Exp Brain Res (2010) 202:867–878
DOI 10.1007/s00221-010-2191-9

RESEARCH ARTICLE

Planning and control of hand orientation in grasping movements

Oliver Herbort · Martin V. Butz

Received: 17 September 2009 / Accepted: 8 February 2010 / Published online: 27 February 2010

Abstract Humans grasp objects in a way that facilitates the intended use of the object. We examined how humans grasp a circular control knob in order to turn it in different directions and by different extents. To examine the processes involved in anticipatory planning of grasps, we manipulated advance information about the location of the control knob and the target of the knob-turn. The forearm orientation at the time of grasping depended strongly on the knob-turn, with the direction of the knob-turn having a stronger effect than the extent of the knob-turn. However, the variability of the forearm orientations after the knob-turn remained considerable. Anticipatory forearm orientations began early during the grasping movement. Advance information had no influence on the trajectory of the grasp but affected reaction times and the duration of the grasp. From the results, we conclude that (1) grasps are selected in anticipation of the upcoming knob rotation, (2) the desired hand location and forearm orientation at the time of grasping are specified before the onset of the grasp, and (3) an online programming strategy is used to schedule the preparation of the knob-turn during the execution of the grasp.

Keywords Grasping · Knob-turning · Motor planning · Anticipatory modifications of movements · Kinematics

Introduction

In our daily lives, we often grasp objects to interact with them. In such situations, redundant degrees of freedom of the body are used to align the grasping movement to the upcoming interaction with the object (Gentilucci et al. 1997; Johnson-Frey et al. 2004). For example, in order to displace an object, we select a grasp that not only enables to lift the object but also to place it comfortably at a new location or to manipulate the object with the necessary accuracy (Marteniuk et al. 1987; Rosenbaum et al. 1990; Short and Cauraugh 1999). The present study investigates how humans grasp and turn a circular control knob. The circular knob can be grasped with different degrees of forearm supination or pronation—and thus different hand orientations—dependent on the direction and extent of the subsequent turning movement. With this task, we address how the CNS adjusts the forearm angle to facilitate the upcoming knob-turn, which planning mechanisms are adopted to realize such anticipatory adjustments, and how the planning of the grasp and the knob-turn are scheduled.

Regarding the first question, a large body of studies investigated if humans grasp a bar with either a supine or pronated forearm depended on subsequent rotations or transportations of the bar (e.g. Rosenbaum et al. 1996; Short and Cauraugh, 1999; Steenbergen et al. 2000; Weigelt et al. 2006). In these experiments, participants had to choose between two possible grasps, for example, grasping a horizontal bar with either an “overhand” (forearm pronated) or “underhand” (forearm supinated) grip (e.g. Rosenbaum and Jorgensen 1992). Thus, the experiments urged participants to make a selection between two very distinct grasps, raising the question how humans select from a continuous range of possible forearm angles when grasping an object for manipulation. Indeed, experiments

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Electronic supplementary material The online version of this article (doi:10.1007/s00221-010-2191-9) contains supplementary material, which is available to authorized users.

O. Herbort (✉) · M. V. Butz
Department of Psychology, University of Würzburg,
Röntgenring 11, 97070 Würzburg, Germany
e-mail: oliver.herbort@psychologie.uni-wuerzburg.de

that required participants to grasp and rotate a hexagonal or octagonal knob showed that healthy humans tend to use a range of different grasps dependent on upcoming rotation movements (Haggard 1998; Mutsaarts et al. 2006). Here, we extend previous work by requiring participants to grasp and turn a circular knob, which does not afford specific forearm angles when grasped (see Zhang and Rosenbaum 2008 for a related task). Thus, we address the question how participants adjust the forearm during grasping in a task that does not constrain the angle of the forearm at the time of grasping by the shape of the object. Furthermore, we record the forearm angle throughout the grasping movement to gather information on the time course of anticipatory forearm rotations.

Second, we address how grasping movements are planned. To execute a grasping movement, the CNS has to control several parameters, such as the position of the hand, the orientation of the hand, or the configuration of the fingers. Thereby, some parameters are critical to initiate a successful grasping movement, whereas other parameters are not. To grasp a knob, the location of the control knob in extra-personal space has to be necessarily processed. However, for a successful grasp, the hand orientation does not necessarily need to be adjusted to the intended knob turn because grasping the knob in the first place does not afford a specific hand orientation.

Two different modes of movement planning could be employed to prepare the coordination of a grasping movement. On the one side, an integrated movement plan could be generated (Loukopoulos et al. 2001; Rosenbaum 1980), which incorporates coordinated trajectories or goal states for all controlled parameters, including critical (i.e. location) and non-critical (i.e. hand orientation) parameters. This implies that movement planning cannot be completed and movements cannot be initiated until all parameters are available to the participant.

On the other side, the trajectories of different parameters could be planned and executed independently. In this case, the transport of the hand may be initiated independent of the rotation of the hand once the location of the knob is specified to the participant. As it is not critical to rotate the hand in a specific way for grasping the knob, a “default-plan” for the orientation of the hand could be employed that is unspecific to the upcoming knob-turn. For example, reaching movements can be initiated if the location of the target is roughly specified and are adjusted online once the precise target location is presented to the participant (Favilla 1997).

