

The contribution of cognitive, kinematic, and dynamic factors to anticipatory grasp selection

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Received: 16 July 2013 / Accepted: 20 January 2014
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Abstract Object-directed grasping movements are usually adjusted in anticipation of the direction and extent of a subsequent object rotation. Such anticipatory grasp selections have been mostly explained in terms of the kinematics of the arm movement. However, object rotations of different directions and extents also differ in their dynamics and in how the tasks are represented. Here, we examined how the dynamics, the kinematics, and the cognitive representation of an object manipulation affect anticipatory grasp selections. We asked participants to grasp an object and rotate it by different angles and in different directions. To examine the influence of dynamic factors, we varied the object's weight. To examine the influence of the cognitive task representation, we instructed identical object rotations as either toward-top or away-from-top rotations. While instructed object rotation and cognitive task representation did affect grasp selection over the entire course of the experiment, a rather small effect of object weight only appeared late in the experiment. We suggest that grasp selections are determined on different levels. The representation of the kinematics of the object movement determines grasp selection on a trial-by-trial basis. The effect of object weight affects grasp selection by a slower adaptation process. This result implies

that even simple motor acts, such as grasping, can only be understood when cognitive factors, such as the task representation, are taken into account.

Keywords Anticipatory actions · Grasping · End-state comfort effect · Dynamics · Kinematics · Task representation

Introduction

Humans and other animals manipulate objects in a manner that outperforms any state-of-the-art robot arm in terms of dexterity and efficiency. Part of our manual intelligence becomes evident when early aspects of a movement sequence are aligned to the requirements of subsequent actions. In the domain of object manipulations, for example, body postures are adjusted in anticipation of external loads (Wing et al. 1997), the speeds of prehension movements are adjusted to intended object manipulation even in infants (Claxton et al. 2003), and tools are grasped task dependently (Herbort 2012).

One particularly well-studied movement sequence is the (anticipatory) grasping and subsequent rotation of an object (Rosenbaum et al. 1990; for a review see Rosenbaum et al. 2012). It is frequently observed that when participants are asked to rotate an object, they rotate the hand in the direction opposite to the intended object rotation before grasping the object, if possible. This behavior enables humans (and monkeys) to keep the arm in a central range of motion during the object rotation, consequently increasing movement speed and accuracy (Rosenbaum et al. 1996; Short and Cauraugh 1999).

Even though this so-called end-state comfort effect has been reported in the past decades across different age

Electronic supplementary material The online version of this article (doi:10.1007/s00221-014-3849-5) contains supplementary material, which is available to authorized users.

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groups, in various clinical populations, tasks, and some non-human species, the precise mechanisms that implement this behavior in the central nervous system remain unclear. Here, we address to which extent dynamic, kinematic, and cognitive variables contribute to anticipatory grasp selections.¹

Object manipulations have at least three different aspects, pertaining to the cognitive representation of the task, the object manipulation's kinematics, and the object manipulation's dynamics. Even though these factors are interdependent, they can be separated to some extent. On the one side, these concepts can be separated to the extent that a specific representation of a task can be implemented with different kinematics (e.g., when making a paper ball, Todorov and Jordan 2002) and that movements with similar kinematics can be implemented with different dynamics (e.g., in force field adaptation, Gandolfo et al. 1996). On the other side, in visuomotor adaptation tasks, it can be shown that kinematics and dynamics are learned independently (Krakauer et al. 1999). Likewise, learning the kinematics and dynamics of object manipulations can be dissociated (Lukos et al. 2008; Zhang et al. 2010).

The first aspect in our focus is the task representation. The task represents the specific state or change of the environment that the participant intends to bring about. It thus refers to the end of an object manipulation, in contrast to the movements that provide the means of the object manipulation. It has been shown that these representations may affect also low-level aspects of grasping movements (Bock and Steinberg 2012). Moreover, movements that have to comply with identical dynamic and kinematic constraints can vary tremendously in terms of planning or initiation times depending on the goal to be achieved with them. For example, a supination of the left forearm might be hard to be combined with a spatially asymmetric pronation of the right forearm. However, once these movements are carried out to achieve the same object manipulation, they are easily combined (Kunde and Weigelt 2005; c.f. Hughes and Franz 2008; Hughes et al. 2012).

Secondly, the task kinematics, such as the postures assumed during a movement, need to be taken into account. It has been suggested that the kinematic level is central to planning reaching and grasping movements (Aflalo and Graziano 2007; Rosenbaum et al. 2001).

Thirdly, the dynamics of the task (e.g., which loads and forces are encountered) need to be considered to generate appropriate patterns of muscle activity. For this case, the literature is mixed. On the one side, it is a well-documented finding that participants adjust their grasp to properties

of the object bearing on movement dynamics, such as its weight or center of mass (Crajé et al. 2011; Sartori et al. 2011). On the other hand, these adjustments seem to be modulated only slightly or not at all by the intended object manipulation. For example, Sartori et al. (2011) observed how participants grasped an empty or full bottle for lifting or pouring. Whereas finger placements depended on the object weight, it did not interact with the task (c.f. van der Wel and Rosenbaum 2010). By contrast, Crajé et al. (2011) provided evidence for finger adjustments that were specific to particular combinations of object weight and intended object manipulation. Thus, whereas grasps are adjusted to the mass or mass distribution of objects, there is a mixed evidence for adjustments of grasps to specific combinations of object manipulations and object weights.

By now, anticipatory grasp selections have been mainly discussed in terms of the arm (and hand) kinematics or, more specifically, the postures assumed during critical parts of an object manipulation (e.g., Johnson 2000; Rosenbaum et al. 2012). However, varying the (instructed) object manipulation affects not only the arm kinematics of object manipulation but also the task representation and the dynamics of the object manipulation. Indeed, recent experiments have cast doubt on the notion that anticipatory grasp selections can be fully understood from a kinematic perspective. In these experiments, participants used very dissimilar postures to accomplish short object rotations (e.g., 45°) in different directions, even though this was not necessary to accomplish the task (e.g., Herbolt and Butz 2010, for a review see Herbolt 2013). Thus, the postures assumed during the object manipulation movement do not seem to be the defining factor of the grasp selection in this case.

