be more flexible and weighted differently among participants. This differentiated weighting leads to task- and subject-specific constraint hierarchies and is reflected in inter-individual differences in grasp selection.

Keywords Grasping · Motor planning · Multi-segment sequences · End-state comfort · Inter-individual differences · Action selection

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Introduction

More than 50 years ago, Napier stated that "during the performance of a purposive prehensile action […], it is the nature of the intended activity that finally influences the pattern of the grip" (1956). Consequently, what an individual plans to do with an object can be inferred from the way that the object is initially grasped. Since Napier's seminal work, several researchers have largely confirmed this assumption and shown that initial grasp postures are strongly influenced by the action goal of the task (e.g., Herbort and Butz 2012; Hughes et al. 2012a, c; Rosenbaum et al. 1990; Seegelke et al. 2011; Zhang and Rosenbaum 2008). For example, in Zhang and Rosenbaum (2008), participants performed an object sliding task in which they placed their hand on top of an object and moved it from a start position to one of five target positions. The authors found that initial hand orientation was inversely related to final hand orientation, indicating that participants selected initial grasp postures that afforded more comfort when the object was moved to the target position (i.e., end-state comfort effect). The end-state comfort effect has been reliably reproduced during a variety of unimanual object manipulation tasks that require second-order planning (i.e., grasping an object and one subsequent displacement), and thus is considered a prominent action selection constraint (i.e., a factor that consistently influences initial grasp choice, see Rosenbaum et al. 2012, 2013). More generally, these findings have led to the inference that initial grasp postures are selected in anticipation of future goal postures, and that actions are represented in terms of goal states (see Schütz-Bosbach and Prinz 2007, for a review).

Until recently, however, surprisingly little work has examined action selection constraints on anticipatory grasp posture planning during tasks that require higher-order planning (i.e., multi-segment sequences; Rosenbaum et al. 1990; Haggard 1998; Hesse and Deubel 2010; Seegelke et al. 2012, 2013). In one study (Hesse and Deubel 2010), participants reached and grasped a cylinder, placed it on a target circle, and subsequently grasped and displaced a bar that was positioned in one of three orientations. The authors found that the orientation of the bar at the end of the movement sequence influenced the grip orientation that participants used when grasping the cylinder, and that grip orientation in these early movement segments was systematically shifted toward the final grip orientation (i.e., when grasping the bar).

Seegelke et al. (2013) have provided further evidence that grasp posture planning extends to three-segment object manipulation sequences. In their task, participants grasped a cylindrical object from a home position, placed it at a first target position, and subsequently placed it at a second target position. The location of the first target position was fixed and required either 90° clockwise or counterclockwise object rotation (with respect to the home position). The second target positions were arranged in a semi-circular fashion around the first target position and required 0°, 45°, 135°, or 180° object rotation between the first and second target position. Congruent with previous studies (e.g., Haggard 1998; Hesse and Deubel 2010), it was found that initial grasp postures were influenced by the specific requirements of both the first (i.e., intermediate) and the second (i.e., final) target positions, which the authors took as evidence that each element was considered when planning the action sequence. The authors also found that adjustments in initial grasp postures depended on the temporal order of the targets, such that grasp postures were more strongly adjusted to the requirements of the first, rather than the second target position (i.e., a "planning gradient"). These findings demonstrate that the planning of initial grasp postures during multi-segment object manipulation tasks is contingent upon biomechanical (i.e., spatial target position) as well as cognitive (i.e., planning gradient) constraints, and that the relative importance of these constraints relies on a flexibly hierarchy (van der Wel and Rosenbaum 2010; Hughes and Franz 2008).

In the study of Seegelke et al. (2013), the required object orientation was predetermined at both the first and second target positions. The task was designed to include conditions in which participants could not select initial grasp postures that allowed them to adopt comfortable postures at both target positions. Results showed that the adjustment of initial grasp postures was stronger to the first target position as compared with the second target position, leading to the inference that participants were more concerned with satisfying intermediate-state comfort rather than end-state comfort.

In comparison with the wealth of research on second-order grasp posture planning, there has been very little research on higher-order motor planning during multi-segment object manipulation. The lack of research in this area is surprising given that movements in everyday tasks do not occur in isolation, but are often embedded within a larger action sequence. Consequently, the aim of the present study was to examine the influence of final target position on grasp posture planning during a three-segment object manipulation task in which the required object orientation at the intermediate (first) target position was unconstrained. To this end, we modified the three-segment object manipulation task used in Seegelke et al. (2013), such that the object orientation at the first (intermediate) target position was not defined but could be freely chosen by the participants (similar as in Hesse and Deubel 2010). Thus, participants grasped a cylindrical object from a home position, placed it at an intermediate target position in a freely chosen orientation, and subsequently placed it at one of four final target positions in a predetermined orientation. We were specifically interested in whether participants would adjust their initial grasp postures such that they would adopt comfortable postures at the intermediate target position (i.e., intermediate-state comfort) and/or final target position (i.e., end-state comfort).