To distinguish between the integrated planning and independent planning hypothesis, we provided advance information about the location of the knob (critical to grasp the knob) and the target of the knob-turn (not critical to grasp the knob) before the onset of a choice reaction signal, which completely specified the required response. For the integrated planning hypothesis, we expect that the time to finish movement planning depends strongly on the advance information condition because a plan for all parameters needs to be generated in all advance information conditions, but conditions vary in the amount of planning that can be done before the onset of the choice reaction signal. As the movement plans in all conditions incorporate all movement parameters and might thus be similar or even identical, we expect little differences in movement kinematics. For the independent control hypothesis, movement planning can be completed and movements can be initialized as soon as information about the location of the to be grasped knob is available, regardless if information about the knob-turn specifies a desirable hand orientation. Hence, we expect little differences in the time required to finish planning and initiate the movement between conditions that provide similar advance information about the knob location (i.e. no advance information and advance information about knob-turn). However, as the initiation of the hand transport and the hand orientation are independent, we expect different movement kinematics between conditions. For example, if the knob location is specified before the knob-turn (and thus the hand orientation at grasping), we expect anticipatory forearm rotations with a later onset and reduced magnitude when compared to in the condition where participants have time to plan the hand orientation in advance.

Finally, the grasp-and-turn movement is a sequential movement, whose individual segments could be planned either as a whole before movement onset or by adopting an online planning strategy, in which the knob-turn is planned during the execution of the grasp (Rosenbaum et al. 1987). To test if movement planning occurs during the execution of the grasp, we analyzed if features of and advance information about the knob-turn interfere with the execution of the grasp.

Method

Of the 41 students of the University of Würzburg who participated in the experiment fulfilling a course requirement, data from 38 (29 women, 9 men, age ranging from 19a to 34a, $m = 22$a) participants were included in the analysis (see “Results” section). All participants were unaware of the purpose of the study and had normal or corrected-to-normal vision. According to the handedness scale of the Lateral Preference Inventory (Coren, 1993), all but four participants were right-handed (mean score = 2.9).

Apparatus and stimuli

After giving informed consent, participants were seated in front of a table, on which a start key, two control knobs,

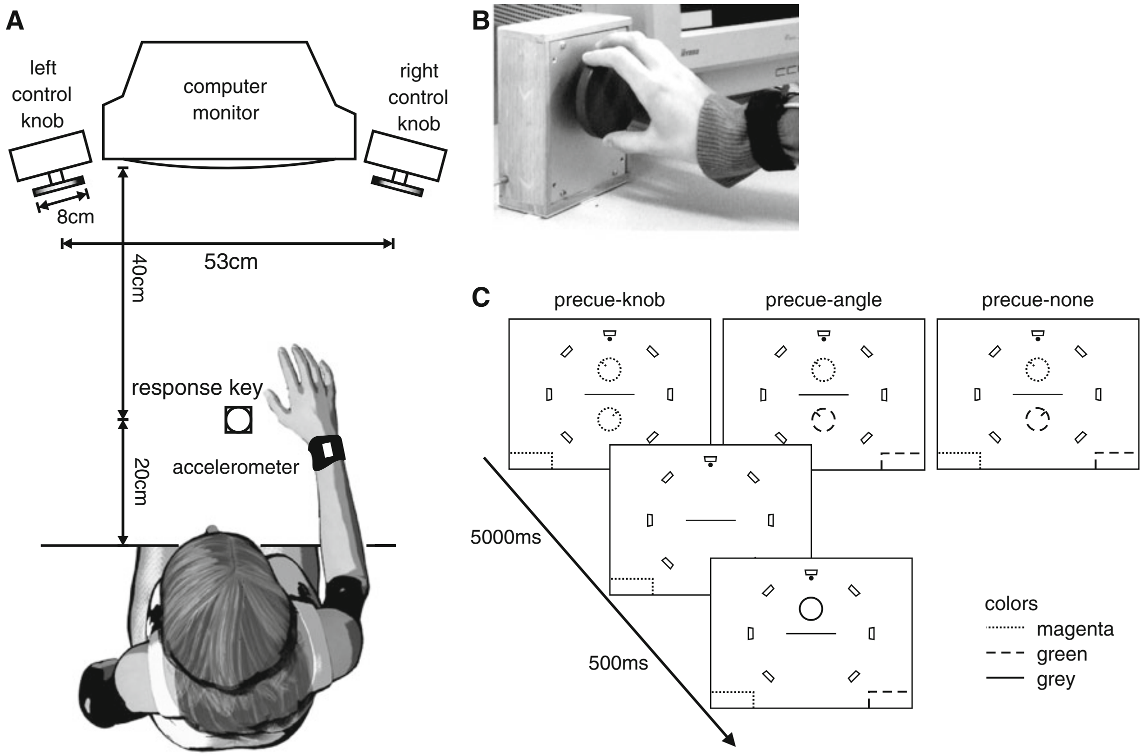

Fig. 1 **a** the arrangement of the start key, control knobs, and computer monitor; **b** photograph of the left control knob being grasped; **c** exemplar procedures of the stimulus presentation for the three different advance information conditions (*the different line* styles indicate *different colors*)

and a computer monitor were placed. Figure 1a shows the experimental setup. A 17-inch computer monitor (1,024 × 768 pixel, 100 Hz) was located at a distance of 60 cm from the edge of the table. A response key (2 cm × 2 cm) was placed 40 cm before the computer monitor on the midline axis of the participant. The two control knobs were placed to the left and right of the computer screen so that they faced the participant. The plastic control knobs had a diameter of 8 cm and a depth of 1 cm (Fig. 1b). The center of the control knobs was 10 cm above the table surface.