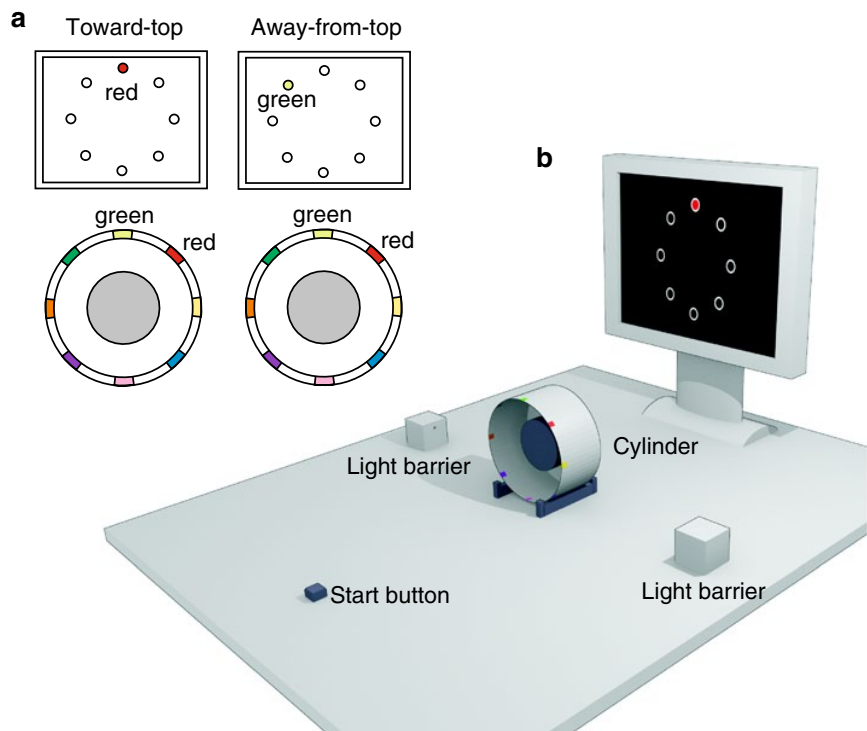
By contrast, the rotation direction per se may have a considerable influence on the task representation and the task dynamics. On the cognitive side, the direction of the movement is probably the most salient factor. Direction is not only a crucial factor for the specification of movements (Rosenbaum 1980), but it is also associated with, for example, motivational factors. For example, moving a joystick toward the body can be coded as an approach movement in some contexts but as an avoidance movement in others (Eder and Rothermund 2008; Neumann et al. 2014).

On the dynamics side, pronation and supination of the forearm require different muscle groups. Moreover, the postures in which maximal pronation and supination torques can be produced are rather different (O'Sullivan and Gallwey 2002). This suggests that rotation direction per se may be an important aspect from the perspective of movement dynamics.

In conclusion, the finding that the direction of an object rotation per se has a considerable effect on grasp selection, even though it matters little from a kinematic perspective, suggests that the task representation or the dynamics of the object manipulation may play a critical role. Hence, we

¹ With grasp selection, we refer to the orientation of the hand and forearm when grasping the object.

Fig. 1 **a** The figure shows a toward-top stimulus and an away-from-top stimulus (*top*) that both instruct a 45° counterclockwise rotation, given the corresponding cylinder positions (*below*). The *color* names were not shown during the experiment. **b** The setup consisted of a start button, a open cylinder placed on a socket, a light barrier used for detecting cylinder lifts and placements online, and a monitor



investigated which factors primarily contribute to the selection of grasp orientation preceding the rotation of an object. We varied the arm kinematics, dynamic, and also representational properties of the task. Participants were asked to rotate a cylinder by a certain degree. The arm kinematics were varied by instructing different rotation angles, even though this manipulation might also affect task dynamics and the task representation. Additionally, the dynamics of the rotation were varied by requiring participants to rotate a light or heavy object. To vary a representational variable, rotations were framed either as rotation toward a 12 o'clock position or as rotations away from a 12 o'clock position.

We expected that if mainly the arm kinematics determined grasp orientation selection, neither the cylinder weight nor the task framing should affect grasp selections. If dynamic factors (co-)determined the grasp selection, we expect a difference in the grasp orientation preceding manipulations of the light and heavy object. For example, participants might be inclined more strongly to grasp the heavy object with a posture supporting the generation of pronation or supination torques than the light object. Finally, if the representation of the task (co-)determined grasp selection, then the framing of the task should influence grasp selection. Conceivably, a toward-top stimulus may suggest that the cylinder needs to be moved from a deflected to a, what can be said, canonical “top” orientation, increasing the tendency to also deflect the forearm when grasping the cylinder. Conversely, moving an object

away from the top orientation might reduce the impact of the anticipated object manipulation on grasp selection.

Methods

Participants

Fourteen women and two men with a mean age of 24 years ($SD = 3.4$) gave informed consent and participated in the study. Visual inspection of the data revealed that the behavior of the two men did not differ qualitatively from that of the women. According to the handedness scale of Coren's (1993) Lateral Preference Inventory, all were right handed (average handedness score of 3.8).

Apparatus and stimuli

Figure 1 shows the setup and exemplar stimuli. Participants had to lift and rotate a cylindrical object. Two different cylinders were used throughout the experiment. The heavy cylinder weighed 363 g and was made of plastic; the light cylinder weighed 122 g and was made of cardboard. The estimated moment of inertia of the heavy cylinder equated almost four times the light cylinder's moment of inertia ($0.00142 \text{ m}^2 \text{ kg}$ vs. $0.00037 \text{ m}^2 \text{ kg}$). The cylinders had identical measures. Both were open at the front side, were white, had a diameter of 15 cm, and were 8 cm deep. The

plastic cylinder was painted white. The cardboard cylinder was coated with white plastic foil. Colored markings (1 cm × 1 cm) were distributed in 45° steps at the front rim, both at the inside and at the outside (green, red, yellow, blue, pink, violet, orange, green, as shown in Fig. 1). Both cylinders could be grasped and manipulated by a round knob (8 cm in diameter, 1 cm width) that protruded 4 cm from the cylinders' backside. The cylinder in use was placed in a socket on the table surface. We used a freely moveable cylinder to minimize the participants' possibility to readjust the grasp during the object movement and consequently encourage anticipatory grasp selections. A start button was placed 40 cm in front of the socket. A computer monitor positioned behind and slightly above the socket showed instructions and stimuli. A light barrier was positioned 5 cm above the table surface (Fig. 1). It was used to detect the lifting and placing of the cylinder for the online control of the experiment.