Methods

Grasping task

Participants

Twenty individuals from Bielefeld University (5 men, 15 women, mean age = 22.70 years, SD = 3.16) participated

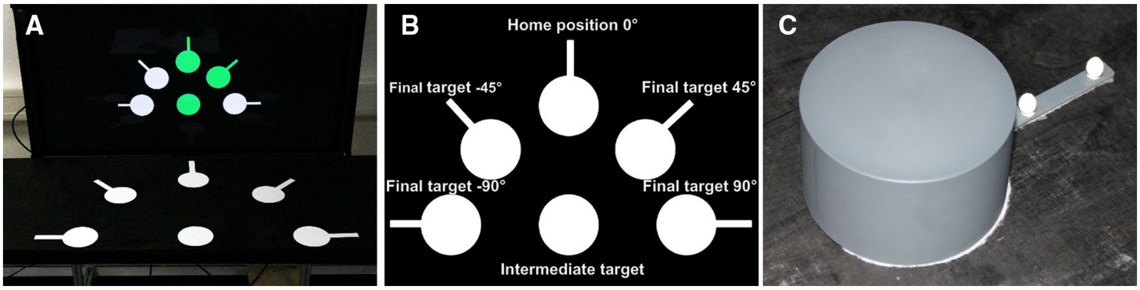

Fig. 1 Experimental setup and stimuli. **a** Front view of the experimental setup. Exemplary stimulus indicating a sequence in which the object is to be placed to the 45° final target. **b** Top view of the experimental setup including target labels. **c** Manipulated object

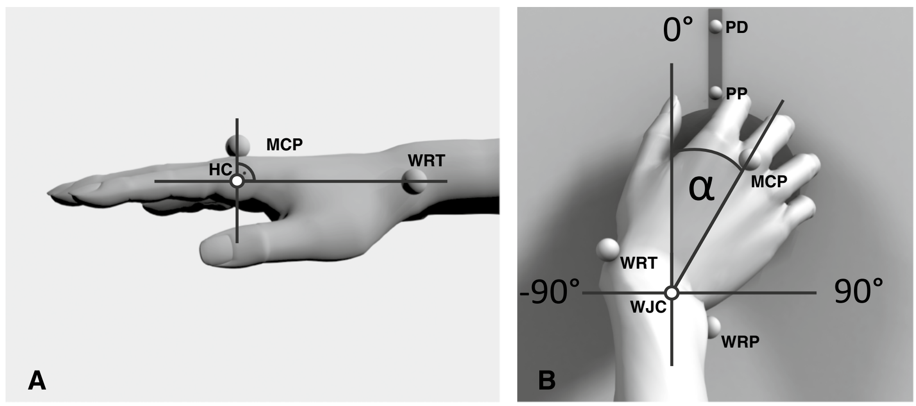

Fig. 2 Calculation of HC (**a**) and hand orientation angle (**b**)

in exchange for 5 € compensation. All participants were right-handed (mean score = 99.35, SD = 2.91) as assessed using the Revised Edinburgh Handedness Inventory (Dragovich 2004). Participants reported 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.

Apparatus and stimuli

The experimental apparatus was similar to that used in a previous study (Seegelke et al. 2013) and is shown in Fig. 1a and b. The setup was positioned on a height-adjustable shelf (200 cm × 60 cm). The home, intermediate, and final positions consisted of white paper circles (11 cm in diameter) that were taped flat to the surface of the shelf. The home and final positions had outward extending paper protrusions (9 cm × 2 cm) and were arranged in a semicircle, each separated by 45°. Viewed from the participant's perspective, the home position was located at 0°(up), while the final positions were located to the left (i.e., at −90° and −45°) and to the right (i.e., 45° and 90°). The intermediate position was a white target circle (11 cm in diameter) and was located midway between the −90° and 90° final targets and 7 cm from the edge of shelf. The manipulated object was a grey PVC cylinder (5 cm in height, 10 cm in diameter, 566 g in weight) with a protrusion (8.5 cm × 1 cm) that extended from the bottom of the object (Fig. 1c).

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 setup (bird's eye view) and displayed the required final target position (Fig. 1a). Stimulus presentation was controlled via Presentation® (Neurobehavioral Systems).

Kinematic data were collected from three retro-reflective markers (14 mm in diameter) 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. Two markers (10 mm in diameter) were placed on the object protrusion [5 cm (PP) and 0.5 cm (PD) from the tip of the protrusion, Fig. 2]. Kinematic data were recorded using an optical motion capture system (VICON Motion Systems, Oxford, UK) consisting of ten Bonita cameras with 200 Hz temporal and 1 mm spatial resolution.

