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The continuous end-state comfort effect: weighted integration of multiple biases

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Abstract The grasp orientation when grasping an object is frequently aligned in anticipation of the intended rotation of the object (end-state comfort effect). We analyzed grasp orientation selection in a continuous task to determine the mechanisms underlying the end-state comfort effect. Participants had to grasp a box by a circular handle—which allowed for arbitrary grasp orientations—and then had to rotate the box by various angles. Experiments 1 and 2 revealed both that the rotation's direction considerably determined grasp orientations and that end-postures varied considerably. Experiments 3 and 4 further showed that visual stimuli and initial arm postures biased grasp orientations if the intended rotation could be easily achieved. The data show that end-state comfort but also other factors determine grasp orientation selection. A simple mechanism that integrates multiple weighted biases can account for the data.

The continuous end-state comfort effect: weighted integration of multiple biases

In everyday life, we usually act with the consequences of our behavior in mind. In manual actions, this enables us to adapt early movements in a course of actions to the requirements of later ones. This capability is a prerequisite to be able to carry out longer chains of actions effectively, which is often necessary to achieve our goals. Consider the example of grasping a spoon and using it. Dependent on if we want to eat soup, stir the soup, or hand the spoon to someone, we grasp it in different ways. If an unsuitable grasp is selected, the intended action may only be carried out with awkward movements or even not at all. To avoid such undesirable situations, humans appear to predict future events and consider them during motor planning (Bubic et al. 2010; Pezzulo et al. 2008). Motor planning can be defined as a process that selects a particular movement—among the often infinite number of alternatives—to achieve one's current goals. To succeed, this process needs to consider current contextual factors, such as the current body posture, the presence of obstacles, and the next body state to be reached. However, as discussed, motor planning also needs an anticipatory component, which considers the requirements of subsequent movements, thus enabling the effective execution of sequential actions.

The end-state comfort effect

A classical way to study anticipatory motor planning in the domain of grasping is the end-state comfort paradigm (Rosenbaum et al. 1990). Rosenbaum and colleagues asked their participants to place a horizontally oriented bar either on its left or right end and observed how the participants grasped the bar. If the task was to place the bar on its right end (i.e. turn the bar 90° clockwise), the participants grasped the bar with a prone forearm ("overhand grip"). If the task was to put the bar on its left end (i.e. turn the bar 90° counterclockwise), the participants grasped it with a supine forearm ("underhand grip"). This result demonstrated that the participants used the redundant degrees of

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freedom of their arm to select a grasp orientation (i.e. orientation of the hand when grasping the object) that enabled not only to grasp the object but also to terminate the rotation movement in a comfortable posture. Thus, the end-state comfort paradigm provides a powerful tool to investigate how sequential actions are planned. By now, the original findings have spawned a broad and growing body of research (c.f. Rosenbaum et al. 2007). The basic end-state comfort paradigm has been applied to assess motor planning in different age groups (e.g. Adalbjornsson et al. 2008; Thibaut and Toussaint 2010), with clinical populations (e.g. Hughes 1996; Steenbergen et al. 2000; van Swieten et al. 2010), in monkeys (Chapman et al. 2010; Weiss et al. 2007), and also for different continuous tasks (Cohen and Rosenbaum 2004; Schütz et al. in press; Zhang and Rosenbaum 2008).

Using the bar transport paradigm and its variations (e.g. Rosenbaum et al. 1992, 1993), several intertwined factors have been proposed that determine anticipatory grasp orientation[1] in object rotation tasks (besides the position and the orientation of the bar relative to the person who wants to grab it). First, the grasp orientation before the rotation depends strongly on the intended object rotation (e.g. Rosenbaum et al. 1990) and assures that the arm rests in a comfortable position after the object rotation. It is of course possible that participants do not actually strive to optimize comfort itself, but exploit properties of arm postures that are correlated with comfort. For example, in a comfortable posture, the forearm can also be pronated or supinated more quickly and exert stronger torques than in an awkward posture (Matsuoka et al. 2006; O'Sullivan and Gallwey 2005; Rosenbaum et al. 1996). The dependency of the grasp orientation on the to-be-executed rotation is modulated also by the precision requirements at the end of the rotation. High precision requirements attenuate the influence of the rotation on the grasp orientation, whereas low precision requirements may even eliminate it (Rosenbaum et al. 1996; Short and Cauraugh 1999). In the latter case, the influence of other factors on the grasp orientation may increase. Most prominently, recent grasp orientation selections tend to be conserved (Kelso et al. 1994; Schütz et al. in press; Short and Cauraugh 1999; c.f. Cohen and Rosenbaum 2004; Weigelt et al. 2009; Rosenbaum et al. 2006). In sum, the grasp orientation when grasping an object strongly depends on the anticipated rotation of the object if precision requirements are high. If precision requirements are low, however, the influence of the anticipated consequences of a rotational movement may decrease or even vanish.

[1] With the term "anticipatory grasp orientations", we refer to grasp orientations that have an anticipatory component.

The end-state comfort effect has been widely studied and different reasons have been proposed, why such behavior might be beneficial (e.g. Rosenbaum et al. 1996). However, the mechanisms that bring about this phenomenon are still not well understood. Thus, in this paper, we address potential mechanisms that could bring about the end-state comfort effect. In the following, we discuss two potential mechanisms that could underlie the end-state comfort effect. In Experiments 1 and 2, we contrast these two hypotheses of grasp orientation selection for object manipulation in a continuous task. Experiments 3 and 4 scrutinize possible additional effects of task-irrelevant visual and motor factors on grasp orientation selection. Finally, we will discuss potential optimality criteria and propose a simple mechanistic model for their implementation.

Possible mechanisms underlying the end-state comfort effect

Currently there are only very limited proposals on the detailed mechanisms underlying the end-state comfort effect. Thus, we bootstrap our exploration by contrasting two hypotheses, which can be derived from the literature. These rather distinct hypotheses will serve as a starting point and might finally both prove to be insufficient.

End-state comfort optimization hypothesis

A prominent approach to explain motor behavior is the optimal control framework (Engelbrecht 2001; Flash and Hogan 1985; Harris and Wolpert 1998; Todorov 2004; Wolpert and Ghahramani 2000). According to this approach, free parameters of a movement are chosen so that they minimize or approximately minimize an additional intrinsic cost function. This function is called objective function or optimality criterion. The approach has been particular successful in describing simple arm or eye movements (Harris and Wolpert 1998). As optimal control is a well-accepted framework for understanding motor behavior and end-state comfort is frequently discussed as a key determinant of grasp orientation selection, it seems straight forward to postulate that an optimal controller strives to maximize end-state comfort (at least if precision requirements are high). In the following, we will refer to this hypothesis as the "*end-state comfort optimization*" hypothesis. This hypothesis has three implications. First, it implies that humans prefer to end movements in postures that are as comfortable as possible or at least highly comfortable. Second, it implies that humans are actually able to realize this preference by generating optimal initial grasp orientations. Third, it implies that the end-state comfort criterion provides a clear preference for (ideally) one or at least a restricted range of postures (c.f. Johnson 2000; O'Sullivan and Gallwey 2005). Please note, that if this hypothesis cannot be confirmed, it does not imply that all three implications are necessarily invalid.

Even though this formulation of the hypothesis might seem overly strict and denies the influence of other variables than end-state comfort, there are good reasons to start from this point. First, the hypothesis is directly derived from a prominent framework for theories of motor control (optimal control) and a frequently proposed criterion for grasp orientation selection (end-state comfort). Second, the end-state comfort effect is frequently discussed in terms of optimization processes (Johnson 2000; Short and Cauraugh 1999; Rosenbaum et al. 1996; Schütz et al. in press; van der Vaart 1995). Thirdly, end-state comfort is discussed as an ecologically valid objective, because it is also correlated with movement speed or movement precision (Rosenbaum et al. 1996; Short and Cauraugh 1999).

Prototypical grasp orientations

On the other end of the scale, we speculated that the end-state comfort effect might be realized by a rather simple planning mechanism (Herbort and Butz 2010). We speculated that grasp orientations may be determined heuristically by selecting among a few prototypical grasp orientations based on the category of action. An example for action categories might be all clockwise or all counterclockwise object rotations. We will refer to this as the "prototypical grasp orientations" hypothesis. We proposed this hypothesis because participants' forearm orientations upon grasping a to-be-rotated dial depended strongly on the direction of the subsequent dial-turn, whereas the actual extent of the dial-turn had only a small influence on grasp orientations. Furthermore, a strong difference between grasp orientations preceding even very short dial-turns in either clockwise or counterclockwise direction was found despite the fact that this difference in grasp orientation was not crucial to perform the required turns and even slowed down the requested fast action execution. Similar results were obtained in comparable experiments (Robert et al. 2009; van der Vaart 1995). Finally, this hypothesis is interesting because it offers a very simple explanation for a seemingly complex phenomenon.

Implications and predictions

Both hypotheses differ considerably. Theoretically, the end-state comfort optimization hypothesis implies that precise information about the reach-grasp-and-turn movement is required and that an (unspecified) optimal movement planning process is applied. In contrast, the prototypical grasp orientations hypothesis simply implies that the initial grasp orientation selection is the result of a heuristic, which takes only the direction of the object rotation into account. Behaviorally, the end-state comfort optimization hypothesis implies that movements end in the most comfortable posture—or a restricted range of comfortable postures—but the prototypical grasp orientations hypothesis allows for a considerable variability of end postures. The cartoon charts in Fig. 1 contrast how the grasp orientation before and after the rotation of an object should depend on the angle of the rotation (a) if grasp orientation is not adjusted at all to upcoming rotations, (b) if the optimization of end-state comfort hypothesis applies, and (c) if the prototypical grasp orientations hypothesis applies. The charts show that both hypotheses predict a reduction of the range of grasp orientations after the rotation as compared to no adjustment of the grasp orientation before rotation. Otherwise, the predicted data patterns look fundamentally different. Most prominently and somewhat counter-intuitively, the prototypical grasp orientations hypothesis predicates that even rotations of rather small extents should have a considerable effect on grasp orientation. To distinguish between the hypotheses, we recorded participants' grasp orientation selections in a continuous task, before rotating an object by different extents and directions.