Rotations were instructed with stimuli that consisted of eight white circles (diameter 1.6 cm) that were arranged on an imaginary circle (diameter 18 cm) on a black background (Fig. 1a). One of them was filled with one of the eight colors that could be found on the rim of the cylinder. The remaining seven were filled with black. The cylinder had to be rotated in such a way that the position of the colored circle on the display corresponded to the position of the patch with the same color on the cylinder. For example, if a red circle was shown at 0° (12 o'clock) on the screen, participants had to move the red patch on the cylinder to the 0° position. Two different stimulus types were used: *toward-top* and *away-from-top stimuli*. Toward-top stimuli instructed a rotation by X degrees with a circle in the 0° position on the screen that had the same color as the patch on the cylinder in the $-X$ degree position before the rotation. Figure 1a (left) shows an example in which a rotation of 45° is instructed by displaying a red circle in the 0° position of the stimulus. In away-from-top stimuli, a rotation by X degrees was indicated with a circle in the X degrees position on the screen that had the same color as the patch in the 0° position on the cylinder. Figure 1a (right) shows an exemplar away-from-top stimulus, instructing a rotation of 45°. In each trial, the specific color of the colored circle on the screen was selected based on the orientation of the cylinder, which resulted from the last trial.

Procedure

After giving informed consent, the participants were seated in front of the table and familiarized with the experimental setup. Participants were seated so that they had to lean slightly forward with the trunk to grasp the dial with a stretched arm. A trial of the experiment began when the participant pressed the start button with the index finger of the right hand. After a fixation cross was presented for 1,000 ms, either a toward-top or away-from-top stimulus was

presented. Participants were instructed to grasp the knob inside the cylinder, lift the cylinder by at least 5 cm, rotate it according to the stimulus, place it back into the socket, and move the hand back to the start button. If participants rotated the cylinder incorrectly, did not raise the cylinder out of the socket, or took longer than 10 s, error feedback was given. If the movement was performed correctly, positive feedback was provided.² If participant released the start button before stimulus onset, the trial was restarted. If the cylinder was oriented in such a way that neither color was within 10° of the 12 o'clock position, participants were asked to reposition the cylinder. Otherwise, the next trial began with the cylinder oriented as placed by the participant.

Three independent variables were manipulated. First, the rotation angle of the cylinder could be 135°, 90°, 45°, -45°, -90°, and -135° (positive angles denote counter-clockwise rotations). Second, the cylinder weight could be light or heavy. Third, the stimulus types could be toward-top or away-from-top. Additionally, we included conditions in which the cylinder only had to be lifted (rotation angle = 0°) for comparison. Note that for the lifting condition toward-top and away-from-top stimuli were identical. The experiment consisted of two parts. Each part had four blocks of 26 trials. In each block, each combination of rotation angle and stimulus type was presented twice (=24 trials), plus two repetitions of the lifting condition. The different trial types were presented in random order. Half of the participants had to move the light cylinder in the first part of the experiment and the heavy cylinder in the second part. For the other half of the participants, the order was reversed. The entire experiment consisted of 208 trials and took approximately 45 min.

Data reduction and analysis

The movements of the cylinder and the participant's forearm were recorded with an electromagnetic motion tracker at a sampling rate of 100 Hz (Ascension TrakStar). One sensor was fixed to the distal end of the forearm of the participants, and one sensor was attached to the backside of the cylinder. We took care of giving the sensor cables enough play not to hinder the participants' movements or the rotation of the dial. For data analysis, the motion data of the sensors were smoothed with a second-order bidirectional Butterworth filter (10 Hz). For more accurate identification of movement onsets and offsets, the data were resampled to 1,000 Hz.

² If participants were within 3° of the target orientation the message "Ausgezeichnet!!!" (German for "Excellent!!!") appeared. Within 3°–7.5°, the message "Sehr gut!!!" ("Very good!!!") appeared. Within 7.5°–15°, the text "Gut, aber zu weit links/rechts." ("Good, but too far to the left/right") appeared, depending on the direction of the error. If errors exceeded 15°, the text "Fehler" ("error") was shown. If participants were too slow or did not lift the cylinder, the text "Schneller oder Rad höher anheben" ("Faster or lift cylinder higher") appeared.

The following variables were extracted. The reaction time (RT) was defined as the time from stimulus onset to the release of the start key. The onset of the cylinder rotations was defined as the time point at which the cylinder rotation or translation exceeded first 30°/s or 30 cm/s, whatever came first. The offset of the cylinder rotations was defined as the last time points at which the cylinder was last rotated with at least 30°/s or translated with at least 30 cm/s, whatever came last. The duration of the grasping movement (MT_{GRASP}) was defined as the time from the release of the start key to the onset of the cylinder rotation. The duration of the rotation (MT_{ROT}) was defined as the time from rotation onset to rotation offset. The most important variable, the grasp orientation FO_{GRASP} was defined as the orientation of the forearm relative to an external coordinate system at the onset of the cylinder rotation (positive angles denote supination, a value of 0° corresponds to the forearm orientation when placing the hand flat on the table surface). FO_{GRASP} mostly reflects pronation and supination of the forearm, because participants were seated in a way that required them to grasp the knob with a stretched arm.³ Moreover, FO_{GRASP} is highly correlated with the orientation of the hand and fingers, as revealed by high Pearson's correlation coefficients (computed over the trials of each participant) between the rotation of the cylinder and the rotations recorded at the forearm (mean $r = 0.98$). In the current experiment, about two-third of the cylinder rotation was caused by arm movements and one-third by finger movements. The absolute error (AE) of cylinder rotations was defined as the absolute difference between the final position of the cylinder and its target position as depicted by the stimulus.

Altogether, 21 trials (or 0.6 %) were excluded from analysis because they could not be segmented. From the remaining trials, 76 trials (or 2.3 %) were excluded for one of the following reasons: the movement was slower than 10 s, the deviation from the target cylinder orientation exceeded 15°, the cylinder was not lifted, the cylinder was incorrectly placed, or the time to complete the object manipulation ($RT + MT_{GRASP} + MT_{ROT}$) differed by more than two standard deviations from the average in the respective condition (treating the first two and second two blocks of each part of the experiment separately).

³ This is supported by the data in two ways. First, at the time of grasping, the yaw (left–right) and pitch (up–down) angle of the forearm with respect to an external coordinate system revealed little variability over the trials of each participant (mean $SD_{yaw} = 7.3^\circ$, mean $SD_{pitch} = 6.6^\circ$, for comparison, the mean of the participants' SD of FO_{GRASP} was 66.4°). Second, on average, the difference between the highest and lowest yaw and pitch angle recorded during each cylinder rotation was 8.9° and 13.9°, respectively. The low variability of the forearms position shows that the forearm was stretched or only slightly flexed when grasping and moving the object, suggesting that FO_{GRASP} reflects mostly pronation and supination of the forearm.