Procedure

Upon arrival, participants were seated in front of the table and an accelerometer, which recorded forearm orientation, was attached to their right forearm. The experiment consisted of six training trials to familiarize the participant with the experimental task and three blocks of 72 trials, which were separated by pauses of at least 60 s. Through out the experiment, the screen displayed a digital representation of the knob on a black background (Fig. 1c). A small, grey, and round cursor (diameter 3 mm) that could move on an imaginary circular path (diameter 17 cm) displayed knob motion. Outside of the circle on which the cursor could move, seven trapezoid target areas were displayed in a circular arrangement at −135°, −90°, …, 135° (18 mm × 4 mm). Additionally, a color was assigned to each control knob (left: magenta, right: green). The colors corresponding to the knobs were displayed by filled rectangles (42 mm × 15 mm) at the lower left and right corner of the screen.

The procedure of each trial was as follows. If the participant did not already press down the start key at the beginning of the trial, she or he was requested to do so by a short message presented on the computer monitor. Once the start key was pressed down, two circular precueing stimuli (diameter 16 mm) appeared on the computer monitor in a vertical arrangement, separated by a thin, grey, and horizontal line (length 40 mm). Each precueing stimulus corresponded to a specific knob turning movement. The color (magenta or green) of each precueing stimulus indicated if the left or right knob had to be turned. An inset (length 4 mm) inside the circle pointed to the location the knob should be turned (−135°, −90°, −45°, 45°, 90°, or 135°).

In the precue-knob condition, both precueing stimuli had the same color and corresponded to turning movements of the same extent but in different directions, thus informing the participant about the knob, with which the response had to be carried out. In the precue-angle condition, the precueing stimuli had different colors but corresponded to turning movements of the same extent and direction, thus informing participants about the turning movement but did not provide information about the knob, with which the response had to be carried out. In the precue-none condition, the precueing stimuli had different color and corresponded to turning movements of the same extent but in different directions. In this case, the participants could not know in advance which knob to turn and in which direction. After 5 s, the precueing stimuli disappeared and one of them was replaced 500 ms later by the choice reaction signal, which was a grey circle of the same size as the precueing stimuli. Participants were instructed to execute the movement that corresponded to the replaced precueing stimulus as fast as possible after the onset of the choice reaction signal. Participants first had to grasp one of the control knobs with the thumb opposing the fingers of the right hand (Fig. 1b) and then turn it toward the indicated target with a single motion and without readjusting the grasp. The knob turning movement was displayed on the computer screen by the motion of the cursor, where 1° of wheel motion resulted in 1° of cursor motion. Once the average angular velocity of the knob fell below 20°/s for at least 500 ms, the movement was considered finished. If the final cursor position was within 6° distance to the target angle, the word "richtig" (German for "correct") was displayed for 1 s in green letters. If the final cursor position deviated more then 6° from the target angle, the word "falsch" (German for "wrong") was displayed for 3 s in red letters. Finally, if the duration of the reaching movement, defined as the time between the release of the start key and the first time the wheel rotation exceeded 20°/s, was longer than 1 s, the words "bitte schneller" (German for "faster, please") were displayed for 3 s in red letters. After the feedback was presented, the next trial began.

The 72 trials of each experimental block were combinations of the three advance information conditions (precue-knob, precue-angle, precue-none), six target angles (−135°, −90°, −45°, 45°, 90°, or 135°), two control knobs (left or right), and the location of the to be executed precueing stimulus (above or below line). The trials were presented in a randomized order. In sum, each combination of advance information, target angle, and knob was repeated two times in each block and six times throughout the experiment, resulting in 216 trials altogether.

Data recording, data reduction and analysis

The forearm orientation was recorded with a three-axis accelerometer that was attached to the dorsal side of the distal end of the right forearm. The low-pass filtered (5 Hz) forearm supination measurements had a resolution of 0.5°. Rotations of the knobs were measured with incremental rotary encoders (resolution 1.3°). The knob angle signal was digitally processed by a zero-phase 2nd order 10 Hz low-pass Butterworth filter. The forearm angle and movements of the control knobs were recorded with a sampling rate of 100 Hz. We corrected for possible slip of the sensor during the course of the experiment by subtracting the estimate of a participant-wise linear regression of trial on the supination of the arm at movement onset for each trial.