Procedure

After entering the laboratory, participants filled out the informed consent and handedness inventory. Participants' arm length and hip height were measured, and the markers were placed on the right hand. The shelf was adjusted to hip height, and the home and target circles were arranged so that their distance from the intermediate position was 60 % of the participants' arm length. The participant stood in front of the experimental setup so that the right shoulder vertically coincided with the home and intermediate target position.

At the beginning of each trial, the experimenter placed the object on the home position. To ensure that the experimenter's grasp did not influence the participants' grasp choice (cf. Wilson and Knoblich 2005), the experimenter always grasped the side of the object with the thumb and middle finger when bringing it back to the home position. The message "Put your hand to the start position!" (in German) was displayed on the monitor, and the participant placed the hand on the shelf 10 cm to the right of the intermediate target with the fingers pointing up (12 o'clock position). A fixation cross was then displayed for 500 ms, and after a random time interval (500–1,500 ms), the stimulus was presented for 500 ms. When the stimulus appeared, the participant grasped the object from the home position, placed it at the intermediate position, and then at the final target position, as indicated by the stimulus. The participant then brought the hand back to the start position and waited for the next trial to begin.

The orientation of the object at the intermediate position was not prescribed, but could be freely chosen by the participant. Participants were told to grasp the object by placing their palm on top of the object so that the fingers were arranged around the sides of the cylinder, and not to change the selected grasp throughout the trial. The instructions also emphasized that the task should be performed at a comfortable speed, and movement accuracy was stressed. Each final target was presented ten times in a randomized order, yielding a total of 40 trials. A session lasted about 30 min.

Data analysis

The 3-D coordinates of the retro-reflective markers were reconstructed and labeled. Any missing data (<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).[1] Kinematic variables were calculated using a custom-written MATLAB program (The MathWorks, Version R2010a). Grasp postures were quantified by calculating hand orientation angles. To this end, 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 [vector 1 (V1) = MCP–WJC) and a second one passing through the wrist [vector 2 (V2) = WRP–WRT]. The hand center (HC) was defined on a plane normal to V1 × (V2 × V1),[2] positioned palmar from MCP at a distance of 19.5 mm which corresponds to (average hand thickness + marker diameter)/2 in a way that (HC–WJC) and (HC–MCP) formed a right angle (Fig. 2a). The hand orientation angle was calculated as the projection of the vector pointing distally from WJC to HC on the shelf plane (Fig. 2b). 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. Similarly, the object orientation angle was calculated as the projection of the vector pointing distally from PP to PD on the shelf plane.

For each trial, the time series was divided into three movement segments. The initial movement segment was defined as the time period between when the hand left the start position and the time period when the hand grasped the object. The intermediate movement segment was defined as the time period between when the object was lifted from the home position and the time period when the object was placed to the intermediate target position. The final movement segment was defined as the time period from when the object was lifted from the intermediate target position to the time period when the object was placed to the final target position.

Movement onset of each segment was determined as the time of the sample in which the resultant velocity of the hand (WJC) exceeded 5 % of peak velocity of the corresponding phase. Movement offset was determined as the time of the sample in which the resultant velocity dropped and stayed below 5 % of peak velocity of the corresponding phase. Initial, intermediate, and final hand and object orientation angles were extracted at movement offset of the corresponding segment.

Trials performed in the non-instructed manner (e.g., 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 <1 % of the data, and were approximately equally distributed across condition.

Assessment of grasp comfort

To quantify comfortable grasp postures, we obtained an independent measure of grasp comfort at each position (i.e.,

[1] The Woltring filter is commonly used in the analysis of motion capture data and is equivalent to a double Butterworth filter. The benefit to the Woltring filter is that higher-order derivates can be calculated from the analytic derivative of a polynominal spline.

[2] Here, the symbol × is used to denote the cross product of two vectors.

home position, intermediate target position, final target positions −90°, −45°, 45°, and 90°) using a separate pool of participants ($n = 15$, mean age = 25.60, SD = 4.08, 10 women, 4 men). All participants were right-handed (mean score = 100.00, SD = 0.00), reported normal or corrected to normal vision, and did not have any neurological or neuromuscular disorders. The experiment was conducted in accordance with local ethical guidelines and conformed to the declaration of Helsinki.

The experimental setup and motion capture analysis were identical to that used in the grasping task. At the start of each trial, the experimenter placed the object on a target position and participants reached out with their right hand and grasped the object with a grasp posture they considered to be most comfortable. Participants then removed their hand from the object and placed their hand back to the side of the body. Participants performed five comfortable grasp postures at each target position, yielding a total of 30 trials, which were presented in a randomized order. Hand orientation angles of the comfort task were analyzed and compared to the hand orientation angles of the grasping task.