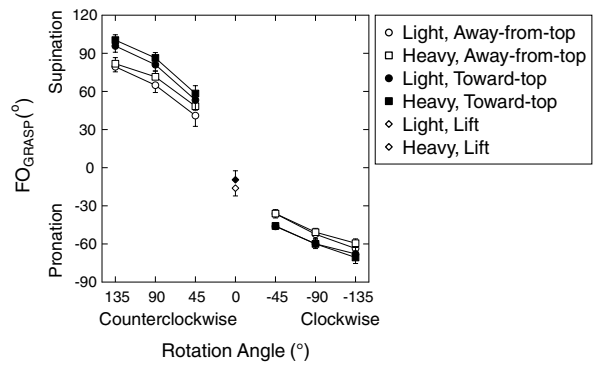


Fig. 2 Forearm orientation when grasping the knob (FO_{GRASP}) dependent on rotation angle, weight, and stimulus type. *Positive rotation angles* denote counterclockwise rotations; *positive forearm orientations* denote supination. *Error bars* reflect the standard error (between participants) of the mean

Results

We averaged the values of FO_{GRASP} , RT, MT_{GRASP} , MT_{ROT} for each experimental condition. The data of the first two blocks and the second two blocks of each part of the experiment were treated separately. The dependent variables (FO_{GRASP} , RT, MT_{GRASP} , MT_{ROT} , AE) were then subjected to an analysis of variance with the within-subject factors rotation angle ($-135^\circ, -90^\circ, -45^\circ, 45^\circ, 90^\circ, 135^\circ$), cylinder weight (light, heavy), stimulus type (toward-top, away-from-top), blocks (1 + 2, 3 + 4), and the between-subject factor group (light cylinder first, heavy cylinder first).⁴ All effects that are significant at the 0.05 level are reported. Please note that the five-factor ANOVA yields a large number of results. To achieve a global alpha of 0.05, individual comparisons needed to be significant at an alpha level of 0.0016.

Forearm orientation at grasping

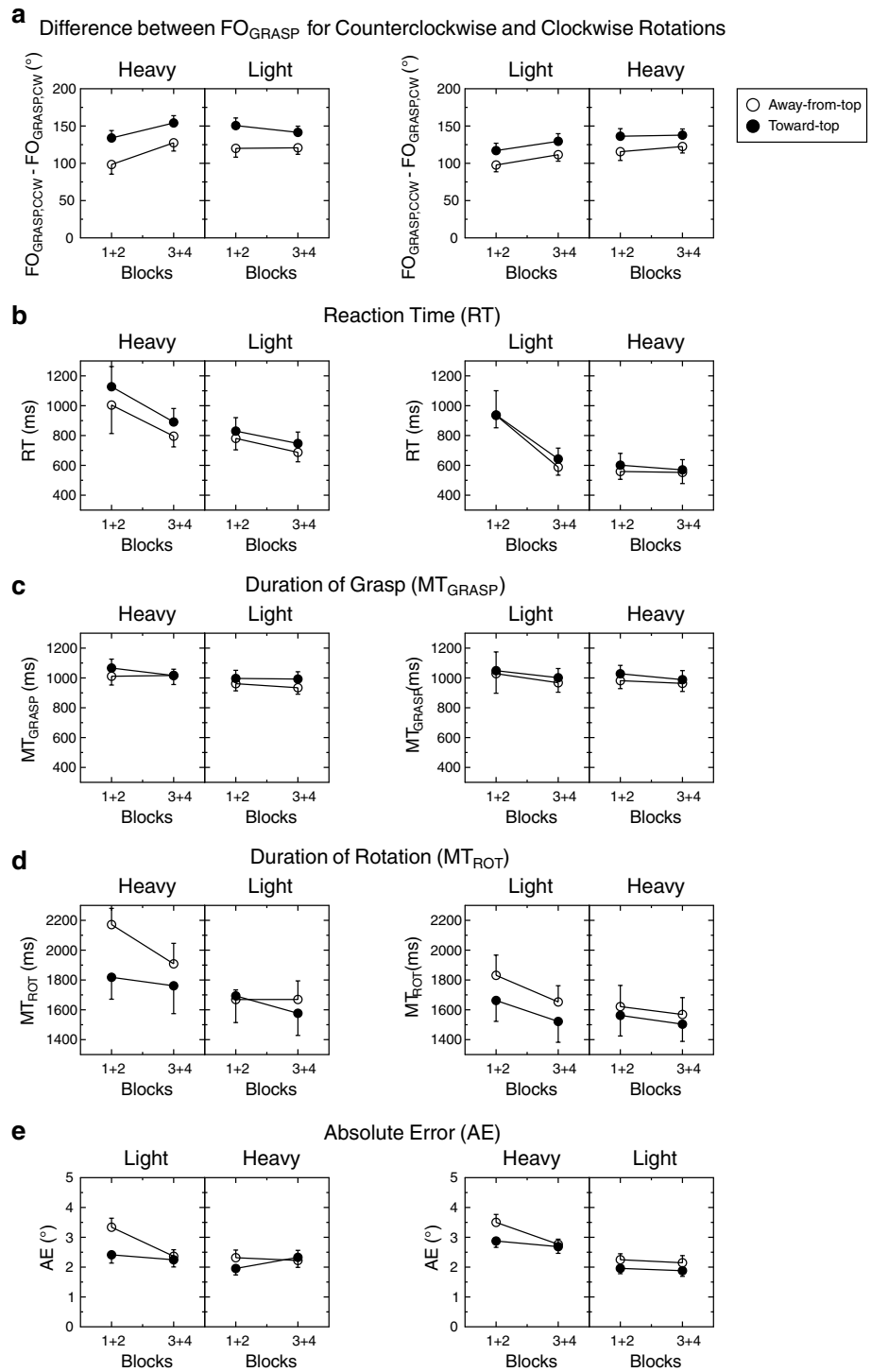
Figure 2 shows the forearm orientation at rotation onset (FO_{GRASP}) dependent on the rotation angle, averaged over all blocks. Figure 3a plots the difference between the mean FO_{GRASP} for counterclockwise and clockwise rotations, split by stimulus type, blocks, and group of participants.

Effects of rotation angle

FO_{GRASP} depended on the rotation angle, $F(5,70) = 356.3$, $p < 0.001$, $\eta_p^2 = 0.962$. Participants used a supine grasp before counterclockwise rotations and a prone grasp before clockwise rotations. This finding is commonly described as “end-state comfort effect.” Contrast analyses

⁴ Greenhouse–Geisser corrected p values but uncorrected dfs are reported.