The percentage of errors (PE) due to erroneous knob-turns or operations of the wrong knob was computed for each participant and each combination of advance information condition, knob, and target angle. For each trial and each participant, we recorded the reaction time (RT), defined as the interval between the onset of the choice reaction signal and the release of the start key. The following movement was partitioned into a grasping segment and a turning segment. The grasping segment was defined as the movement between the release of the start key and the onset of the rotation of one of the knobs, which was defined as the first time point when knob rotation rate exceeded 20°/s. We extracted the duration of the grasping segment (MT_{GRASP}) and the forearm supination at the end of the grasping segment (SUP_{GRASP}). The turning segment was defined as the movement from the end of the grasping segment to the moment when the knob rotation rate dropped and stayed below 20°/s. We computed the duration of the turning segment (MT_{TURN}) and extracted the magnitude and time to peak knob acceleration, velocity, and deceleration, relative to the onset of the turning segment (PA_{TURN}, $TTPA_{TURN}$, PV_{TURN}, $TTPV_{TURN}$, PD_{TURN}, $TTPD_{TURN}$). Finally, we extracted the forearm supination at the end of the turning segment (SUP_{TURN}).

Before statistical testing, we removed data from trials in which participants responded incorrectly (7.6%)[1] or too slow ($RT > 1{,}000$ ms, $MT_{GRASP} > 1{,}000$ ms, or $MT_{TURN} > 2{,}000$ ms, 9.7%). We further removed trials in which participants did not follow the instruction to not readjust the grasp during turning, defined as trials in which forearm supination correlated with knob rotation by less than 0.75 during the turning segment (8.4%) or turned the wheel by more than 180° to reach a goal (e.g. turning the knob 270° clockwise to point to a 90° counterclockwise target, 1.7%). Finally, we excluded data if we could not clearly identify the peak of acceleration, velocity, or deceleration of the turning movement (6.5%). We had to exclude data of three participants who were unable to provide at least one valid trial for each combination of target angle, knob, and advance information. The remaining 38 participants provided on average 81.5% (SD = 8.5%) valid trials. Please note that the participants received positive feedback in 85.6% (SD = 5.3%) of all trials because trial validity was determined by the offline data analysis. The dependent variables were averaged for each participant and each combination of advance information, target angle, and knob. The averages were submitted to repeated measures ANOVAs

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[1] More than one exclusion criterion may apply to each trial.

Table 1 shows the results of the ANoVA for RT, PE, MT_{GRASP}, SUP_{GRASP}, MT_{TURN}, and SUP_{TURN} with the within-subject factors advance information, target angle, and knob as well as the result of subsequent contrast analysis (indented rows)

Factor/contrast/interaction		RT		PE		MT_{GRASP}		SUP_{GRASP}		MT_{TURN}		SUP_{TURN}	
	df	*F*	*p* >	*F*	*p* >	*F*	*p* >	*F*	*p* >	*F*	*p* >	*F*	*p* >
Advance information	2,74	48.7	.001	8.3	.01	7.6	.01						
Precue-knob	1,37	82.5	.001	8.3	.01	8.7	.01						
Precue-angle	1,37	32.4	.001	18.5	.001	13.6	.01						
Target angle	5,185	3.1	.05	3,9	.01	9.8	.001	190.1	.001	333.1	.001	128.0	.001
Direction	1,37					6.3	.001	202.8	.001			96.0	.001
Extent ccw	1,37			6.3	.05			82.8	.001	750.5	.001	320.6	.001
Extent cw	1,37	10.5	.01			35.6	.01	54.0	.001	570.1	.001	259.4	.001
Knob	1,37	9.2	.01			110.5	.001	181.6	.001	182.2	.001	114.1	.001
Target angle × knob	5,185					24.5	.001					13.4	.001
Direction × knob	1,37					65.7	.001					13.2	.01
Extent ccw × knob	1,37											33.1	.001
Extent cw × knob	1,37											17.3	.001
Advance information × target angle × knob	10,370	3.3	.01			3.0	.01						
Precue-knob × extent cw × knob	1,37	6.6	.05										
Precue-knob × extent ccw × knob	1,37					6.1	.05						
Precue-angle × extent cw × knob	1,37	8.8	.01			5.2	.05						
Precue-angle × direction × knob	1,37	15.8	.001			9.2	.01						

with the within-subject factors advance information (precue-knob vs. precue-angle vs. precue-none), target angle (−135° vs. −90° vs. … vs. 135°) and knob (left vs. right).[2] In case of significant effects of the advance information condition, we computed contrasts between the precue-knob or precue-angle condition and the precue-none condition. In case of significant effects of target angle, we computed contrasts between the target angles −135° and −45° to evaluate if there were effects of the extent of counterclockwise target angles (extent ccw), contrasts between the target angles 45° and 135° to evaluate if there were effects of the extent of clockwise target angles (extent cw), and contrasts between counterclockwise (−135°, −90°, −45°) and clockwise (45°, 90°, 135°) target angles to evaluate if there were effects of the direction of the turning movement.

Results

In this section, only significant differences are discussed. The results of the statistical tests for RT, PE, SUP_{GRASP}, MT_{GRASP}, SUP_{TURN} and MT_{TURN} are reported in Table 1. (Means and standard deviations are provided in online resource 1). Table 2 shows the parameters and statistical evaluation of the knob-turning movement.