Altogether, we conducted four experiments. In Experiment 1, we tested the proposed hypotheses under conditions in which participants should be motivated and have the resources to carefully plan grasp orientations. Experiment 2 tested whether grasp orientation selection depends on the range of movements required throughout an experimental session. Experiments 3 and 4 tested if the grasp orientation is susceptible to the visual representation of the task or to the arm posture before grasp onset.

Experiment 1

In Experiment 1, we tried to match our procedures with the original bar paradigm (Rosenbaum et al. 1990) but we allowed for continuous grasp orientation selection in the pronation–supination range. Thus, participants had to grasp a circular dial attached to a box, which did not afford a specific grasp orientation, in order to turn the box by different extents and in different directions (Fig. 2). Moreover, we established conditions that should facilitate and encourage participants to plan their actions carefully. As in Rosenbaum et al.'s (1990) experiment, the box was a freely movable but rigid object, which gave maximal intuition on

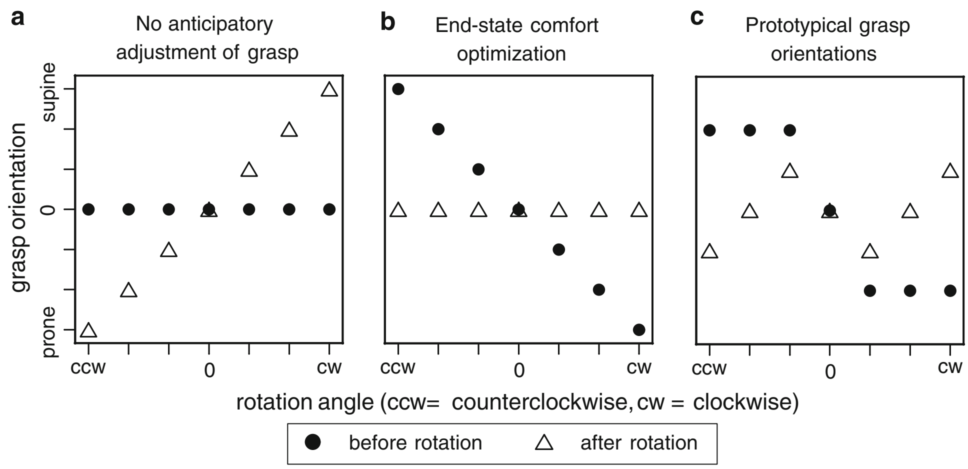


Fig. 1 Relationship between intended object rotation and grasp orientation before and after object rotation, **a** if grasp orientation is not adjusted to the rotation, **b** for the optimization of end-state comfort hypothesis, **c** for the prototypical grasp orientations hypothesis

how forearm movements will affect box movements and, unlike supported objects such as dials, it required participants to firmly grasp the handle throughout the turning movement and thus limited the possibility to compensate for poor initial adjustment of the grasp orientation. Furthermore, the turned box had to be placed into a cradle that was just slightly larger than the box, requiring an accurate positioning movement at the end of the turn. This was done because high accuracy demands at the end of the movement enhance the end-state comfort effect (Rosenbaum et al. 1996). Furthermore, there was no emphasis on reaction time or movement speed in the experiments, to give participants the time to plan their movements carefully. Finally, participants had the opportunity to increasingly adapt their grasp orientations from one trial to the next because the different required box rotations were presented in a blocked design. These experimental procedures were thus better suited to facilitate optimal motor planning than previous experiments on the continuous end-state comfort effect (e.g. Herbort and Butz 2010; Robert et al. 2009).

We expected that if the grasp orientation is selected to optimize end-state comfort, then grasp orientations should resemble those in Fig. 1b. In this case, the grasp orientation when the box is first grasped should depend strongly and linearly on the direction and the extent of the box rotation. Moreover, the grasp orientation at the end of the box rotations should always be in the middle of the pronation–supination range and depend little or not at all on the extent or direction of the box rotation. On the other hand, if the prototypical grasp orientations hypothesis is closer to the mark, we expect a data pattern similar to Fig. 1c, in which the grasp orientation when the box is first grasped depends strongly on the movement direction but only little or not at all on the extent of the box rotation. Furthermore, in the latter case we do not expect the grasp orientation at the end of the box rotation to be approximately independent of extent and direction of the box rotation.

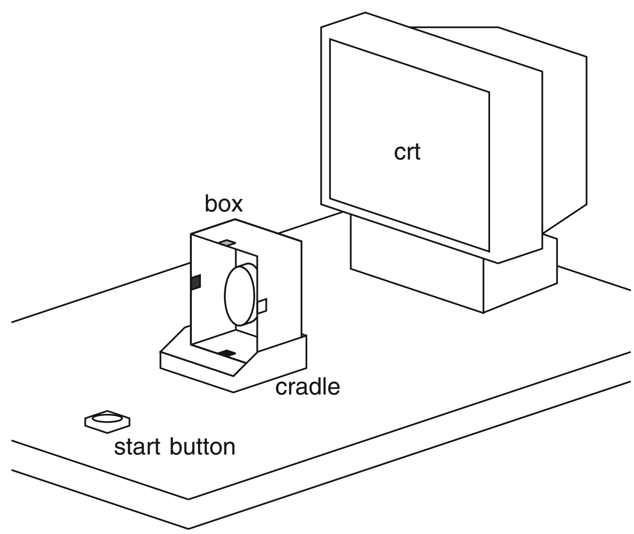


Fig. 2 Apparatus consisting of the start button, the box with the circular handle, the box' cradle, and the CRT

Method

Participants

Ten students of the University of Würzburg (8 women, 2 men, $M_{\mathrm{Age}} = 22$, age range 19–24) participated in Experiment 1 as a course requirement. According to Coren's (1993) Lateral Preference Inventory, eight participants were right-handed and two were left-handed.

Apparatus and stimuli

Figure 2 shows the general setup of the experiments. In all experiments, participants were required to grasp and rotate a cardboard box. The squared box (15 cm × 15 cm × 6 cm; 155 g) was open on the side facing toward the participant. The box could be grasped at a plastic dial (8 cm diameter) inside the box, which was fixed to the box' backside. Additionally, small patches of different colors (1 cm × 1 cm) were attached to each side of the box to help participants turn the box by the correct extent. During the experiment, the box was placed in a cradle that was open to the front and had small cardboard barriers on its left, right (1.5 cm height), and back side (3 cm height). A micro-switch inside the cradle registered if the box was placed in the cradle or not. A start button was placed between the participant and the cradle. A 17–in. CRT monitor was placed behind the cradle to deliver instructions to the participant. The box did not block the view of the monitor. Participants were seated in a chair, which was placed in such a way that the participants had to lean forward slightly, to be able to reach the dial with a stretched arm.

Procedure

After giving informed consent, the participants were seated in front of the experimental setup and were familiarized with the task. The experiment required the participants to turn the box by seven different rotation angles: −270°, −180°, −90°, 0°, 90°, 180°, or 270°, where a negative sign denoted a clockwise turn. In the 0° condition, participants were instructed to lift the box for approximately 2 s without turning it. The experiment was partitioned into 14 blocks of 5 trials. The trials of one block always required identical turning movements. Each type of block was presented once in the first half and once in the second half of the experiment but otherwise the sequence of blocks was randomized for each participant. Throughout the session, an experimenter in the room assured that the participants did not alter the seat position and always grasped the box firmly with a stretched arm.

Each block began with the presentation of an instruction on the CRT that informed the participant by which angle he or she had to turn the box in the next trials as well as a reminder of the experimental procedure. A trial began when the participant placed the right hand flat on the table surface and thereby pressed the start button with the right index finger. The so assumed forearm orientation was defined as 0°. After pressing the key, only the instruction to turn the box by a certain angle after the onset of a tone remained on screen (e.g. "Nach dem Ton, drehe die Schachtel bitte um 180° im Uhrzeigersinn", German for "After the tone, turn the box by 180° clockwise, please."). 1,100 ms after the onset of this instruction, a tone (880 Hz for 200 ms) signaled the participant to grasp the dial inside the box with the right hand, lift it, turn it, and place it back into the cradle. After that, feedback was displayed on the screen for 1,000 ms. If the participant did not turn the box by the correct angle, a message informed about the error. If participants needed more than 10 s to complete the movement, they received the message to move faster. If they executed the movement correctly, the text "gut gemacht" (German for "well done") was displayed. After that, the participant moved the right hand back to the start button and the next trial was initiated once the button was pressed. Participants were neither instructed to execute the movements with a particular speed nor to grasp the box with a specific grasp orientation.

Data recording and analysis

The grasp orientation was operationalized by recording the forearm orientation with a three-axis accelerometer that was strapped to the participant's right forearm proximal to the wrist. Thus, the measurement reflects the overall orientation of the distal forearm with respect to the table surface, which may, in principle, be caused by forearm pronation or supination, elbow adduction or abduction, or movements of the torso. As the participants could reach the dial only with a stretched arm, the measurements reflect mostly forearm pronation and supination. Even though fixating the accelerometer to the forearm did not enable measuring the hand's orientation directly, we used this method because in this way, no sensors at the fingers hindered the participants' interactions with the dial. Moreover, previous studies have shown that the orientation of the forearm is highly correlated with the orientation of the hand and thus a suitable operationalization (Herbort and Butz 2010; Marotta et al. 2003).