Fig. 3 Difference between FO_{GRASP} for counterclockwise and clockwise rotations **a** RT, **b** MT_{GRASP} , **c** MT_{ROT} , **d** AE, and **e** by stimulus type. The *left column* shows the data for the participants who started with the heavy cylinder; the *right column* shows the data for the participants who started with the light cylinder. *Error bars* reflect the standard error (between participants) of the mean



revealed that this finding is significant for the comparisons of all opposing rotation angles (45° vs. -45° , 90° vs. -90° , and 135° vs. -135°), all $F(1,14) \geq 196.7$, all

$ps < 0.001$, all $\eta_p^2 \geq 0.934$. The main effect of rotation angle increased from blocks 1 and 2 to blocks 3 and 4, $F(5,70) = 8.0$, $p < 0.001$, $\eta_p^2 = 0.364$. This increase in the

end-state comfort effect was significant for the contrast for each pair of opposing rotation angles, all $F(1,14)s \geq 5.4$, all $ps \leq 0.036$, all $\eta_p^2 \geq 0.277$.

Effects of stimulus type

Interestingly, participants tended to use a more supine grasp in toward-top trials than in the away-from-top trials, $F(1,14) = 4.8$, $p = 0.046$, $\eta_p^2 = 0.255$. FO_{GRASP} s differed more between clockwise and counterclockwise rotations in toward-top trials than in the away-from-top trials, as signified by the interaction between rotation angle and stimulus type, $F(5,70) = 17.7$, $p < 0.001$, $\eta_p^2 = 0.558$. This effect was significant for each pair of opposing rotation angles, all $F(1,14)s \geq 15.3$, all $ps \leq 0.002$, all $\eta_p^2 \geq 0.521$. The interaction between rotation angle, stimulus type, and block reached significance, $F(1,14)s = 3.0$, $p = 0.047$, all $\eta_p^2 \geq 0.176$. This effect is not systematic for all rotation angles and can be attributed to a decrease in the effect of stimulus type on the end-state comfort effect from blocks 1 + 2 to blocks 3 + 4 for 135° rotations.

Effects of cylinder weight

FO_{GRASP} did not depend significantly on the cylinder's weight, $F(1,14) = 1.8$, $p = 0.206$, $\eta_p^2 = 0.112$. Likewise, there was no significant interaction between rotation angle and cylinder weight, $F(5,70) = 1.1$, $p = 0.334$, $\eta_p^2 = 0.07$. However, there were significant interactions between rotation angle, weight, and group, $F(5,70) = 4.1$, $p = 0.041$, $\eta_p^2 = 0.226$, and rotation angle, weight, block, and group, $F(5,70) = 5.8$, $p = 0.008$, $\eta_p^2 = 0.292$. Inspection of the data revealed that these interactions can be best understood as follows. In contrast to blocks 3 and 4, in which the end-state comfort effect was consistently larger for the heavy object, in blocks 1 and 2, the end-state comfort effect was larger for whatever weight was presented in the second part of the experiment. No other effect or interaction reached significance ($ps \geq 0.063$),⁵ nor was there a significant difference between both groups.

Effects of stimulus type versus cylinder weight

To directly compare the effect of cylinder weight and stimulus type, we computed two variables Δ stimulus and Δ weight, which reflect how changing the stimulus or the

cylinder's weight, respectively, affects FO_{GRASP} on average.⁶ Again, both variables were computed for the first two and second two blocks of each part of the experiment. On average, when instructed with a toward-top stimulus, participants rotated the forearm more against the direction of cylinder rotation than when instructed with an away-from-top stimulus, blocks 1 + 2, Δ stimulus = 13.3° (SD = 10.3°), $T(15) = 5.2$, $p < 0.001$, $g = 1.292$; blocks 3 + 4, Δ stimulus = 10.1° (SD = 9.4°), $T(15) = 4.3$, $p = 0.001$, $g = 1.073$. The cylinder weight had no effect on grasp selection in blocks 1 and 2, Δ weight = -0.2° (SD = 14.8°), $T(15) = 0.0$, $p = 0.968$, $g = -0.011$. In later blocks, the heavy cylinder caused participants to rotate the forearm more against the direction of cylinder rotation than the light cylinder, Δ weight = 4.8° (SD = 8.0°), $T(15) = 2.4$, $p = 0.029$, $g = 0.605$. Paired t tests revealed that Δ stimulus is significantly larger than Δ weight in the first two blocks of each part of the experiment, $T(15) = 2.7$, $p = 0.016$, $g = 0.681$, but not in the second two blocks, $T(15) = 1.6$, $p = 0.133$, $g = 0.397$. Thus, whereas the stimulus type affects the magnitude of the difference between grasps for clockwise and counterclockwise rotations (or the magnitude of the end-state comfort effect) throughout the experiment, the effect of the cylinder weight is smaller and emerges only after having interacted with the object for a while.

Short summary

The analysis of the grasp orientation when lifting the object revealed several main findings. First, grasp selections depended on rotation angle, replicating the end-state comfort effect. Second, grasp selections depended on the stimulus type throughout the experiment. Participants showed a larger end-state comfort effect in toward-top trials than in away-from-top trials. Third, also the weight of the object affected grasp selections, even though to a lesser degree than the stimulus type and only if participants had some experience handling the objects. As a result, participants showed a larger end-state comfort effect when handling the heavy object. Fourth, the end-state comfort effect increased during the first blocks of the first part of the experiment, regardless of the weight of the cylinder used initially.

⁵ Descriptively, the cylinder presented in the first part tended to be grasped more supine, with the exception of away-from-top trials in blocks 3 + 4, resulting in a marginally significant interactions between weight, group, block (and stimulus type), $p = 0.069$ (and $p = 0.063$, respectively). No other effect approached significance, all $ps \geq 0.206$.

⁶ Δ stimulus = $0.5 \times [(FO_{CCW,TOWARD-TOP} - FO_{CCW,AWAY-FROM-TOP}) + (FO_{CW,AWAY-FROM-TOP} - FO_{CW,TOWARD-TOP})]$; Δ weight = $0.5 \times [(FO_{CCW,HEAVY} - FO_{CCW,LIGHT}) + (FO_{CW,LIGHT} - FO_{CW,HEAVY})]$; where $FO_{X,Y}$ denotes FO_{GRASP} averaged over all other factors than implied by X and Y . For examples, $FO_{CCW,TOWARD-TOP}$ refers to the FO_{GRASP} averaged over all counterclockwise target angles and both weights.