Planning

RT

Figure 2a shows that participants reacted 51 ms faster in the precue-knob and 28 ms faster in the precue-angle condition than in the precue-none condition. Furthermore, RTs were 11 ms lower for right-knob trials than for left-knob trials. Finally, there was an unsystematic increase of RT in left-knob trials with target angle 135° in the precue-none condition, which resulted in a significant main effect of the target angle and significant interactions between advance information, target angle, and knob.

PE

On average, the participants responded incorrectly in 6.0% of all trials. Participants responded correctly more frequently in the precue-knob and the precue-angle condition than in the precue-none condition. Additionally, PE was modulated by the target angle, with more errors being made for movements to the −135° target than to the −45° target. Neither the main effect of knob nor any interaction reached significance.

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[2] If the assumption of sphericity was violated as indicated by Mauchly's Test of Sphericity, dfs were Greenhouse-Geisser-corrected. For the sake of clarity, we report uncorrected dfs.

Table 2 shows the mean (SD) time to and magnitude of peak acceleration (TTPA, PA), peak velocity (TTPV, PV), and peak deceleration (TTPD, PD) for the different target angles and both knobs as well as F- and p-values of significant main effects (target angle, knob), interactions, and contrasts (direction, extent cw [clockwise], extent ccw [ccounterlockwise])

Knob	Target angle	TTPA	PA	TTPV	PV	TTPD	PD
Left	−135°	85 (24)	3,537 (921)	214 (35)	430 (78)	356 (56)	−2,548 (847)
	−90°	71 (14)	3,072 (802)	181 (30)	342 (61)	301 (47)	−2,198 (798)
	−45°	54 (9)	2,176 (598)	150 (25)	213 (43)	263 (44)	−1,621 (546)
	45°	61 (22)	2,003 (523)	160 (38)	204 (38)	280 (55)	−1,512 (439)
	90°	75 (27)	2,728 (645)	195 (40)	318 (54)	343 (65)	−2,032 (599)
	135°	84 (20)	3,334 (939)	225 (41)	421 (80)	381 (77)	−2,564 (982)
Right	−135°	93 (15)	3,767 (1,029)	204 (27)	469 (86)	337 (60)	−2,869 (972)
	−90°	89(25)	3,182 (911)	190 (27)	370 (72)	305 (48)	−2,651 (953)
	−45°	66 (13)	2,104 (438)	154 (17)	220 (34)	264 (35)	−1,759 (447)
	45°	68 (15)	2,018 (528)	163 (25)	216 (37)	277 (42)	−1,779 (536)
	90°	92 (22)	2,837 (666)	208 (38)	350 (56)	332 (56)	−2,439 (668)
	135°	107 (31)	3,241 (867)	243 (41)	447 (78)	381 (58)	−2,808 (880)

ANOVA	df	F	p	F	p	F	p	F	p	F	p	F	p
Target angle	5,185	39.3	>.001	157.1	>.001	114.7	>.001	486.4	>.001	101.1	>.001	74.3	>.001
Direction	1,37			29.4	>.001	21.2	>.01	11.9	>.01	30.9	>.001		
Extent ccw	1,37	185.2	>.001	242.0	>.001	231.7	>.001	766.7	>.001	174.7	>.001	164.2	>.001
Extent cw	1,37	73.9	>.001	292.7	>.001	576.3	>.001	800.2	>.001	241.9	>.001	125.5	>.001
Knob	1,37	60.8	>.001			6.3	>.05	40.5	>.001			36.4	>.001
Interaction	5,185	2.9	>.05	3.0	>.05	3.6	>.01	4.8	>.001				
Direction	1,37					5.6	>.05						
Extent ccw	1,37			9.9	>.001	5.5	>.05	17.2	>.001				
Extent cw	1,37	8.2	>.01										

Both, RTs and PEs reveal that participants responded faster and made fewer errors in the precue-knob and precue-angle condition than in the precue-none condition. Thus, providing advance information about the to be turned knob or the target angle facilitates movement initiation.

Grasping segment

MT$_{GRASP}$

The duration of the grasping segment MT$_{\mathrm{GRASP}}$ was on average 638 ms (Fig. 2b). Participants grasped the knob slightly faster in the precue-knob (13 ms) and in the precue-angle (11 ms) condition than in the precue-none condition. MT$_{\mathrm{GRASP}}$ for grasping the right knob was 78 ms higher than for grasping the left knob. Additionally, we found an effect of advance information, which was strongly modulated by the direction of the knob-turn and the location of the knob. In general, grasps preceding counterclockwise turns took longer than grasps preceding clockwise turns in right-knob trials, but grasps preceding clockwise turns took longer than grasps preceding counterclockwise turns in left-knob trials. However, this interaction was significantly weaker in the precue-angle condition than in the precue-none condition, whereas there were no differences between the precue-knob and precue-none condition. Likewise, the effect of the extent of knob-turns was modulated by the location of the knob and the advance information condition. As both, the advance information condition and features of the subsequent knob-turn modulated MT$_{\mathrm{GRASP},}$ differences in movement planning strategies between the advance information conditions may partly account for the interaction between knob and target angle.