Results

Mean initial hand orientation angles were 6.6°, 3.6°, −10.3°, and −17.9° and inversely related to the final target positions −90°, −45°, 45°, and 90° (see Fig. 3). Pairwise comparisons showed that initial hand orientation angles in the grasping task differed from the comfortable initial hand orientation angles (obtained from the grasp comfort assessment) for all required final target positions (all $p < 0.05$; absolute differences between comfortable initial hand orientation angles and initial hand orientation angles in the grasping were 9.4°, 6.4°, 7.5°, and 15.1° for the final target positions −90°, −45°, 45°, and 90°, respectively, see Fig. 3).

To examine the extent to which intermediate hand and/or object orientation angles were adjusted to the required final target positions, a repeated measures multivariate analysis of variance (RM MANOVA) was performed with final target position as the factor, and intermediate hand and object orientation angles as dependent variables.[3] Analysis revealed that required final target position influenced the grasp-object orientation at the intermediate target position, $F(6,14) = 3.835$, $p = 0.018$. To assess the contribution of the dependent variables to the main effect, separate follow-up univariate ANOVAs were conducted on intermediate hand orientation angles and on intermediate object orientation angles. Analyses indicated that mean intermediate hand orientation angles (−19.2, −13.0°, −10.0°, −9.4°) were similar regardless of required final target position, $F(3,57) = 2.553$, $p = 0.124$ (Fig. 4a).

In contrast, mean intermediate object orientation angles (−26.0°, −13.4°, 10.3°, 20.5°) were influenced

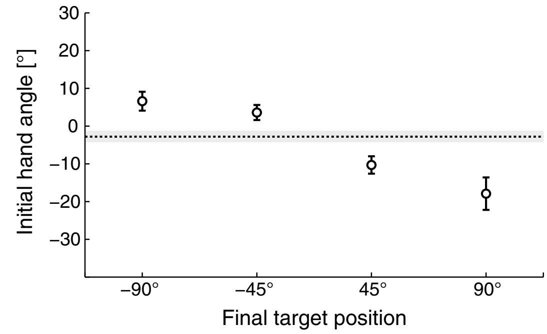

Fig. 3 Mean initial hand orientation angles (±1 SE) as a function of final target position. The *dashed line* represents the mean of the comfortable initial hand orientation angles ± 1 SE (*grey background*)

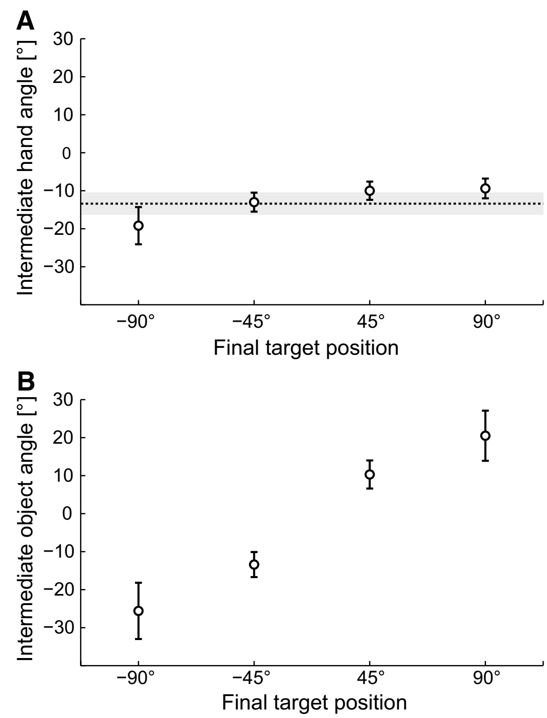

Fig. 4 **a** Mean intermediate hand orientation angles (±1 SE) and **b** mean intermediate object orientation angles (±1 SE) as a function of final target position. The *dashed line* represents the mean of the comfortable intermediate hand orientation angles ± 1 SE (*grey background*)

[3] Given that participants were instructed to maintain the initially adopted grasp posture throughout the entire movement sequence, intermediate hand and object orientation angles cannot be assumed to be independent. To account for this interdependency, we initially performed a RM MANOVA on intermediate angels.