Reaction time, duration of grasp, and duration of rotation

Reaction time

Figure 3b shows that RTs tended to be shorter when away-from-top stimuli were presented than when toward-top stimuli were presented, even though this main effect did not reach significance, $F(1,14) = 3.9$, $p < 0.067$, $\eta_p^2 = 0.220$. RTs decreased from the earlier blocks to the later blocks, $F(1,14) = 25.4$, $p < 0.001$, $\eta_p^2 = 0.645$. Reaction times were larger for whatever object had to be manipulated in the first part, as signified by the interaction between weight and group, $F(1,14) = 37.0$, $p < 0.001$, $\eta_p^2 = 0.725$. Furthermore, the interaction was stronger in the early blocks than in the later blocks, as signified by the interaction between weight, block, and group, $F(1,14) = 11.9$, $p < 0.004$, $\eta_p^2 = 0.459$. The interaction was also stronger for counterclockwise rotations than clockwise rotations, as signified by the interaction between rotation angle, weight, and group, $F(1,14) = 3.3$, $p = 0.043$, $\eta_p^2 = 0.189$. No other main effect or interaction reached significance, all $ps \geq 0.084$.

Duration of grasp

Figure 3c shows that MT_{GRASP} s tended to be shorter when away-from-top stimuli were presented than when toward-top stimuli were presented, even though this effect did not reach significance, $F(1,14) = 4.5$, $p = 0.052$, $\eta_p^2 = 0.244$. MT_{GRASP} s depended on rotation angle, $F(5,70) = 3.7$, $p = 0.029$, $\eta_p^2 = 0.210$. Contrast analyses revealed that MT_{GRASP} s were shorter for short rotations than for far rotations, $F(1,14) = 5.1$, $p = 0.040$, $\eta_p^2 = 0.268$, and shorter for clockwise than for counterclockwise rotations, $F(1,14) = 5.4$, $p = 0.036$, $\eta_p^2 = 0.277$. The main effect of rotation angle was modulated by stimulus type, $F(5,70) = 4.8$, $p = 0.008$, $\eta_p^2 = 0.256$. Whereas MT_{GRASP} s depended strongly on the rotation angle when a toward-top stimulus was presented, this dependency was virtually absent when away-from-top stimuli were presented, $F(1,14) = 13.6$, $p = 0.0020$, $\eta_p^2 = 0.493$. Finally, the difference between the two stimulus types increased over blocks when moving the light cylinder but decreased when moving the heavy cylinder, $F(1,14) = 5.8$, $p = 0.030$, $\eta_p^2 = 0.294$. No other effect reached significance, all $ps \geq 0.139$.

Duration of rotation

Figure 3d shows that MT_{ROT} s were slower when away-from-top stimuli were presented than when toward-top stimuli were presented, $F(1,15) = 5.7$, $p = 0.031$, $\eta_p^2 = 0.290$. MT_{ROT} s were larger for whatever object had to be manipulated in the first part, as signified by the interaction between weight and group, $F(1,14) = 10.6$, $p < 0.006$,

$\eta_p^2 = 0.431$. This size of this interaction was larger in away-from-top trials than in toward-top trials, $F(1,14) = 8.4$, $p < 0.012$, $\eta_p^2 = 0.374$. No other effect reached significance, all $ps \geq 0.068$.⁷

Short summary

In sum, it can be stated that reaction times and the duration of object rotations decreased during the experiment. Grasping movements tended to be faster if the rotation angle was short, however only when toward-top stimuli were presented.

Absolute error

Figure 3e shows that the AE was affected by the independent variables in a complex pattern of interactions. Despite this wealth of effects, please note that the maximum AE in any cell of the ANOVA table was only 4° and thus rather small.

Movements in the toward-top conditions were more accurate than those in the away-from-top conditions, however only in the early blocks, as signified by a main effect of stimulus type, $F(1,14) = 13.0$, $p = 0.003$, $\eta_p^2 = 0.482$, and the interaction between stimulus type and block, $F(1,14) = 10.8$, $p = 0.005$, $\eta_p^2 = 0.436$. The advantage of toward-top trials was also limited to short rotations, $F(5,70) = 2.6$, $p < 0.043$, $\eta_p^2 = 0.158$. Errors were larger for whatever object had to be manipulated first, as signified by the interaction between weight and group, $F(1,14) = 11.5$, $p < 0.004$, $\eta_p^2 = 0.452$. This interaction was larger in early blocks, $F(1,14) = 5.7$, $p < 0.034$, $\eta_p^2 = 0.290$. Errors depended on the target angle, descriptively, because errors were slightly higher for -90° rotations than for the other rotations angles, $F(5,70) = 2.6$, $p < 0.040$, $\eta_p^2 = 0.158$. This effect was modulated by a number of interactions. The heavy cylinder first group was more accurate than the light cylinder first group, but only for rotations of -135° , $F(5,70) = 3.1$, $p < 0.012$, $\eta_p^2 = 0.197$. Only in early blocks, the heavy cylinder was moved more accurate than the light one for -135° and vice versa for 135° , resulting in a significant interaction between rotation angle and weight, $F(5,70) = 3.1$, $p < 0.030$, $\eta_p^2 = 0.180$, and rotation angle, weight, and blocks,

⁷ MT_{ROT} s tended to decrease from the earlier blocks to the later blocks ($p = 0.068$). The interaction between rotation angle and stimulus type approached significance ($p = 0.070$). This interaction was neither based on a consistent effect of the rotation direction ($p = 0.210$) nor amplitude ($p = 0.438$). The three-way interaction between weight, group, and stimulus trials was modulated marginally by block ($p = 0.080$). All other effects did not approach significance (all $ps \geq 0.173$).

$F(5,70) = 2.8$, $p < 0.038$, $\eta_p^2 = 0.165$. Finally, the interaction between rotation angle, stimulus type, blocks, and group reached significance, $F(5,70) = 3.2$, $p < 0.020$, $\eta_p^2 = 0.187$. Descriptively, this interaction can be attributed to comparatively inaccurate movements in toward-top trials compared with away-from-top trials, which were present only in 135° rotations on the later blocks of the light cylinder first group and comparatively inaccurate movements in away-from-top trials compared with toward-top trials, which were present only in -90° rotations on the later blocks of the heavy cylinder first group. No other effect reached significance (all $ps \geq 0.072$).⁸

As an ANOVA of only the data of blocks 3 and 4 revealed no significant main effects or interactions, we would not like to interpret the complex pattern of effects associated with stimulus type, weight, and rotation angle. Thus, in sum, what can be said is that AEs decreased during the first blocks of the first part of the experiment and were on average rather low. No clear and systematic advantage of any stimulus type, weight, or target angle emerged.