The low-pass filtered (5 Hz) forearm orientation measurements had a resolution of 0.5°. The orientation of the box was measured by a self-constructed electromagnetic motion tracking device that was accurate enough to provide feedback about the orientation of the box. The box' motion tracking device was connected with the recording equipment by a long, thin, and flexible cable that did not hinder lifting or turning the box. The forearm and box orientation were recorded with a sampling rate of 100 Hz. To correct for displacement of the forearm orientation sensor during the course of the experiment, we subtracted the estimate of a linear regression of trial number on the forearm orientation before movement onset for each trial for each participant. This also had the effect that for all participants, the forearm orientation of 0° corresponded to the forearm orientation in which the hand rests flat on the horizontal table surface. In the following, positive forearm angles denote a supine, negative forearm angles a prone forearm position.

From the recordings, we extracted the forearm orientation when the participant started to lift the box (FO_{LIFT}, at release of the micro-switch in the cradle). Additionally, the forearm orientation when the box was placed back into the cradle (FO_{PLACE}, at depression of the micro-switch in the cradle) was recorded because this variable reflects the effects of the initial grasp orientation selection on the final grasp orientation. Data from altogether 20 trials (2.9%) were excluded from the analysis because either the box was turned by an incorrect angle, the movement was not finished within 10 s after the start signal, the forearm orientation deviated more than 10° from the zero orientation at the onset of the start signal, or the forearm orientation at lifting deviated by more than 2.5 SD from the participants mean for the respective target angle.

Results

Biomechanics of the forearm and hand rotation

First, we analyzed which arm segments contribute to the rotation movement. To this end, we related the rotation of the forearm during the box rotation to the rotation of the box itself, which reflects the total rotation caused by trunk, arm, wrist, and fingers. We computed correlations between the actual rotation angle of the box and the angle covered by the forearm orientation between lifting and placing the box for each subject over all trials of a session. The correlations were almost perfect, ranging between $r = 0.9877$ and $r = 0.9992$. Thus, the forearm orientation explains most of the variance of the overall rotation caused by the rotation of trunk, wrist, arm, and fingers. Moreover, the percentage of the contribution of wrist and fingers depended only little on the extent of the box rotation. To estimate the contribution of wrist and fingers to the box rotation, we divided the angle between FO_{PLACE} and FO_{LIFT} by the rotation angle of the box for each trial (except for rotation angles of 0°). The averaged ratio of 0.743 (SD = 0.080) reveals that the wrist and finger movements contributed about 25% of the overall rotation. As participants executed the rotation with an almost stretched arm, the remaining 75% were mostly caused by forearm pronation and supination. Most importantly, the data show that the forearm orientation is a reliable operationalization of the grasp orientation. The contribution of the forearm rotation to the overall rotation in Experiment 1 exceeded previous accounts, which showed that wrist and fingers as well as the forearm contributed roughly equally when grasping or manipulating objects (Herbort and Butz 2010; Marotta et al. 2003). Most likely, the higher forearm contribution results from the task, which requires—unlike in the previous experiments—that the fingers support the grasped object.

Forearm orientation at lifting and placing

Figure 3 shows that participants' grasp orientations upon lifting the box (FO_{LIFT}) and placing the box (FO_{PLACE}) depended strongly on the intended box rotation. To statistically evaluate the effect of the rotation angles on FO_{LIFT} and FO_{PLACE}, we computed repeated measures ANOVAs with the within subject factor rotation angle, with factor levels −270°, −180°,…, 270°. The effect of the differences between adjacent rotation angles on the dependent variables was compared with paired *t* tests. The results of the ANOVA and the *t* tests are reported in Table 1. Participants grasped the box with a supine forearm before counterclockwise turns and a prone forearm orientation before clockwise turns. However, the participants' grasp selection did not compensate for the forearm rotation required to turn the box and thus also FO_{PLACE} depended strongly on the rotation angle. An ANOVA with within subject factors rotation angle and repetition (levels: 1st, 2nd,…, 5th) revealed that FO_{LIFT} was not adjusted systematically during the blocks of five consecutive turns in the same direction, main effect of repetition: $F(4,36) = 0.91$, $p = 0.47$, interaction between rotation angle and repetition, $F(24,216) = 0.59$, $p = 0.94$. Online Resource 1 lists means and standard deviations of FO_{LIFT} and FO_{PLACE} for all trial types.

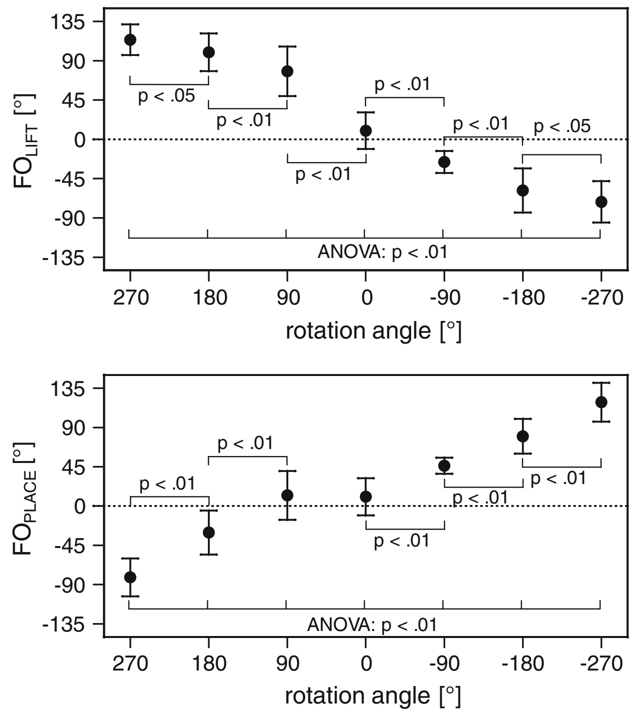


Fig. 3 FO_{LIFT} (*top*) and FO_{PLACE} (*bottom*) for different rotation angles in Experiment 1. Positive FO_{LIFT} and FO_{PLACE} denote supine forearm orientations. Positive rotation angles denote counterclockwise turns. *Error bars* show ± 1 SD (between subjects)

Effect of direction and rotation angle

A look at the relationship between the rotation angle and FO_{LIFT} reveals a discontinuity between FO_{LIFT}s for clockwise and counterclockwise turns. FO_{LIFT} depended

Table 1 Results of ANOVAs with the within-subject factor rotation angle and post-hoc paired *t* tests of the variables FO_{LIFT} and FO_{PLACE}

	ANOVA		Post-hoc paired *t* tests											
			270°/180°		180°/90°		90°/0°		0°/−90°		−90°/−180°		−180°/−270°	
	$F(6,54)$	p^a	$T(9)$	p	$T(9)$	p	$T(9)$	p	$T(9)$	p	$T(9)$	p	$T(9)$	p
FO_{LIFT}	158	<0.01	2.3	<0.05	8.1	<0.01	8.9	<0.01	6.0	<0.01	4.3	<0.01	2.3	<0.05
FO_{PLACE}	83.3	<0.01	−9.1	<0.01	−12	<0.01	0.26	0.80	−4.8	<0.01	−4.5	<0.01	−7.3	<0.01

[a] Greenhouse-Geisser corrected *p* values are reported

Table 2 Comparision between Δ_{ROT}, Δ_{DIR} and $\Delta_{DIR + ROT}$ for Experiments 1, 3, and 4

Experiment	$\Delta_{DIR + ROT}$ m (SD)	Δ_{ROT} m (SD)	Δ_{DIR} m (SD)	Paired *t* test $\Delta_{DIR + ROT}$ vs. Δ_{ROT}			Paired *t* test Δ_{DIR} vs. Δ_{ROT}		
				df	*T*	*p*	*df*	*T*	*p*
Exp. 1	104° (29.6°)	40.9° (17.1°)	62.9° (38.2°)	9	5.2	<0.01	9	1.4	0.21
Exp. 3[a]	108° (32.8°)	35.0° (20.0°)	73.0° (47.4°)	14	6.0	<0.001	14	2.3	0.04
Exp. 4[a]	98.1° (29.4°)	25.9° (12.6°)	72.1° (28.1°)	14	10	<0.001	14	5.6	<0.001

[a] Averaged over arrow start positions (Experiment 3) and forearm orientations before onset of the grasp (Experiment 4)

apparently stronger on the direction of the rotation than on the extent of the rotation. This can be seen as the difference between FO_{LIFT}s for the rotation angles −90° and 90° was larger than the difference between FO_{LIFT}S for rotation angles −90° and −270° or 90° and 270°, although the compared rotation angles all differ by 180°. To quantify the discontinuity, we assumed that the forearm orientation resulted from the combination of a linear effect of rotation angle and an additional effect of rotation direction[2]. The effect of a 180°-difference in rotation angle between turns in the same direction ($\Delta_{ROT} = 0.5 \times [FO_{LIFT,270°} - FO_{LIFT,90°} + FO_{LIFT,-90°} - FO_{LIFT,-270°}]$) only reflects how grasp orientation changes, when the rotation angle is changed by 180° and the direction remains the same. In contrast, the difference between +90° and −90° rotations ($\Delta_{DIR + ROT} = FO_{LIFT,90°} - FO_{LIFT,-90°}$) reflects how grasp orientation changes when the rotation angle is changed by 180° and the direction is changed. To estimate the influence of the direction alone, we subtracted both values ($\Delta_{DIR} = \Delta_{DIR + ROT} - \Delta_{ROT}$). Table 2 reports means and standard deviations of Δ_{DIR}, Δ_{ROT}, and $\Delta_{DIR + ROT}$. Paired *t* tests show, that there is a significant influence of the direction of the rotation. However, the numerically larger effect of direction does not significantly exceed the effect of rotation angle.