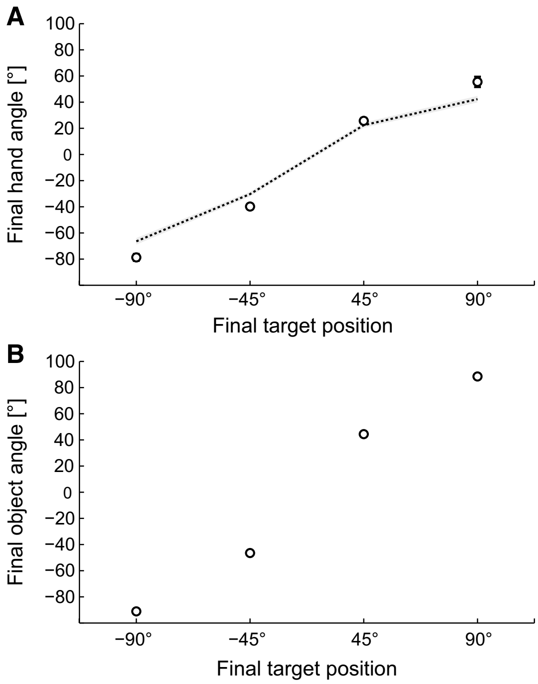

Fig. 5 **a** Mean final hand orientation angles (±1 SE) and **b** mean final object orientation angles (±1 SE) as a function of final target position. The *dashed line* represents the mean of the comfortable final hand orientation angles ± 1 SE (*grey background*)

by the required final target orientation, $F(3,57) = 11.783$, $p = 0.002$ (Fig. 4b). Post hoc tests confirmed that all comparisons, except between the −90° and −45° final target orientation ($p = 0.052$), were significant (all $p < 0.05$).

Pairwise comparisons between the intermediate hand orientations obtained during the grasping task and the comfortable intermediate hand orientation angles (obtained from the grasp comfort assessment) revealed no significant differences (all $p > 0.3$), indicating that intermediate hand orientation angles in the grasping task were similar to the most comfortable intermediate grasp postures (see Fig. 4a).[4]

Final hand orientation angles (−78.7°, −39.8°, 25.7°, 55.5°) strongly depended on the required final target position (see Fig. 5). A 2 task (grasping, comfort) × 4 final target position (−90°, −45°, 45°, 90°) RM ANOVA revealed a significant main effect of final target position [$F(3,99) = 1{,}111.531$, $p < 0.001$] and a significant task × final target interaction, $F(3,99) = 12.755$, $p < 0.001$. Post hoc pairwise comparisons (Bonferroni corrected) showed that final hand orientation angles in the grasping task differed from the most comfortable final hand orientation angles (obtained from the grasp comfort assessment) for the −90°, −45°, and 90° (mean difference range = 9.5°–13.2°, all $p < 0.05$), but not the 45° final target position (mean difference = 3.3°, $p = 0.299$, see Fig. 5a).

Final object orientation angles were close to the required final target angles, and absolute final object placement error (measured in degrees) did not differ between the four final target positions, $F(3,57) = 1.661$, $p = 0.202$ (see Fig. 5b).

In sum, the data indicate that participants planned the action sequence to ensure comfortable hand orientations at the intermediate (i.e., intermediate-state comfort), but not at the home (i.e., initial-state comfort) and final target position (i.e., end-state comfort; except at the 45° final target position). In addition, intermediate object orientation angles but not intermediate hand orientation angles were steered toward the final target positions.

Upon closer inspection, the data revealed inter-individual differences in the adjustment of initial grasp postures. To examine the magnitude of differences in initial grasp posture adjustment, linear regressions for initial hand orientation angles on the final target positions were conducted separately for each participant. The slopes of these regressions provide an estimate of the degree of initial grasp posture adjustment and ranged from 0.000 (no adjustment) to −0.429 (strong adjustment). A median split was applied to divide participants into two groups: the strong adjusters (mean slope = −0.246, range = 0.348) and the weak adjusters (mean slope = −0.033, range = 0.069). To statistically quantify whether the participants stemmed from two distinct populations (i.e., strong adjuster or weak adjusters), Ashman's D (Ashman et al. 1994) was used to test for a bimodal distribution of the slope values. Ashman's D is calculated as

$$D = \frac{|\mu_1 - \mu_2|}{[\frac{\sigma_1^2+\sigma_2^2}{2}]^{1/2}}$$

where μ_1, μ_2 are the means and σ_1, σ_2 are the standard deviations, and $D > 2$ is required for a clean separation between the two distributions. Ashman's D was 2.72, thus indicating that the two distributions were cleanly separated.

T test analyses revealed that the differences between the strong and weak adjusters were not related to participants' age [$t(18) = -0.555$, $p = 0.586$], hip height [$t(18) = -1.419$, $p = 0.173$], arm length [$t(18) = -1.068$, $p = 0.300$] or gender [$\chi^2(1) = 2.4$, $p = 0.121$]. Consequently, differences cannot be traced back to the obtained participant characteristics.

[4] Notably, the difference between intermediate object orientation and intermediate hand orientation angle was larger for the −90° and −45° final target positions (difference = 6.8° and 0.4°, respectively) compared to the 45° and 90° target positions (difference = 20.3° and 30.0°, respectively). These differences reflect the generally stronger adjustment in initial grasp postures to the 45° and 90° final targets and are likely to result from biomechanical asymmetries in the range of motion of the arm.