Discussion

We addressed the question which factors contribute to the anticipatory selection of grasps in order to effectively manipulate an object. We suspected that the direction and extent of a required object rotation affect not only the arm kinematics of the object manipulation, but also the task representation and the movement dynamics. To isolate dynamic and representational factors, identical object rotations had to be executed with objects of different weights (affecting arm movement dynamics but not necessarily arm kinematics) and instructed with different stimulus types (affecting the task representation but not necessarily arm kinematics). It was found that grasp selections depended on the direction and extent of the upcoming object rotation, replicating earlier findings (e.g., Herbolt and Butz 2010, 2012; Rosenbaum et al. 1990, 2012). Additionally, the task representation affected grasp selections early on. However, the weight of the cylinder affected grasp selections only after participants had interacted with the specific cylinder for a while. These results show that the analysis of arm kinematics alone is not sufficient to understand anticipatory actions.

Dynamics

One possible reason for the small effect of cylinder weight could be that the objects had too similar weights or were

generally too light. However, we do not think that this is the case. On the one hand side, the heavy object had almost four times the light object's moment of inertia. That is, to accomplish identical rotations with both objects, almost four times larger torques had to be produced when moving the heavy object as compared to the light object.

On the other hand side, participants had to produce considerable torques to accomplish the task. In the $\pm 135^\circ$ trials, the acceleration of the object peaked on average at $1,400^\circ/s^2$ and at least at $2,500^\circ/s^2$ in the 5 % of trials with the fastest accelerations. For the heavier object, this implies that, on average, peak torques of 2.0 Nm were produced. In 5 % of trials, peak torques even exceeded 3.5 Nm. Given that participants were instructed to move the object with a stretched arm, these values correspond to about 17–30 % of the maximal pronation and supination torques that male adults can exert (O'Sullivan and Gallwey 2002).⁹ Considering that participants had to move each object over 100 times, thereby exerting considerable torques, it seems unlikely that the objects were too light or too similar in weight to elicit substantial weight-related effects. Of course we cannot exclude that cylinder weight might affect grasp selections more strongly for other movements than rotation or that other manipulations of dynamics might affect rotation movements as well. Still, comparatively small effect of the cylinder weight is remarkable and deserves further exploration.

Task representation

We manipulated the task representation using two different sets of stimuli to instruct the rotations. Whereas away-from-top stimuli suggested that the object was to be rotated away from the 12 o'clock position, the toward-top stimuli suggested that the object needed to be rotated toward the 12 o'clock position. In the following, we want to address whether the stimulus type genuinely affected the task representation. Alternatively, the different stimulus types could have affected kinematic variables in so far as different grasp selections for the different stimulus types might have improved object visibility or attentional factors.

Rosenbaum et al. (1992) noted that grasp posture might not only be selected with respect to the arm movement but also so that critical parts of the object are not occluded by the arm. However, we think it is unlikely that properties of the movement kinematics pertaining to the perception of the object caused the effect of stimulus type. First, the colored patches were placed on the rim of the cylinder,

⁸ The effect of block approached significance ($p = 0.72$, all other $ps \geq 0.089$).

⁹ As our participants were mostly female, these values are likely to underestimate the exerted torques in the task respective the maximum torques our participants would be able to produce.

so that the hand did not occlude any of the patches (except the patch at the 6 o'clock position, which was irrelevant in all conditions). Moreover, the participants were seated in such a way that all patches relevant to the task were visible. Second, also the data do not support such an explanation. If different end positions of the target patch had different visibility, then the differences in errors and rotation times between the stimulus types should increase with the extent of the rotation. If anything, then the reverse was found in the data. Third, visibility of the target patches can be expected to be worst at the -135° and 135° position. However, AEs tended to be lowest for object rotations by $\pm 135^\circ$. Indeed, several participants reported that they used the socket, which was close to the $\pm 135^\circ$ positions to precisely position the cylinder. In sum, the data do not indicate that the visibility of the patches on the cylinder was affected by the stimulus type in our experiment. Therefore, the observed effect of stimulus type cannot be attributed to kinematic factors pertaining to the visibility of the cylinder or socket.

It is frequently observed in object manipulation tasks that participants align the thumb with the functional part of an object, regardless of the intended object manipulation (Herbort and Butz 2011; Rosenbaum et al. 1992). One explanation for this so-called thumb-toward bias is that it facilitates attending concurrently to hand and object, both of which are attended during object manipulations (Collins et al. 2008). Thus, it might be possible that the effect of the stimulus type on grasp selection was driven by the tendency to align the thumb—or in our task more likely the index finger—with the attended colored patch on the cylinder. However, this seems unlikely for a number of reasons. First, in the away-from-top condition, the grasp orientations selected for rotations by $+45^\circ$ and -45° differ considerably, even though it would be easily possible to align the index finger with the patch at the 12 o'clock position and rotate the object. Moreover, if participants tended to align the index finger with the attended colored patch, the effect of stimulus type on grasp selection should increase with rotation angle. This was not the case.¹⁰ Hence, also attentional demands during the object manipulation cannot account for the effect of stimulus type.

In sum, the effect of stimulus type on the grasp orientation cannot be attributed to kinematic factors relating to motor, perceptual, or attentional demands of the object manipulation. Thus, it seems rather likely that the representation of the task as such affected the participants' grasp selections.

¹⁰ An inspection of single-trial data revealed that the absence of the effect of stimulus type on FO_{GRASP} cannot be explained by the effect being present in a subset of trials and being subsequently averaged out in the aggregated data.

Task kinematics

The relationship between grasp orientation on the one side and rotation angle and extent on the other side found here is comparable to that reported in other studies (for a review see Herbort 2013). As previously reported, the effect of the extent of the rotation is relatively small. In contrast, the difference between the grasps selected for the 45° and -45° is rather strong, even though these rotations can be easily brought about. The weighted integration of multiple biases model provides an account for these results (Herbort and Butz 2012). According to the model, the grasp orientation is the weighted average of a rotation direction-specific grasp orientation, a task independently preferred grasp orientation, and grasp orientations resulting from processing task-irrelevant information. With a participant-wise mean R^2 of 0.995 ($SD = 0.006$), this model provides a tight fit to the relationship between rotation angles and grasp orientations in the current experiment (details on the model and the fit to the current data are provided as electronic supplement).

Interaction between the task representation, kinematics, and dynamics

It was observed that the task kinematics, the task representation, and the task dynamics affected grasp selections. The direction and extent of the object rotation and the stimulus type had a strong impact on the grasp on a trial-to-trial basis. In contrast, other variables affected grasp selection on a slower time scale. A consistent effect of the object weight only emerged after having interacted with the cylinder for several minutes. Likewise, during the first blocks of the experiment, the magnitude of the end-state comfort generally increased, irrespective of which object was handled. This raises the question of how these different factors determine grasp selection.