Discussion

Experiment 1 investigated the continuous end-state comfort effect in a task that should motivate and facilitate participants to adjust grasp orientations before lifting the box as well as possible to their liking. The results revealed that participants' grasp orientations depended strongly on the direction of the subsequent box turn but also on the rotation angle. Participants selected very different grasp orientations when required to turn the box by −90° versus 90°, even if both rotations could in principle be executed without adapting the grasp orientation to the subsequent box turn at all. Moreover, the differences in the grasp orientation before turns of an extent of 90°, 180°, or 270° were comparatively small, especially when one considers that it is much more difficult to turn the box by 270° than by 90°. The data replicate previous experiments on the continuous end-state comfort effect (Herbort and Butz 2010; Robert et al. 2009; van der Vaart 1995).

With regard to possible explanations for the determination of grasp orientation, this experiment provides mixed results. On the one hand, the high variability of the grasp orientations at the end of the box rotations between conditions does not fit the predictions of the end-state comfort optimization hypothesis. On the other hand, there was a significant influence of the extent of the turn on the grasp orientation, which is incompatible with the prototypical grasp orientations hypothesis. Thus, neither of the proposed hypotheses is able to fully account for the data without modification.

[2] The rotation angle can assume both positive and negative values

Experiment 2: context

Experiment 1 seemed to contradict the notion that strictly those grasp orientations are selected that result in the most comfortable arm postures at the end of the box rotation. However, one might object that the comparatively strong difference between the grasp orientations preceding clockwise and counterclockwise turns resulted only because participants reused movement plans or avoided re-planning. In fact, it has been shown that when objects are grasped, features of previous movements are conserved (Cohen and Rosenbaum 2004; Kelso et al. 1994; Rosenbaum and Jorgensen 1992; Schütz et al. in press; Weigelt et al. 2009). Thus, it is possible that the influence of previously executed movements obscures anticipatory grasp orientation selections according to the optimization of end-state comfort hypothesis and that behavior would be different, if the influence of this effect was removed. If this would be the case, the excursion of the grasp orientations before turns of small extents should be larger than predicted by the end-state comfort optimization hypothesis because it is likely that turns of larger extent had to be executed previously. Likewise, grasp orientations before turns of large extent should be smaller than predicted by the optimization of end-state comfort hypothesis because it is likely that rotations by a small extent have been executed previously. This would result in a data pattern similar to the one found in Experiment 1.

Alternatively, subjects might have been tempted to adopt the strategy of only slightly adjusting an average suitable grasp orientation for each rotation direction to lessen the burden of motor planning. As the direction of the turning movement might have been a salient feature of the experimental procedure from the viewpoint of the participants, also such an averaging effect does not seem to be an unlikely explanation.

Thus, the requirement to turn the box by different extents in Experiment 1 might obscure the participants' ability to finely adjust the grasp orientation to an intended rotation and optimize comfort after the rotation. Even though the blocked trial structure of Experiment 1 reduced the potential influence of the context, Experiment 2 tests if the requirement to rotate the box by different extents in a session biased participants toward generating average grasp orientations for clockwise and counterclockwise turns. In this case, the data pattern of Experiment 1 resulted due to the presentation of different rotation extents in the same session and participants should behave differently if only rotations by one specific extent would be required throughout a session. If this was the case and participants only had to turn the box by 90° throughout a session, we would expect participants to generate less prone or supine grasp orientations than in Experiment 1 but if participants only had to turn the box by 270° throughout a session, we would expect them to generate more prone or supine grasp orientations than in Experiment 1. However, if the data pattern of Experiment 1 did not result from a tendency to generate average grasp orientations or from carry-over effects from previous trials, we would expect that the range of possible rotation extents of an experimental session does not affect grasp orientations. Thus, Experiment 2 uses the same procedure as Experiment 1, but this time data of three independent groups of participants was collected, each of which had to turn the box by an extent of either 90°, 180°, or 270°. The average grasp orientation before lifting the box of the participants of Experiment 2 is then compared to the grasp orientations exhibited by the participants of Experiment 1.

Method

Participants

Thirty students of the University of Würzburg (27 women, 3 men, $M_{\mathrm{Age}} = 21$, age range 19–44) participated in Experiment 2 as a course requirement. According to Coren's (1993) Lateral Preference Inventory, 28 participants were right-handed and 2 were left-handed. The participants were assigned to three groups, which did not differ significantly with respect to age, sex, or handedness and which did not differ from the participants of Experiment 1, $F_{\mathrm{age}}(3,36) = 0.60$, $p = 0.62$, $F_{\mathrm{LPI}}(3,36) = 0.38$, $p = 0.77$, $\chi^2_{\mathrm{sex}} = 0.69$, $p = 0.88$.

Procedure

Whereas in Experiment 1 the extent of the required turns was varied in a within-subject design, in Experiment 2 the extent of the required turns was varied between subjects by randomly assigning each participant to one of three groups. In each group, participants had to turn the box by only one extent (90° in the 90°-group, 180° in the 180°-group, and 270° in the 270°-group) in either clockwise or counterclockwise direction (8 blocks of 5 identical trials) or lift the box (2 blocks of 5 identical trials). The blocks were presented in randomized order. The trial procedure and the instructions of Experiment 1 and 2 were identical otherwise. After applying the same criteria as in Experiment 1, data from altogether 107 trials (7.1%) were excluded from the analysis.

Results

Figure 4 shows the data of Experiment 1 and Experiment 2 (see Online Resource 1 for means and standard deviations of FO_{LIFT} and FO_{PLACE}). The participants of the 90°-group show very similar differences between FO_{LIFT}s preceding clockwise and counterclockwise turns as do the participants in 90° and −90° conditions in Experiment 1. The same holds for the 180°-group and the 270°-group of

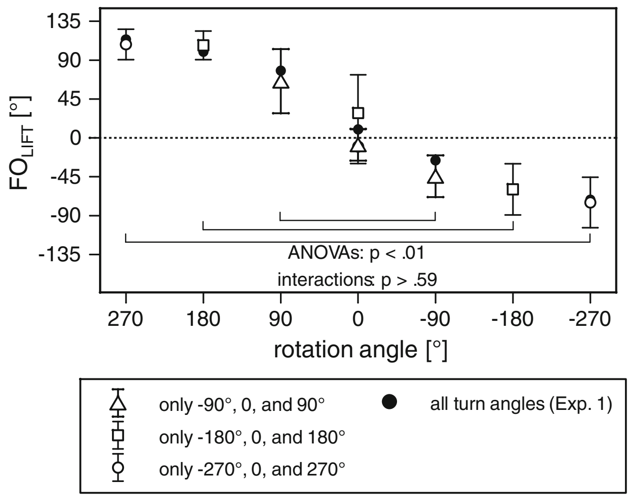


Fig. 4 FO_{LIFT} for the three groups of Experiment 2 (*empty diamonds, squares, and circles*) and of Experiment 1 (*black circles*) for different rotation angles. Positive FO_{LIFT} denote supine forearm orientations. Positive rotation angles denote counterclockwise turns. *Error bars* show ± 1 SD (between subjects of Experiment 2)

Experiment 2 when compared to the respective conditions in Experiment 1. To statistically test for any differences, we compared the FO_{LIFT}s preceding an either clockwise or counterclockwise turn (i.e. we did not compare the 0° condition) of each group of Experiment 2 with the respective data of Experiment 1 with three ANOVAS with within-subject factor turn direction (clockwise vs. counterclockwise) and between subject factor experiment (Experiment 1 vs. Experiment 2). For example, the ANOVA for the 90°-group compared FO_{LIFT}s preceding turns of 90° and −90° in participants of Experiment 1 and Experiment 2. Table 3 reports the results of the ANOVAs. There were main effects of turn direction for all groups, indicating strong end-state comfort effects. Most importantly, the interaction between turn direction and experiment was far from significant for the three ANOVAs. Thus, the magnitude of the end-state comfort effect did not differ significantly between Experiment 1 and 2.[3] Even if a non-significant result does not imply that there are no differences between groups, we are confident that we can reject the hypothesis that participants tended to produce average grasp orientations for each turn direction in Experiment 1. In this case, we would expect a smaller difference between FO_{LIFT}S for rotation angles of 90° and −90° in Experiment 2 than in Experiment 1 and a greater difference between FO_{LIFT}S for rotation angles of 270° and −270° in Experiment 2 than in Experiment 1. The numerical data, however, showed the exact opposite pattern.

[3] The effect of the context is unlikely to be cancelled out by the different ratios of women and men participating in Experiments 1 and 2 (c.f. Fischman 1998), because similar results are obtained if only women are included in the analysis (for all interactions $p > 0.23$).

Table 3 Results of ANOVAs with the within-subject factor turn direction and between subject factor experiment

Group	Rotation angles	Experiment		Turn direction		Interaction	
		$F(1,18)$	p^a	$F(1,18)$	p^a	$F(1,18)$	p^a
90°-group	90° vs. −90°	3.4	0.08	147	<0.01	0.13	0.72
180°-group	180° vs. −180°	0.19	0.67	446	<0.01	0.31	0.59
270°-group	270° vs. −270°	0.40	0.54	648	<0.01	0.32	0.86

[a] Greenhouse-Geisser corrected *p* values are reported

Discussion

Experiment 2 revealed that the selection of the grasp orientation in each trial did not depend on the range of box rotations or grasp orientations that were required throughout the experimental session. The strong difference between grasp orientations before clockwise and counterclockwise box rotations in Experiment 1 did not emerge because participants tended to produce averaged grasp orientations and were thus biased away from grasping the box according to the end-state-comfort optimization hypothesis. Thus, Experiment 2 replicated the discontinuous relationship between grasp orientation and required object rotation, which was already present in Experiment 1.