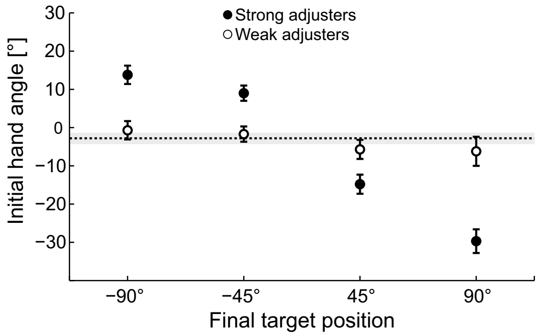

Fig. 6 Mean initial hand orientation angles (±1 SE) as a function of final target position and group (strong vs. weak adjusters). The *dashed line* represents the mean of the comfortable initial hand orientation angles ± 1 SE (*grey background*)

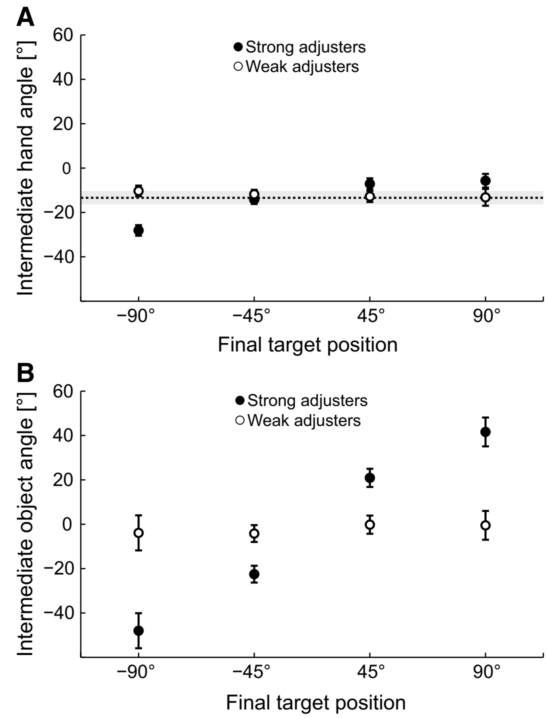

Fig. 7 **a** Mean intermediate hand orientation angles (±1 SE) and **b** mean intermediate object orientation angles (±1 SE) as a function of final target position and group (strong vs. weak adjusters). The *dashed line* represents the mean of the comfortable intermediate hand orientation angles ± 1 SE (*grey background*)

To examine whether the magnitude of initial hand orientation adjustment influenced the planning for comfortable grasp postures differently for these two groups, hand orientation angles of the weak and strong adjusters were compared to hand orientation angles obtained in the assessment of grasp comfort (comfort group) at each position (i.e., home, intermediate, final) using mixed effect ANOVAs. Differences in initial, intermediate, and final hand orientation angle were assessed using separate mixed effect ANOVAs with the factors group (strong adjusters, weak adjusters, comfort) and final target position (−90°, −45°, 45°, 90°). Differences in intermediate and final object orientation angles were examined using separate mixed effect ANOVAs with the factors group (strong adjusters, weak adjusters) and final target position (−90°, −45°, 45°, 90°).

For initial hand orientation angles, analysis revealed a significant main effect of final target position [$F(3,96) = 71.931$, $p < 0.001$] and a significant final target × group interaction, $F(6,192) = 48.747$, $p < 0.001$ (see Fig. 6). Post hoc pairwise comparisons (Bonferroni corrected) showed that initial hand orientation angles of the strong adjusters differed significantly from both the weak adjusters and the comfort group for each required final target position (all $p < 0.05$). In contrast, initial hand orientation angles were similar for the weak adjusters and the comfort group (all $p = 1.0$).

For the intermediate hand orientation angles, there was a significant main effect of final target position [$F(3,96) = 4.153$, $p = 0.047$], and a significant group × final target interaction, $F(6,192) = 5.786$, $p = 0.006$ (see Fig. 7a). Post hoc tests (Bonferroni corrected) revealed that intermediate hand orientation angles for the −90° final target position differed significantly from the other three final target positions (all $p < 0.01$) for the strong adjusters only. However, and more importantly, there were no significant differences between the three groups for either final target orientation, indicating that all participants adopted intermediate hand orientation angles that were close to the most comfortable intermediate hand orientation angles.

For intermediate object orientation angles, there was a significant main effect of final target position [$F(3,54) = 22.797$, $p < 0.001$], and a significant group × final target position interaction, $F(3,54) = 18.761$, $p < 0.001$ (see Fig. 7b). Post hoc pairwise comparisons (Bonferroni corrected) showed that intermediate object orientation angles were strongly influenced and shifted toward the required final target positions for the strong adjusters (all $p < 0.001$). In contrast, for the weak adjusters, intermediate object orientation angles were similar regardless of required final target position (all $p = 1.0$).