We suggest that the factors influence grasp selection on different levels. We proposed that participants specify each object rotation in terms of the direction and extent of the object rotation (Herbort and Butz 2012). It is updated on a trial-by-trial basis as indicated by the presence of the end-state comfort effect. In the current experiment, the representation of direction and extent is biased by the type of stimuli it was extracted from. Hence, grasp selections were modulated by the stimulus type.

During movement planning, the specified rotation direction and extent—as well as the object location, shape, and so on—need to be converted in a specific grasp posture by an inverse model. We suggest that the inverse model is continuously adapted to the task by evaluations of the outcomes of cylinder rotations. It is unclear which precise factors drive the adaptation process, but it can be assumed that the actual end postures after object rotation play a role

(Rosenbaum et al. 2012). In this way, the kinematics and dynamics of the arm and finger movements (not necessarily the kinematics of cylinder movement) required in the present task determined the mapping from the goal representation to the grasp posture. For example, if executing a specific rotation with a specific grasp turned out to be disadvantageous, the mapping from object rotations to grasp postures is updated, possibly resulting in an increase in the end-state comfort during early trials.

In sum, we suggest that grasp selection is based on the specification of the object rotation, including extent and direction. These variables are then mapped onto a specific posture for grasping. The mapping is continuously updated by evaluating executed object manipulations, which depend on the involved kinematics and dynamics of the arm movements.

Conclusion

In the current experiment, we delineated the influence of cognitive, kinematic, and dynamic factors on the planning of grasp selections in anticipation of a subsequent object manipulation. It was found that the cylinder weight affected grasp selection only after having interacted with the cylinders for some time. In contrast, different task representations, elicited by the use of different stimulus types to instruct otherwise identical object manipulations, affected grasp selections from the beginning. Thus, how participants represent tasks with identical dynamic and kinematic properties is a crucial determinant during grasp selection. Finally, also the direction and extent of the object manipulation had a strong effect on grasp selections. We suggest that the dynamics and kinematics of the arm movement may not be directly considered during planning, but they may tune the grasp selection mechanism as a result of motor learning on a longer time scale. Finally, this research also shows that human movements cannot be understood from the perspective of movement kinematics and dynamics alone. Also variables pertaining to the representation of the task need to be considered.

Acknowledgments This work was funded by Grant HE 6710/2-1 of the German Research Foundation (DFG). We thank Michael Herbert, Albrecht Sebald, and Georg Schüssler for technical support and Wladimir Kirsch for helpful discussions.

Conflict of interest The authors declare that they have no conflict of interest.

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ESM 1: Fitting of Weighted-Integration of Multiple Biases Model to Experimental Data

The Weighted-Integration of Multiple Biases (WIMB) Model is described in (Herbert, 2013; Herbert & Butz, 2012). According to the model, grasp orientation selections in tasks as the present one, can be described by the following equation, when potential task-irrelevant biases are not taken into account.

$$FO_{anti} = \begin{cases} FO_{anti,cw} & \text{for clockwise rotations} \\ FO_{anti,ccw} & \text{for counterclockwise rotations} \end{cases}$$

$$FO_{GRASP} = \frac{w_{anti}FO_{anti} + w_{default}FO_{default}}{w_{anti} + w_{default}}$$

The model has four free parameters. $FO_{anti,cw}$ and $FO_{anti,ccw}$ are the forearm orientations associated to clockwise or counterclockwise rotations. $FO_{default}$ is the forearm orientation that would be used if the object just had to be grasped but not rotated. The weight $w_{default}$ defines how strong the default posture determines the executed grasp. The weight of the anticipatory posture bias w_{anti} is defined as the extent of the rotation.

We fitted the free parameters of the model to the average grasp orientations (irrespective of weight and stimulus type) for the seven rotation angles (-135°, -90°, -45°, 0°, 45°, 90°, -135°) for each participant. The data was fitted with the constraint that $w_{default}$ is positive and that $FO_{anti,cw}$, $FO_{anti,ccw}$, and $FO_{default}$ are in the range of -200° to 200°. Figure ESM-1a shows that the model provides on average a good fit to the data. The average R^2 of the models fits is .9948 (SD = .0064). Figure ESM-1b plots empirical grasp orientations against fitted grasp orientations for each rotation angle and each participant. The chart reveals that the model also fits the empirical data closely on the participant level.

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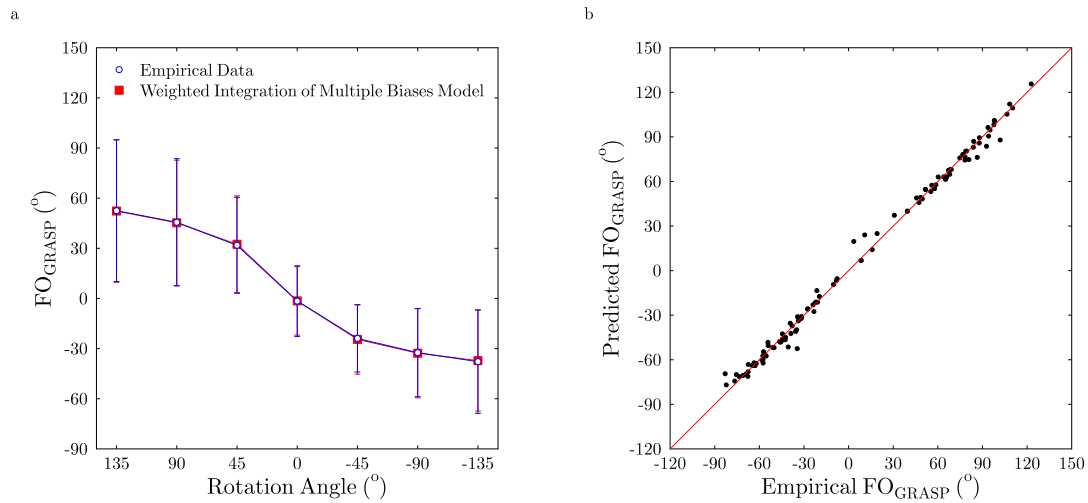


Fig. ESM-1 a) The figure shows the empirical mean grasp orientation and the mean of the participant-wise predictions of the WIMB model by rotation angle. Error bars show between-subject standard deviations. b) The figure shows predicted grasp orientations by empirical grasp orientations for each participant and each rotation angle. The model provides a perfect fit for points that fall on the red line.