Experiment 3: visual task representation

Experiments 1 and 2 revealed that neither of the initially proposed hypotheses could account for the data. Both, the end-state comfort optimization and prototypical grasp selection hypotheses have in common that grasp orientation selection is determined exclusively by motor properties of the task (anticipated end-posture or rotation direction, respectively). To test, if this strict motor focus limited the initial hypotheses, in Experiment 3 we examined to which extent the selection of the grasp orientation is affected by non-motor criteria. If grasp orientation selection took only motor factors into account, then it should not be possible to alter the grasp orientation by instructing identical rotations with different stimuli.[4] Thus, we used a set of circular arrows to cue box rotations. Each arrow suggested that the box was to be grasped with the fingers at the arrow's start position and was to be rotated according to its length and direction. An arrow starting at the right of the

[4] Grasp selection may be biased by optical illusions (Crajé et al. 2008). However, here we did not want to create an illusion that distorted the perceived orientation of the object that was to be grasped, but wanted to suggest a certain way of grasping and turning the box to the participants.

box suggests a supine grasp, the arrow starting left of the box suggests a prone grasp, and the arrow starting on top of the box suggests a neutral grasp. If the arrow starts below the box, it could suggest either an extremely prone or supine grasp. If grasp orientation selection was exclusively based on motor factors, as predicated by both initial hypotheses, it should not be affected by the visual instruction of the rotation movement. On the other hand, if grasp orientations were modulated by perceptual factors, potential explanations for grasp orientation selection would have to take also non-motor factors into account.

Method

Participants

Fifteen adults (9 women, 6 men, $M_{\text{Age}} = 26$, age range 21–48) participated in Experiment 3 for payment (6€). According to Coren's (1993) Lateral Preference Inventory, 12 participants were right-handed, 2 were left-handed, and one was ambidextrous (LPI score = 0).

Stimuli, apparatus, and procedure

Experiment 3 was designed to determine the influence of visual cues on grasp orientation. In the experiment, participants were required to turn the box by rotation angles of −270°, −90°, 90°, or 270°. Each rotation angle could be cued by a circular arrow starting either left, above, right, or below a cartoon of the box. The experiment was split into six blocks, in which each combination of rotation angle and arrow start position was presented 2 times, resulting in 12 repetitions of each trial type in the experiment. The different trial types were presented in trial-wise randomized order.

The same apparatus as in Experiments 1 and 2 was used, with the exception that the box' cradle was elevated by 10 cm. The stimuli that cued the turn of the box consisted of a circle inside a square (representing the box) and an arrow that covered either 90° or 270° of a imaginary circle around the box and that could point in clockwise or counterclockwise direction. The arrow could either start left, above, right, or below the box. The arrow, the square, and the circle were white and were presented on a black background.

A trial began when the participant pressed the start button. Then, a fixation cross appeared for 1,000 ms and after that, the box and the arrow were displayed centrally on the CRT. After the participant carried out the instructed movement, feedback was displayed on the CRT for 1,000 ms. If the participant completed the box turn correctly within 5 s after the onset of the start signal, the text "gut" ("good") was displayed for 1,000 ms on the CRT, otherwise either the text "schneller" ("faster") or "Fehler" ("error") was displayed for 1,000 ms. After applying the same criteria as in Experiment 1, except that the maximal allowable time between the start signal and the end of the box turn was now restricted to 5 s, data from altogether 143 trials (5.0%) were excluded from the analysis.

Results

Figure 5 (top) shows that FO_{LIFT} depended mostly on the rotation angle. A closer look at the data points for each rotation angle reveals, that grasp orientation was also affected by the arrow start position (bottom of Fig. 5, see Online Resource 1 for means and standard deviations of FO_{LIFT} and FO_{PLACE}). Interestingly, the influence of the arrow start position was largest for the more easy rotations by ±90° and smaller for the harder rotations of ±270°. The pattern of the effect of the arrow start position for 90° and −90° rotations shows that the grasp orientation was susceptible to the arrow start position in the predicted way. If the arrow started at the right, FO_{LIFT} was biased to be more supine, if the arrow started at the left, FO_{LIFT} was biased to be more prone. If the arrow started on top of or below the box, FO_{LIFT} laid in between the former two conditions. For rotations of ±270°, there was no systematic impact of the arrow start position. To statistically test the results, we conducted a repeated measures ANOVA with within subject factors rotation angle (−270°, −90°, 90°, 270°) and arrow start position (left, right)[5] for FO_{LIFT} and FO_{PLACE}. Additionally, we conducted post-hoc t-tests to compare the difference between the arrow starts left and arrow starts right condition for each rotation angle. Table 4 reports a significant interaction between rotation angle and arrow start position for FO_{LIFT} and FO_{PLACE}. Finally, also in Experiment 3 a considerable discontinuity between FO_{LIFT} for clockwise and counterclockwise trials was found (Table 2). This time, the influence of the rotation direction significantly exceeded the influence of rotation angle.

Discussion

Experiment 3 showed that the visual cue affected grasp orientation selection. Thus, also perceptual factors play a role in grasp orientation selection. However, the influence of the arrow start position was small compared to the effect of the rotation angle. Most interesting is the finding that a non-motor bias could only be observed when the required rotation of the box was short and hence easy to carry out. One key difference between rotations by a large

[5] Note that we only included the arrow start position left and right because they are the conditions that can be interpreted most easily.

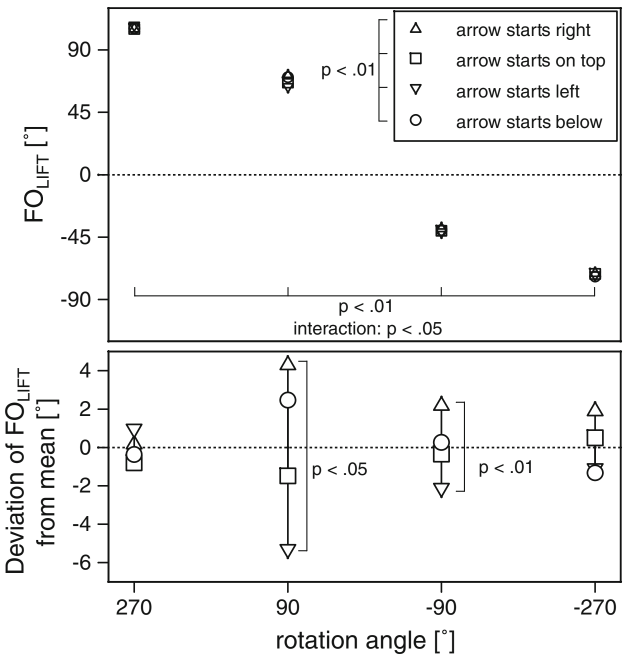


Fig. 5 FO_{LIFT} for different rotation angles and arrow start positions in Experiment 3. In the *upper part* the overall data are presented. The *lower part* magnifies the differences between the arrow start position conditions by showing the deviation of FO_{LIFT}s for the different arrow start positions from the average of each of the rotation angles. Positive FO_{LIFT} denote supine forearm orientations. *Positive rotation angles* denote counterclockwise turns

angle and a small angle is that it is important to carefully select the grasp orientation to be able to rotate the box in the former case but it is not crucial—although possibly advantageous—in the latter case. Thus, during the planning of the grasp, motor factors seem to be taken into account more rigorously for long, difficult rotations. If the movement is easy, the selection of the grasp may be less strictly based on the properties of the rotation movement and also non-motor factors can influence it. Thus, the participants did not only know how to orient the forearm in anticipation of an object rotation but they also knew when it was important to do so. This is in line with the observation that the end-state-comfort effect is more pronounced in bar transportation tasks when the bar transportation requires higher precision (Rosenbaum et al. 1996; Short and Cauraugh 1999).

Experiment 4: posture before start of grasp

If the grasp orientation selection is shielded from task-irrelevant non-motor biases for difficult movements, then also motor factors that are not directly related to the rotation of an object might influence grasp orientation selection only for small rotation angles. In Experiment 4, we tested if the interaction between task-relevant and task-irrelevant variables found in Experiment 3 can be replicated with a task-irrelevant motor factor. One such motor factor is the orientation of the forearm before the onset of the grasping movement. On the one hand, regardless of the forearm configuration at the start of the grasping movement, the forearm can be easily oriented to the requirements of the object rotation before the object is grasped. On the other hand, humans try to assume a posture at the end of a movement that is close to the initial posture to reduce the movement costs (Butz et al. 2007; Rosenbaum et al. 1995; Soechting et al. 1995). Thus, in Experiment 4, we recorded how participants trade off the facilitation of the grasping movement with the facilitation of the box rotation.

Method

Participants

Fifteen adults (10 women, 5 men, $M_{Age} = 29$, age range 21–61) participated in Experiment 4 for payment (6€). According to Coren's (1993) Lateral Preference Inventory, 13 participants were right-handed and 2 were left-handed.