SUP$_{GRASP}$

Figure 2c shows that forearm supination at the time of grasping SUP$_{\mathrm{GRASP}}$ depended strongly on the direction and to a lesser degree on the extent of the subsequent knob-turn. Additionally, participants grasped the right knob generally with a more supine forearm than the left knob. However, SUP$_{\mathrm{GRASP}}$ was unaffected by the advance information condition.

To get an estimate of the consistency of the grasp selection, we computed the SD of SUP$_{\mathrm{GRASP}}$ for each participant, target angle, and knob, which was on average

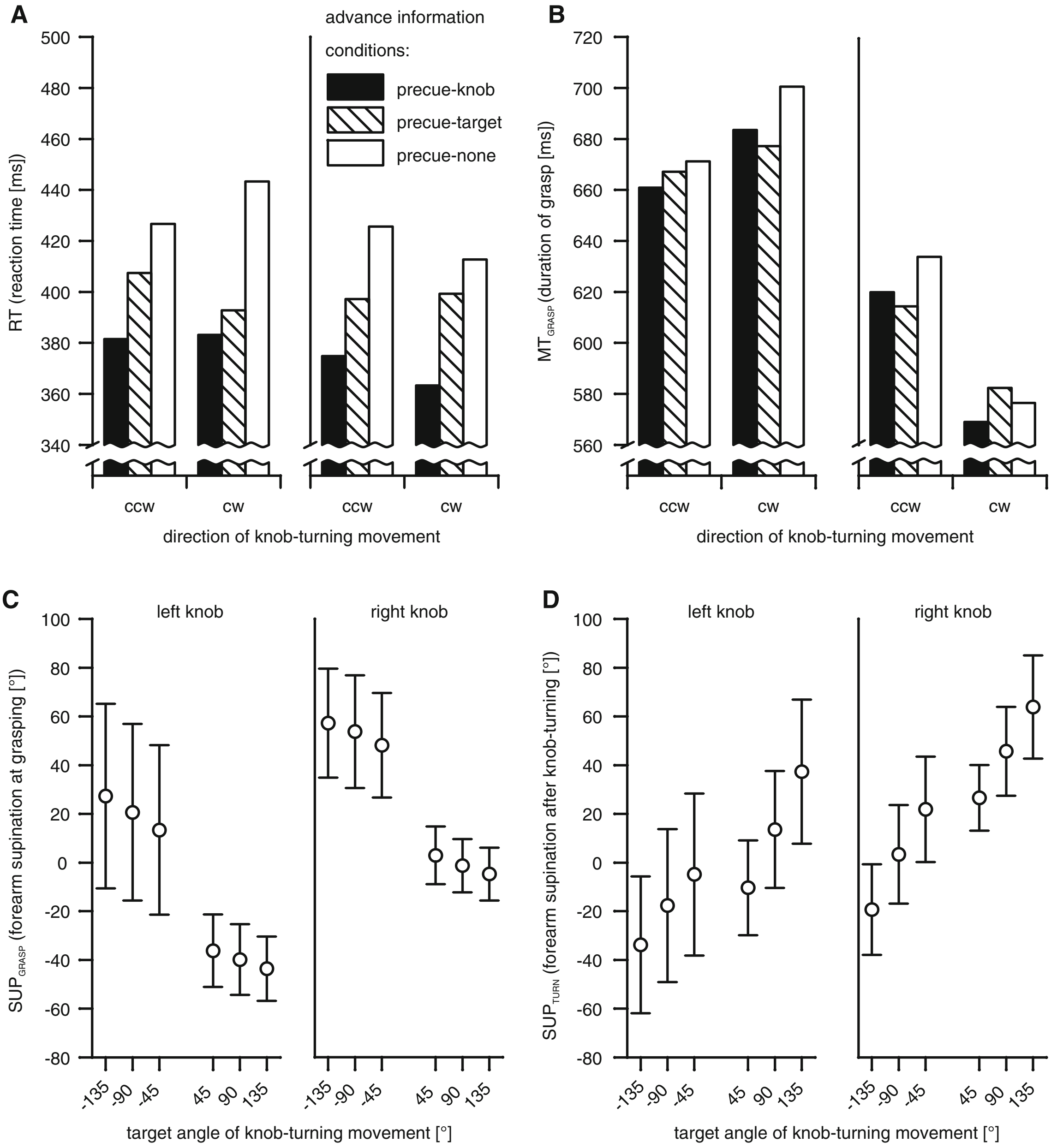

Fig. 2 **a** and **b** show average RT (**a**) and $\mathrm{MT}_{\mathrm{GRASP}}$ (**b**) of movements dependent on knob, advance information conditions, and the direction of the knob-turning movement, ccw = counterclockwise (−135°, −90°, −45°), cw = clockwise (45°, 90°, 135°). **c** and **d** show the average forearm supination (*positive values*) or pronation (*negative values*) when grasping the knob (**c**) and after knob-turning (**d**) dependent on knob and the target angle of the knob-turning movement. *Error bars* show SD

17.3° (SD = 10.9°). Thus, given the range of possible forearm rotations, grasps were selected rather consistently among participants.