For final hand orientation angles, there was a significant main effect of final target position [$F(3,96) = 2{,}254.756$, $p < 0.001$], and a significant group × final target position interaction, $F(6,192) = 27.994$, $p < 0.001$ (see Fig. 8a). Post hoc pairwise comparisons (Bonferroni corrected) showed that final hand orientations of the weak adjusters differed significantly from final hand orientation angles of both the strong adjusters and the most comfortable final hand orientations angles for the −90°, −45°, and 90° final target positions (all $p < 0.01$), but not for the 45° final

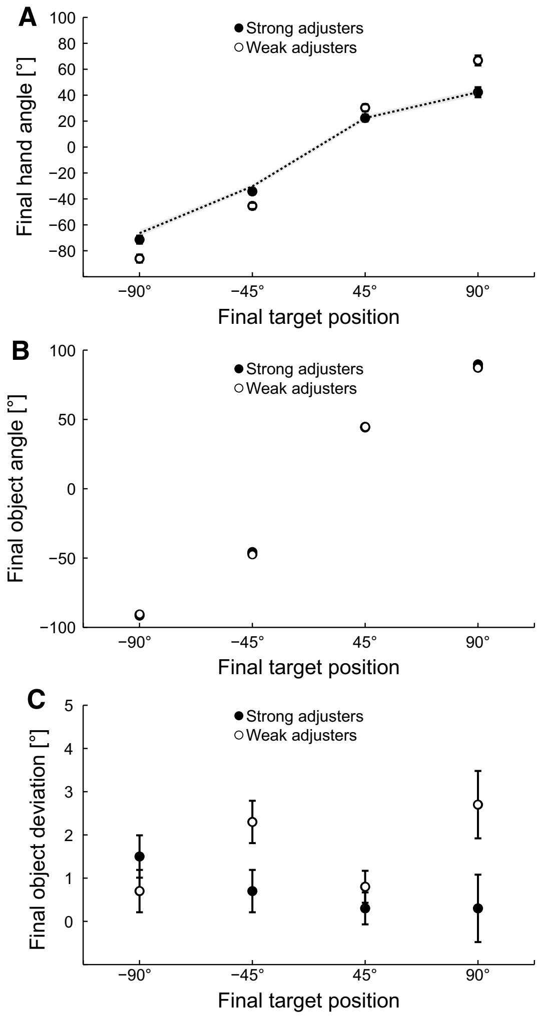

Fig. 8 **a** Mean final hand orientation angles (±1 SE) and **b** mean final object orientation angles (±1 SE) as a function of final target position and group (strong vs. weak adjusters). The *dashed line* represents the mean of the comfortable final hand orientation angles ± 1 SE (*grey background*) **c** mean deviation of final object orientation angles from required final target position angle (±1 SE) as a function of final target position and group (strong vs. weak adjusters)

target position (strong adjusters: $p = 0.071$, comfort group: $p = 0.096$). In contrast, for all final target positions, final hand orientations angles of the strong adjusters did not differ significantly from the most comfortable final hand orientation angles (all $p > 0.6$), indicating that this group of participants satisfied end-state comfort.

Analysis of final object orientation angles revealed a significant group × final target position interaction, $F(3,54) = 5.013$, $p = 0.004$. Post hoc tests indicated that final object orientation angles were significantly less accurate for the weak adjusters compared with the strong adjusters for the final target positions −45° and 90° ($p = 0.025$ and $p = 0.039$, respectively, see Fig. 8b, c).

Discussion

The present study examined grasp posture planning during a three-segment object manipulation task in which the object orientation at the first (intermediate) target position was not constrained. In this study, participants grasped an object from a home position, placed it at an intermediate position in a freely chosen orientation, and subsequently placed it at one of four final target positions in a predetermined orientation.

In general, our results suggest that participants planned the action sequence such that comfortable grasp postures were ensured at the intermediate (i.e., intermediate-state comfort), but not at the home (i.e., initial-state comfort) and at the final target position (i.e., end-state comfort). In addition, intermediate object orientation angles were steered toward the corresponding final target positions. The finding that initial grasp selection and intermediate object orientation ensured mainly intermediate-state comfort, but not end-state comfort, is certainly in line with Seegelke et al. (2013) who reported that grasp postures were more strongly adjusted to the requirements of the first, rather than the second, targets (see also Haggard 1998).

The invariance of intermediate grasp postures suggests that biomechanical characteristics of the arm were taken into account in the motor plan prior to movement onset (Cos et al. 2011, 2012). Specifically, it is likely that only a very limited range of intermediate grasp postures provided sufficient comfort (i.e., even small changes in intermediate grasp posture would place the hand close to the extremes of the range of motion, thus rendering them uncomfortable).