Stimuli, apparatus and procedure

To identify the impact of the forearm orientation before the onset of the grasp on the grasp orientation at lifting, the participants had to turn the box by −270°, −180°, −90°, 0°, 90°, 180°, or 270° (0° only required to lift the box). They started their grasps with a forearm orientation of

Table 4 Results of ANOVAs with the within-subject factor rotation angle and arrow start position as well as post-hoc paired *t* tests between the arrow starts left and arrow starts right condition of the variables FO_{LIFT} and FO_{PLACE}

	ANOVA						Post-hoc paired *t* tests							
	Rotation angle		Arrow start position		Interaction		270°		90°		−90°		−270°	
	F(3,42)	*p*[a]	*F*(1,14)	*p*[a]	*F*(3,42)	*p*[a]	*T*(9)	*p*	*T*(9)	*p*	*T*(9)	*p*	*T*(9)	*p*
FO_{LIFT}	272	<0.01	15	<0.01	4.3	<0.05	−0.60	0.56	2.9	<0.05	3.1	<0.01	1.8	0.09
FO_{PLACE}	370	<0.01	18	<0.01	4.2	<0.05	0.032	0.98	2.9	<0.05	3.3	<0.01	1.3	0.22

[a] Greenhouse-Geisser corrected *p* values are reported

either −15° (more prone), 15°, or 45° (more supine), which are initial postures that were comfortable for most participants. The experiment was split into 6 blocks, in which each combination of rotation angle and start forearm orientation was presented twice, resulting in 12 repetitions of each trial type in the experiment. The different trial types were presented in trial-wise randomized order.

The apparatus was identical to Experiment 3 except that a plastic (polystyrene), semi-spherical (10 cm diameter) button, which participants could press while assuming different forearm orientations, replaced the start button. Each trial of Experiment 4 began with the participants assuming the required start forearm orientation. To help participants orient their forearm, the deviation of the actual forearm orientation from the required start orientation was displayed as horizontal deviation of a square-shaped cursor from a target area on the CRT. The target area was marked by two small, vertical lines and was always presented centrally on the CRT. The participants were instructed to press the start button in such a way, that the cursor was within the target area.

Once the actual forearm orientations was within 2° of the start forearm orientation and the button was pressed for a 1,500 ms interval, in which the cursor stayed on screen for the first 1,000 ms and the screen was blank for the last 500 ms, the imperative stimulus was displayed on the center of the CRT. If the participant released the button during that interval, the forearm orientation procedure started again. The imperative stimulus consisted of a row of one, two, or three white triangles, or a white square on a black background. The white triangle(s) indicated a clockwise turn of the box, if they pointed to the right and a counterclockwise turn if they pointed to the left. A single triangle indicated a turn extent of 90°, two triangles a turn extent of 180°, and three triangles a turn extent of 270°. If a square was displayed, participants were instructed to just lift the box. Feedback was provided as in Experiment 3. After applying the same criteria as in Experiment 3, data from altogether 230 trials (6.1%) were excluded from the analysis. In Experiment 4, we assured that a forearm orientation of 0° corresponded to the forearm orientation that the participants assumed when placing the hand flat on the table by carefully calibrating the position of the accelerometer at the beginning of each session. Due to the nature of the experiment, we could not correct for sensor displacements as in the previous experiments.

Results

The recordings of the forearm orientation at the onset of the start signal showed, that the participants assumed different forearm orientations in the different start forearm orientation conditions ($m_{-15°} = -13.6°$, $SD_{-15°} = 0.571°$, $m_{15°} = 15.4°$, $SD_{15°} = 0.670°$, $m_{45°} = 44.9°$, $SD_{45°} = 0.575°$). The upper part of Fig. 6 shows that Experiment 4 replicated the general pattern of FO_{LIFT} found in Experiments 1–3 (see Online Resource 1 for means and standard deviations of FO_{LIFT} and FO_{PLACE}). The lower part of Fig. 6 shows that FO_{LIFT} was affected mostly by the forearm orientation before the onset of the grasp for short rotations. To statistically test results, we conducted a repeated measures ANOVA with within subject factors rotation angle (−270°, −180°, −90°, 0°, 90°, 180°, 270°) and forearm orientation before the onset of the grasp (−15°, 15°, 45°) for FO_{LIFT} and FO_{PLACE} (Table 5). Additionally, we conducted post hoc *t* tests to compare the difference between the forearm orientations of −15° and 45° before the onset of the grasp for each rotation angle (Table 6). The post hoc *t* tests revealed that for FO_{LIFT} and FO_{PLACE} depended on the forearm orientation before the onset of the grasp for the rotation angles 0° and 90°. Additionally, FO_{LIFT} and FO_{PLACE} depended on the forearm orientation before the onset of the grasp for the −270° rotation. Again, the discontinuity between FO_{LIFT} for clockwise and counterclockwise trials was present (Table 2). As in Experiment 3, the influence of the rotation direction even exceeded the influence of rotation angle.

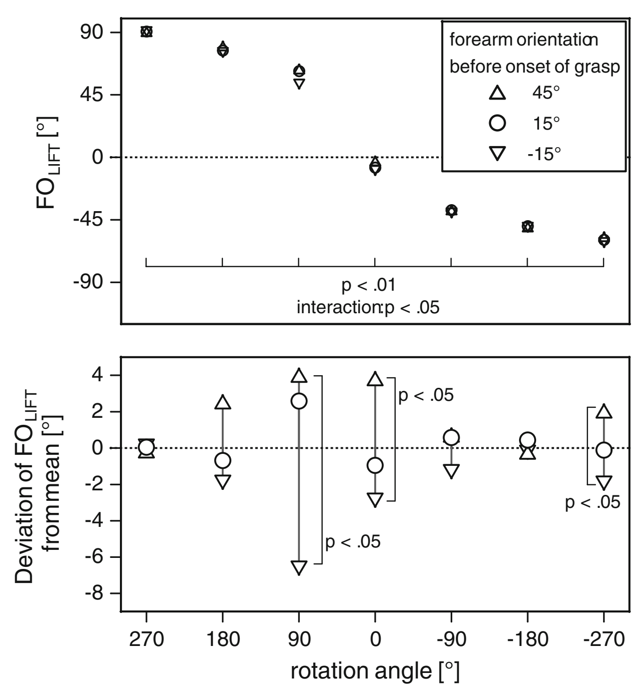


Fig. 6 FO_{LIFT} for different rotation angles and forearm orientations before grasp onset in Experiment 4. In the *upper part* the overall data are presented. The *lower part* magnifies the differences between the conditions with different forearm orientations before grasp onset by showing the deviation of FO_{LIFT}s for the different forearm orientations before grasp onset from the average of each of the rotation angles. Positive FO_{LIFT} denote supine forearm orientations. *Positive rotation angles* denote counterclockwise turns

Discussion

In Experiment 4, the participants had to weigh off if they want to reduce the forearm rotation during the grasping movement and thus let the forearm orientation before the onset of the grasp influence their grasp orientation at lifting, or if they want to adapt the grasp orientation entirely to the requirements of the turning movement to optimize the box transportation. The data showed that the forearm orientation before the onset of the grasp affected the grasp orientation when the box had to be turned by a small amount or only had to be lifted. The data thus replicated the findings of Experiment 3 that variables that were not directly relevant for the turning task biased the selection of the grasp orientation when the required rotation of the box was easy to accomplish. Even in this case, the impact of the forearm orientation before the onset of the grasp was rather small. On the other hand, the data showed that also the arm posture before movement onset modulated the forearm orientation at the grasp. This result is in line with current models for the selection of intermediate arm postures in sequential movements (Fischer et al. 1997; Herbort and Butz 2007).

General discussion

The goal of the present studies was to investigate the mechanisms that determine the selection of the grasp orientation when grasping an object for rotation. By enabling participants to freely select the grasp orientation, it was possible to have a much more detailed look on anticipatory motor planning than in many previous studies. We started our exploration with two rather distinct hypotheses. According to the end-state comfort optimization hypothesis, humans finely tune the grasp orientations before the rotation so that the end-posture of the movement is maximally comfortable. According to the prototypical grasp orientations hypothesis, humans select a prototypical grasp orientation according to the direction of the object rotation.

Table 5 Results of ANOVAs with the within-subject factor rotation angle and initial forearm orientation for FO_{LIFT} and FO_{PLACE}

	ANOVA					
	Rotation angle		Initial forearm orientation		Interaction	
	$F(6,84)$	p^a	$F(2,28)$	p^a	$F(12,168)$	p^a
FO_{LIFT}	142	<0.01	2.7	0.12	2.5	<0.05
FO_{PLACE}	289	<0.01	5.28	<0.05	2.9	<0.05

[a] Greenhouse-Geisser corrected p values are reported

In our experiments, we created experimental conditions that enabled the participants to plan their grasps as well as possible. On the one hand, the task had several features that required participants to plan their grasp orientation carefully. First, participants had to grasp the box without the possibility of rearranging the grasp during the rotation movement because the box had no support. Second, the box had to be placed into a cradle that was just slightly larger than the box itself and thus required a precise placement of the box at the end of the movement, thus fostering the end state comfort effect (Rosenbaum et al. 1996; Short and Cauraugh 1999). Third, the participants were asked to turn the box by up to 270°, which can hardly be executed without using an appropriate initial grasp orientation.

On the other hand, we gave participants many resources to plan the grasp. First, the participants had plenty of time to execute the movements. Second, participants had to repeat the same rotation several times and thus had the possibility to adjust their grasps from one trial to the next in Experiment 1 and 2. Third, as participants had to rotate a rigid object, the relationship between the rotation angle for the box and the required rotation of the grasp was as transparent as possible. Thus, as we created conditions in which participants had both the need to and the possibility to plan the grasp orientations as well as possible, we are confident that the present data show the results of movement planning in close to optimal conditions.

In Experiment 1, it was found that grasp orientation depended strongly on rotation direction but also on the extent of the rotation. This trend was also present in Experiment 3 and 4, in which the influence of the direction was significantly larger than the influence of the rotation angle. Thus, neither the end-state comfort optimization nor the prototypical grasp selection hypothesis fully accounts for the data. Experiment 2 further rejected the possibility that the discontinuity between grasps preceding clockwise and counterclockwise turns resulted because the range of required box rotations biased the participants to reuse similar grasp orientations for all grasps preceding a rotation in the same direction.