Surprisingly, the differences between supinations for movements in the same direction but with different extents differed little, while there was a clear difference between anticipatory supinations preceding rotations in different directions. To quantify this difference, we computed the difference of $\mathrm{SUP}_{\mathrm{GRASP}}$s between trials with different extents of the turning movement but identical directions (i.e. between target angle ± 135° and ± 45°) and the difference of $\mathrm{SUP}_{\mathrm{GRASP}}$s of trials with identical knob rotation extents but different directions (i.e. between −45° and +45°). Please note that in both cases, the absolute difference between target angles is 90°. $\mathrm{SUP}_{\mathrm{GRASP}}$ preceding a knob rotation with an extent of 135° were 9.5° (SD = 6.0°) larger than $\mathrm{SUP}_{\mathrm{GRASP}}$ preceding a rotation with an extent of 45°. In contrast, average anticipatory supinations of grasps preceding knob rotations with an extent of 45° but in different directions differed by 47.4° (SD = 23.3°). A repeated measure ANOVA with factors range of compared target angles (range: ± 135 vs. ± 45, 45 vs. 45) and knob confirmed that the difference is statistically significant and revealed no effect of knob and no interaction, $F(1,37) = 95.2$, $p < .001$.

Trajectory of forearm rotation

The evaluation of the anticipatory forearm supination at the end of the grasping movement revealed no influence of advance information. To test if advance information affects the trajectory of the forearm rotation during grasping, we computed the forearm supination at 25, 50, and 75% of $\mathrm{MT_{GRASP}}$ by linear interpolation and submitted the resulting supination values to repeated measures ANOVAs and subsequent contrast analysis with the same factors and factor levels as the analysis of $\mathrm{SUP_{GRASP}}$.[3] After 25% of the movement time, the analysis revealed significant effects for target angle, $F(5,185)\mathrm{s} \geq 10.9$, p's < .001. Contrast analysis revealed significant influence of direction from 25% of the movement time on, $F(1,37)\mathrm{s} \geq 20.8$, p's < .001. Only after 50% of the movement time, the extent of the turning movements affected arm supination, as revealed by significant effect of the extent of clockwise turns, $F(1,37) = 5.2$, $p < .05$. This effect was further modulated by a significant interaction between target angle and knob based on differences in the effect of the extent of clockwise turns, $F(5,185) = 3.5$, $p < .05$, and $F(1,37) = 9.5$, $p < .01$, respectively. Finally, after 75% of the movement time, contrast analysis revealed significant effects of the extent of both clockwise and counterclockwise turns, $F(1,37)\mathrm{s} \geq 34.6$, p's < .001. At no time was there a significant main effect of advance information or a significant interaction that included advance information. Hence, advance information had no effect on the trajectory of the grasping movement.

To estimate the onset of direction-dependent and extent-dependent anticipatory rotations, we computed the average supination of the forearm after each 20 ms interval by linear interpolation between movement onset and 400 ms for each knob and target angle. We submitted the averages to a repeated measures ANOVA with subsequent contrast analysis, using the factors target angle and knob according to the analysis of $\mathrm{SUP_{GRASP}}$. Already from 80 ms on, target angle had a significant effect on forearm supination, for 80–400 ms all $F(5,185)\mathrm{s} \geq 3.5$, all p's < .05. Contrast analysis revealed that this early effect was based on the direction and not the extent of turning movements, for 80–400 ms, all $F(1,37)\mathrm{s} \geq 6.1$, all p's < .05. Only from 220 and 260 ms on, contrast analysis showed a significant effect of the extent of the counterclockwise and clockwise turns, respectively, 220–400 ms, all $F(1,37)\mathrm{s} > 4.2$, all p's < .05; 260–400 ms, all $F(1,37)\mathrm{s} \geq 4.6$, all p's < .05. The interaction between knob and target angle arose from 140 ms on, 140–400 ms, all $F(5,185)\mathrm{s} > 2.6$, all p's < .05. Contrast analysis revealed significant interaction between knob and the direction but no interactions between knob and the extent, 140–400 ms, all $F(1,37)\mathrm{s} \geq 8.3$, all p's < .01. Thus, forearm rotations depended on the direction of the upcoming movement as early as 80 ms after movement onset. A significant difference between movements in the same direction but with different extents appeared later, only after 220–260 ms after movement onset. To summarize, whereas the forearm angle was strongly adjusted to the knob-turn, it was unaffected by advance information throughout and at the end of the grasp.

Turning segment

MT_{TURN}

The duration $\mathrm{MT_{TURN}}$ for knob turning movements with an extent of 45°, 90° and 135° took on average 473 ms (SD = 50 ms), 630 ms (SD = 65 ms), and 780 ms (SD = 865 ms), respectively (Table 2). $\mathrm{MT_{TURN}}$ depended only on the extent but not on the direction of the turning movement. However, rotations with the left knob took on average 27 ms longer than rotations with the right knob. $\mathrm{MT_{TURN}}$ was not affected by advance information.