Closer inspection of the data revealed the presence of inter-individual differences in initial grasp posture selection, with one subset of participants (i.e., strong adjusters) who adopted comfortable postures at the final target positions (end-state comfort), but not at the home position (initial-state comfort), and another subset (i.e., weak adjusters) who adopted initial grasp postures that satisfied initial-state comfort, but not end-state comfort. Interestingly, intermediate grasp postures were similar regardless of initial grasp adjustment (i.e., weak vs. strong adjusters) and also similar to the most comfortable intermediate grasp postures (i.e., intermediate-state comfort).

The presence of inter-individual differences in initial grasp posture planning has been reported in a number of unimanual (Hughes et al. 2012a; Rosenbaum et al. 1996; Seegelke et al. 2012) and bimanual object manipulation tasks (Fischman et al. 2003; Hughes and Franz 2008; Hughes et al. 2012b), and as in these studies, the presence of inter-individual differences in the present study cannot be readily explained by participants' characteristics (i.e., participants' age, gender, hip height, nor arm length could account for the differences in initial grasp postures adjustment). Although we did not collect data regarding the cognitive abilities of the participants, it is possible that the differences reported in the present study arose from the manner in which the task was perceived or cognitively represented [e.g., perception of precision demands (Rosenbaum et al. 1996; Hughes et al. 2012a) or the reduction of cognitive costs associated with grasp postures planning (Hughes et al. 2012b)]. Convincing evidence that inter-individual differences in motor behavior have a cognitive origin was recently obtained by Stöckel et al. (2012) who examined links between motor planning and the cognitive representation of grasp postures in children aged 7, 8, and 9 years. The major finding to emerge from that study was that the tendency toward comfortable end postures was related to the cognitive representation structure such that children with functionally well-structured representation exhibited a stronger preference for end-state comfort.

The idea that cognitive action representations are required when planning manual actions is a principle tenant in the frameworks of action selection outlined in work from our laboratory (Hughes and Franz 2008; Hughes et al. 2011, 2012b; Seegelke et al. 2011, 2012) and those of other researchers (Rosenbaum et al. 2001, 2013; van der Wel and Rosenbaum 2010). These flexible constraint hierarchy frameworks postulate that movements are guided by the higher-level action goals of the task, with the selection of appropriate actions contingent upon both the action goals of the task and the lower-level action constraints (e.g., grasp postures, kinematic minimization, task conceptualization). Lower-level constraints are given weight factors and ordered hierarchically according to their importance,[5] which depend not only on the action goals of the task, but also upon contextual, conceptual, environmental, and internal influences. That way, the weighting of the constraints defines the task to be performed as represented by the actor (Rosenbaum et al. 2013). For example, in point-to-point reaching movements, task conceptualization is less likely to influence action selection. As such, action constraints such as minimizing mean squared jerk (Hogan 1984; Hogan and Flash 1987), minimizing mean squared torque change (Uno et al. 1989), and minimizing end-point variance (Harris and Wolpert 1998) are assigned higher weights, and thus guide our actions. In contrast, in actions closer to those experienced in everyday life (such as object manipulation tasks), these kinematic minimization constraints are given lower weights. According to such a view, inter-individual differences in task performance are a result of variations in the relative order of action selection constraints between individuals (Seegelke et al. 2011, 2012; Hughes et al. 2011).

Based on the theoretical considerations of these frameworks, it follows that the associated weight factors of the action selection constraints (initial-state, intermediate-state, end-state comfort) differed between individuals. In the present task, strong adjustments in initial grasp posture led to comfortable final postures (i.e., end-state comfort), but not initial-state comfort, whereas the opposite was true for the weak adjusters. Consequently, it is plausible that participants who strongly adjusted their initial grasp postures (i.e., strong adjusters) weighted the tendency to adopt comfortable final postures higher than the tendency to adopt comfortable initial postures. In contrast, it is likely that the weak adjusters gave a higher weight to initial-state comfort as opposed to end-state comfort. In addition, as they selected similar initial grasp postures regardless of the final target position, they also reduced the cognitive costs associated with motor planning (see also Hughes et al. 2012b). Future research should consider manipulating environmental, conceptual, perceptual, cognitive, biomechanical, and personal constraints, as this line of work could shed light on the predominant constraints relating to inter-individual differences during multi-segment grasp posture planning.

In sum, the data of the present study provide further evidence that grasp posture planning is contingent upon multiple constraints that compete with each other during the selection of appropriate grasp postures. Whereas some constraints may take precedence in a given task, others may be regarded more flexible and weighted differently among participants dependent on contextual, environmental, and internal influences. This differentiated weighting leads to task- and subject-specific constraint hierarchies, which, in turn, are reflected in inter-individual differences in the selection of grasp postures.

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[5] In contrast to single-constraint models (e.g., Hogan 1984; Hogan and Flash 1987; Uno et al. 1989; Harris and Wolpert 1998), an important component of these frameworks is that all possible constraints are included, but differ with respect to their assigned weights.

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