With Experiment 3, we tested whether grasp orientation selection was determined exclusively by motor-related criteria. To this aim, we instructed identical motor tasks with different visual stimuli. These stimuli affected grasp selection to some degree but the overall pattern of grasp selection remained the same. Interestingly, the visual representation of the task only influenced those grasp orientations that preceded small turns. This suggests that the grasp orientation selection process was only susceptible to non-motor influences if the to-be-executed rotation could be achieved easily. Experiment 4 replicated Experiment 3 by showing that also motor factors that are irrelevant for

Table 6 Results of post-hoc paired *t* tests between the conditions with the initial forearm orientations of −15° and 45° for each rotation angle for FO_{LIFT} and FO_{PLACE}

	Post-hoc paired *t* tests													
	270°		180°		90°		0°		−90°		−180°		−270°	
	T(14)	*p*	*T*(14)	*p*	*T*(14)	*p*	*T*(14)	*p*	*T*(14)	*p*	*T*(14)	*p*	*T*(14)	*p*
FO_{LIFT}	−0.15	0.88	0.92	0.37	2.7	<0.05	2.2	<0.05	1.2	0.24	0.004	0.98	2.2	<0.05
FO_{PLACE}	−0.33	0.75	0.39	0.70	3.1	<0.01	2.6	<0.05	2.2	<0.05	0.16	0.88	2.2	<0.05

the actual box rotation only modulate the grasp orientations for short rotations. The fact that the context (Experiment 2), the visual stimuli that instructed movements (Experiment 3), and task-irrelevant motor factors (Experiment 4) had only a subtle influence on grasp orientation, if any, the facts that these influences vanished if careful grasp orientation selection was crucial, and that the experimental procedure gave the participants good preconditions to plan the grasp orientation, suggest that participants were bound to produce the observed non-linear pattern of grasp orientations. Hence, in the remainder, we discuss several possible reasons for the emergence of the observed behavioral pattern.

Optimal control of grasp orientation

The optimal control approach provides one answer, why humans reproduce very similar behavior in different situations (Engelbrecht 2001; Todorov 2004). In many motor tasks, including grasping circular objects, not all degrees of freedom of the movement are determined by the task. The optimal control approach suggests that task-irrelevant degrees of freedom are eliminated by imposing the constraint to optimize movements according to additional optimality criteria. Thus, the one movement among the often infinite number of alternatives that is most suitable to solve a motor task is executed. As the results of the experiments showed that end-state comfort is not the only criterion that is optimized, humans possibly strive to optimize other criteria besides end-state comfort. In the following, we discuss potential criteria that might be considered to determine the grasp orientation before object rotations.

Initial posture and end-posture optimization

Besides optimizing the end-posture alone, movement plans could minimize the—possibly weighted—average discomfort of the grasp orientation before and after the rotation. In this case, one would expect that for the lifting movement (0° rotation) the most favorable grasp orientation is selected for lifting and placing. When the rotation angle is increased, it is not possible anymore to assume the most favorable posture before and after rotation. Hence, the unavoidable discomfort to realize the movement has to be shared between the posture before and after rotation. Thus, the further the rotation angle is increased, the further should initial and final grasp orientation deviate from the most favorable posture.

This explanation is more in line with our data than pure end-posture optimization. However, it cannot explain why turns by a small extent were almost entirely compensated for by the initial grasp orientations and had almost no effect on the final grasp orientation (suggesting a very large weight for the comfort of the final posture), while turns by large extents resulted in a considerable contribution of the final posture in the sharing of awkwardness (in contradiction, suggesting at least comparable weights for initial and final posture). Thus, while the observed grasp orientations generally tended to be kept in the mid-range of the pronation–supination range, the assumption that grasp orientations were optimized by a fixed, weighted combination of initial and end-state comfort criteria is inconsistent with the data.

End-state comfort prioritization or ceiling effects

The data could be explained better by assuming that the comfort of the final grasp orientation was optimized for short rotations but that also other factors affected grasp orientation for larger rotations. For example, if it is physically impossible or would require highly awkward postures to completely compensate for the intended rotation, participants might start trading off end-state comfort for initial comfort.[6] Indeed, when only looking at the short rotation angles of 90°, 0°, and −90°, the initial forearm orientation almost completely compensated for the box rotation and hence the final grasp orientation was only slightly affected by the rotation angle (see Online Resource 1). As the rotation angles increased further, the excursion of the initial grasp orientation only grew slightly, possibly

[6] We thank an anonymous reviewer for suggesting this explanation.

approximating the most extreme grasp orientations that participants were willing to adopt. At the same time, the rotations ended in increasingly excursed grasp orientations. In sum, such a ceiling effect or (limited) prioritization of end-state comfort accounts for the behavior observed for very large rotation angles.

Following this reasoning, one could argue that our participants did not optimize end-state comfort because this was anatomically impossible. While this may be the case for the 270° box rotations, humans are principally able to completely compensate for 180° box rotations. This is evident as Robert and colleagues' (2009) participants showed forearm pronation and supination angles in a 360° object rotation task that imply that it is possible to terminate a 180° box rotation in a neutral angle. Thus, even though participants could have maximized end-state comfort in the 180° box rotation conditions, they did not do so. Moreover, the data pattern observed in our experiments closely resembles those of studies on small rotation angles, in which participants apparently even overcompensated for some rotation angles (i.e. participants ended more supine after counterclockwise rotations than after clockwise rotations, Herbort and Butz 2010; van der Vaart 1995). In sum, our findings and previous data suggest that the ceiling effect or prioritization of end-state comfort hypotheses offers only a limited account for the data reported in the current and previous experiments.

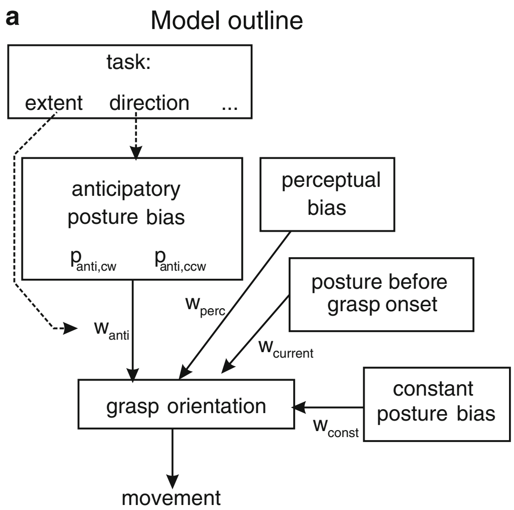
Limits of the optimal control framework

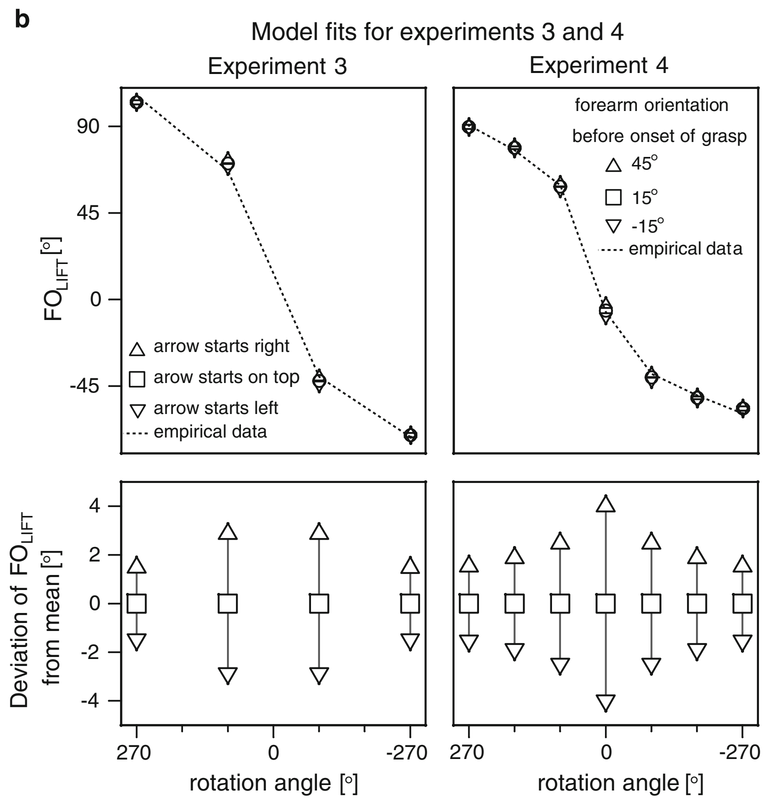
The previous section revealed that the overall data pattern found in Experiments 1–4 can be explained to some extent by assuming that participants only start to trade-off end-state comfort for initial state comfort once the initial grasp orientations that would be required to maximize end-state comfort approaches a boundary. Nevertheless, the explanation in the framework of optimal control has some limitations. First, while it accounts for larger rotation angles, it does not seem to account for smaller angles (Herbort and Butz 2010; van der Vaart 1995). Second, optimal control theory helps to understand why humans move in a specific way by showing that the movements are optimal with respect to an ecologically valid criterion, such as minimal end-point variance (Engelbrecht 2001; Harris and Wolpert 1998). Thus, it is hard to understand the effect of task-irrelevant factors—such as the perceptual representation of the task—in terms of the optimal control framework. One could argue that differences between the visual stimuli may have affected the input to a potential optimal planner but in this case, the interaction between visual stimuli and motor task could not be explained. Third, the optimal selection of the grasp orientation requires that participants have precise information about the kinematics of the forearm rotation that is necessary to rotate the object as instructed during movement planning. Participants in preliminary studies, however, had difficulties rotating a box without colored markers by the correct amount. This indicates that the box rotation is mostly under visual closed-loop control and that precise information about the required forearm rotation is not necessarily available to the participants. Fourth, the optimal control framework provides a descriptive account for the data but does not inform about the mechanisms that realize the behavior.

Weighted integration of multiple biases

We now propose a simple model (weighted integration of multiple biases model) for the selection of grasp orientations. The proposal complements the reasoning in the previous section by providing a possible mechanism that is able implement the observed mixture of initial-state and end-state comfort effect. A model of anticipatory grasp orientation selection should have several features. First, the model should account for the general non-linear relationship between the object rotation and the grasp orientation. Second, the model should account for the interaction of other factors with the grasp orientation selection. Third, the model should be extensible to account, in principle, for other findings related to the end-state comfort effect.

The present experiments suggest that the realized grasp orientations result from the weighted integration of multiple biases, including the rotation direction, the rotation extent, the forearm configuration before reaching, or the perceptual representation of the task. Hence, in the proposed model, the grasp orientation results from the combination of votes for different grasp orientations that may be weighted task-dependently (Fig. 7a). According to the model, when an object has to be rotated, an anticipatory component votes for an anticipatory posture bias dependent on the rotation direction (similar to the prototypical grasp selection hypothesis). However, the anticipatory posture bias is weighted by the difficulty of the task, which might be reflected by the extent of the object rotation but also possibly by other factors. Additionally, perceptual processing of task-related stimuli or the current arm orientation may result in the generation of other posture biases. Finally, other processes that were not explicitly manipulated in our experiments may also have generated votes. For example, it seems plausible to assume that participants generally have a preferred posture for reaching a specific point in space. All the different grasp orientation votes are then combined to the actually realized grasp orientation.





c Means (and standard deviations) of fits and parameter estimates

	Exp. 1		Exp. 3		Exp. 4	
R^2	.984	(.015)	.991	(.012)	.988	(.012)
RMSE	8.5°	(4.3°)	5.7°	(4.5°)	5.6°	(2.3°)
$p_{anti,ccw}$	166°	(35°)	147°	(42°)	131°	(51°)
$p_{anti,cw}$	-109°	(43°)	-106°	(35°)	-75°	(30°)
p_{const}	14°	(21°)	18°	(28°)	-15°	(32°)
w_{irrel}	-	-	7	(8)	32	(83)
w_{const}	138	(71)	117	(77)	82	(51)

Fig. 7 **a** The chart illustrates a simple model of the weighted integration of multiple biases for the determination of the grasp orientation. **b** The mean model predictions for experiment 3 and 4. **c** Means and standard deviations of the model's fit (R^2), RMSE, and estimates for the free parameters

To test this model on the datasets, we expressed it in the following equation, which computes the weighted mean of multiple posture biases:

$$FO_{LIFT} = (w_{anti}p_{anti,dir} + w_{irrel}p_{irrel} + w_{const}p_{const}) / (w_{anti} + w_{irrel} + w_{const}),$$

where FO_{LIFT} is the predicted forearm orientation at lifting, w_{anti} is the weight of the anticipatory posture bias $p_{anti,dir}$, which can be either a clockwise-posture bias $p_{anti,cw}$ or a counterclockwise-posture bias $p_{anti,ccw}$, depending on the direction of the intended rotation, w_{irrel} is the weight of a task-irrelevant posture bias p_{irrel} (arrow start position or arm posture before grasp onset), and w_{const} is the weight for a constant posture bias p_{const}, which results from factors that are not manipulated in the experiment but are likely to affect posture selection. For example, when modeling Experiment 3, the forearm orientation before grasp onset may be part of the constant posture bias, because it was not experimentally manipulated but nevertheless may have influenced grasp orientation selection as was demonstrated in Experiment 4. As w_{anti} should reflect the perceived task difficulty, we set w_{anti} to the extent of the rotation and fitted the values for the five free parameters $p_{anti,cw}$, $p_{anti,ccw}$, w_{irrel}, p_{const}, and w_{const} individually for each participant of Experiments 1, 3, and 4.[7] For experiment 1, in which w_{irrel} was set to zero because no task irrelevant factors were manipulated, the model provides a fit of $R^2 = 0.984$ (SD = 0.015), averaged over all participants (predicting 7 data points with 4 free parameters). The average root mean square error (RMSE) of 8.5° (SD = 4.3°) is low and comparable to the average standard error of FO_{LIFT}s for all combinations of turn angle and participant (SE = 5.2°).

[7] We used the matlab function fminsearchbnd (http://www.mathworks.com/matlabcentral/fileexchange/8277-fminsearchbnd) to determine values that result in the smallest root mean square error for each participant. We constrained the values of $p_{anti,cw}$, $p_{anti,ccw}$, and p_{const} to [−200°,200°]. As each participant provided only three data points in Experiment 2, the model, which has four free parameters in the case of Experiment 2, fits the data trivially ($R^2 = 1.0$).

Unlike Experiment 1, Experiments 3 and 4 manipulated task-irrelevant variables. To fit the model to the data of Experiment 3, we set the irrelevant posture biases p_{irrel} to −90°, 0°, 90°, dependent on the arrow start position (right, top, left, respectively). We did not include the bottom arrow start position because it can be associated to either strongly supine or prone grasps. For experiment 4, we set p_{irrel} to −15°, 15°, or 45° dependent on the forearm posture before grasp onset. Figure 7b shows that the mean model predictions provide a tight fit to the data of Experiment 3 and 4 (predicting 12 and 21 data points, respectively, with 5 free parameters). The model is able to reproduce the characteristic non-linear relationship between rotation angle and grasp orientation as well as the interaction between rotation angle and task irrelevant variables. Additionally, the average fitted values for the anticipatory posture biases (Fig. 7c) coincide with the range of forearm orientations adopted by an independent group of 16 participants, who were asked to rotate their forearms as far as it is comfortably possible or as far as possible (clockwise 123°–142° supination, counterclockwise −76° to −115° supination). Likewise, the estimates for p_{const} are close to the neural position. Thus, the produced estimates for $p_{\mathrm{anti,cw}}$, $p_{\mathrm{anti,ccw}}$, and p_{const} seem plausible. Finally, the w_{const} for Experiment 3 is roughly the sum of w_{const} and w_{irrel} in Experiment 4. This is in line with the interpretation that the posture before grasp onset, which was manipulated in Experiment 4, adds to the other constant biases in Experiment 3.

Extension and evaluation

The model itself could be extended to account for other aspects of grasp orientation selection. For example, if the weight of the anticipatory posture bias was not only determined by movement extent but also by factors such as accuracy requirements, the model could account for the decreased susceptibility of the grasp orientation to task irrelevant factors if precision requirements are high (Rosenbaum et al. 1996; Short and Cauraugh 1999). Likewise, a bias based on the last grasp choice could be introduced to account for hysteresis effects (e.g. Kelso et al. 1994). Moreover, as the model is able to reproduce the characteristic non-linear relationship between rotation angles and grasp orientations, it could further account for other experiments on the continuous end-state comfort effect. Additionally, the model could be extended to discrete grasp orientation tasks by providing a response rule that selects one of the discrete alternatives based on the model's output. Finally, whereas the proposed model explains how the orientation of the forearm is adjusted to forthcoming actions, it remains to be tested whether it also accounts for other anticipatory adjustments in grasping movements, such as the adjustment of the grasp location or hand adduction/abduction (e.g. Cohen and Rosenbaum 2004; Zhang and Rosenbaum 2008).

In sum, the model accounts for the present data and could be extended to accommodate other aspects of grasp orientation selection. Moreover, it relies on the weighting of biases from different sources, which is also a key element of recent models of motor planning (c.f. Butz et al. 2007; Cisek 2006; Erlhagen and Schöner 2002; Herbort and Butz 2007) but also in other domains (e.g. Knill and Pouget 2004). Furthermore, it is a simple mechanism, which integrates information that is directly available through the instruction (rotation direction, rotation extent) or other channels such as vision or proprioception. Thus, it neither requires complex planning mechanisms nor motor simulation abilities (Johnson 2000; Rosenbaum et al. 1995, 2001). In sum, the model is simple, makes few assumptions, and can account for the present data and potentially for other experiments.

Conclusion

The present report extends previous research on anticipatory grasp orientation selection. It shows that the grasp orientation before an object is grasped for rotation depended on several interacting factors. First, the grasp orientation was mostly determined by the intended rotation of the object, showing that the overarching goals of an action sequence strongly determine the kinematics of its constituents. Second, the grasp orientation depended on the arm configuration before the onset of the reach-to-grasp movement, showing an interaction between anticipated and immediate task constraints. Third, also the visual representation of the task influenced the grasp orientation, showing that, besides the immediate or anticipated motor variables, also cognitive variables co-determine grasp orientation selection. While the intended manipulation of the object was the main determinant of the grasp orientation throughout all experimental conditions, the arm configuration before the onset of the grasp and the visual representation of the task only affected grasp orientations if the object rotation could be easily realized. Thus, different motor and non-motor factors are integrated with regard to their importance to determine the orientation of a grasp.

Besides showing the interaction between different factors on grasp orientations, the experiments also delivered a detailed picture on the relationship between intended object rotation and grasp orientation. Interestingly, anticipatory grasp orientation selection was mostly determined by the direction of the intended object rotation whereas the influence of its extent was smaller. This behavior resulted in a considerable variability of the forearm orientations after object rotations. To account for the data we proposed that the arm posture is kept in a comfortable range with a simple mechanism, which is based on the weighted integration of multiple biases. The mechanism selects a grasp orientation based on the intended object manipulation but also allows other factors to bias the realized grasp orientation. The good fit of this simple model suggests that—besides focusing on the criteria, which determine how an action is executed—future research should also focus on further investigating the mechanisms that strive to realize, approximate, or combine these criteria to fully understand human motor behavior.

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