SUP_{TURN}

Figure 2d shows that the forearm supination at the end of the turning segment $\mathrm{SUP_{TURN}}$ depended on extent and direction of the preceding turn. Participants had a more supine forearm position after turning the right knob than the left knob. As can be seen in Fig. 2d, the extent of counterclockwise turns had a stronger effect on $\mathrm{SUP_{TURN}}$ in right-knob trials than in left-knob trials and the extent of clockwise turns had a stronger effect on $\mathrm{SUP_{TURN}}$ in left-knob trials than in right-knob trials. Additionally, the direction of the turn had generally a stronger effect in right-knob trials than in left-knob trials. There was no effect of advance information on $\mathrm{SUP_{TURN}}$. The data show that anticipatory forearm rotations reduced the range of forearm angles after the turning movement and thus kept the rotation of the forearm in a restricted range.

$TTPA_{TURN}$, PA_{TURN}, $TTPV_{TURN}$, PV_{TURN}, $TTPD_{TURN}$, and PV_{TURN}

The top part of Table 2 shows mean $\mathrm{TTPA_{TURN}}$, $\mathrm{PA_{TURN}}$, $\mathrm{TTPV_{TURN}}$, $\mathrm{PV_{TURN}}$, $\mathrm{TTPD_{TURN}}$, and $\mathrm{PV_{TURN}}$ averaged for all combinations of knob and target angle. The lower part of Table 2 shows significant results of the ANOVA and subsequent contrast analysis. The velocity of the turning movements peaked at 30% of the $\mathrm{MT_{TURN}}$, resulting in an

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[3] We do not report the main effect of knob because fast hand movements in different directions during grasping systematically distorted the supination readings of the accelerometer.

asymmetric velocity profile. This suggests that the control of the knob-turn was based on a feedback process (Mackrous and Proteau 2007). The parameters of the knob-turn depended not only on the extent of the knob turn but also on the location of the knob and the direction of the knob turn. This possibly reflects different biomechanical properties of the arm resulting from the recruitment of different muscles in different arm postures. Neither a main effect of advance information nor any interaction containing the factor advance information yielded significant results for any variable.

Discussion

The present study showed that humans adjust the forearm and, thus, the hand orientation when grasping a circular knob to the direction and to a lesser degree to the extent of the upcoming knob-turning movement. Even though the shape of the knob does not constrain the forearm angle at grasping, our participants only used a comparatively small range of possible forearm angles to grasp the knob (cf. Mutsaarts et al. 2006). Advance information did not influence movement kinematics but affected RT and MT_{GRASP}. Thirdly, advance information and the features of the upcoming knob-turn modulated MT_{GRASP}.

Planning

Anticipatory forearm rotations

The results of the present experiment have implications for the integration of different constraints imposed by the grasping and the turning movement. The integration requires a mechanism that selects a grasping movement that further facilitates the knob-turn among all those grasping movements that are suitable to grasp the knob. It has been proposed that this selection is based on "end-state comfort" (Rosenbaum et al. 1990). The end-state comfort effect refers to the finding that humans grasp objects in a way that results in comfortable arm postures after object rotations or displacements (Rosenbaum et al. 1996). Our participants behaved clearly according to the end-state comfort effect because their anticipatory forearm rotations during grasping enabled to keep the forearm angle at the end of the knob-turn in a restricted, central range. However, additional factors have to play a role in the determination of the grasp orientation. If the participants had strictly optimized end-state comfort, we would have expected that forearm angles at the moment of grasping are selected that result in a common end-posture after rotation that is independent of the direction and extent of the knob-turning movement. However, forearm angles differ considerably after knob-turning movements to different target angles. Moreover, the target angle of the knob-turning movement has a larger effect on the forearm angle after knob-turning than on the forearm angle at grasping. Even though participants partially compensated for the upcoming knob-turn during grasping, considerable end-state variability remained. These results imply that even though some aspects of human manual action seem to be strictly optimized (for a review see Todorov 2004), the selection of the grasp orientation does not seem to be subject to such optimization. However, the finding that participants produce movements with good end-state comfort but not optimal end-state comfort is inline with the "constraint hierarchy" hypothesis (Rosenbaum et al. 2001; Rosenbaum et al. 2009). According to this hypothesis, movements are selected that keep different parameters, such as the angle of the forearm, within an acceptable range, but it is not necessarily the "best" possible movement, that is selected for execution.

At the moment, we can only speculate how the specific pattern of anticipatory forearm rotations, which were mostly determined by the direction of the upcoming knob-turning movement, emerged. One possibility is that the motor system generally does not finely tune anticipatory modifications of movements to the requirements of forthcoming actions. However, grip force (Eliasson et al. 1995; Flanagan et al. 1993, Wing and Lederman 1998) or grip aperture during grasping (Short and Cauraugh 1999) are precisely adjusted to upcoming object interactions. A second possibility is that the motor system is well able to combine constraints from different movement segments but was lacking the necessary information. It is possible that our participants did not plan the amplitude of the knob-turning movement very accurately because they had ample time to home in the cursor on the target at the end of the knob-turn. In consequence, the motor system lacks a precise representation of the extent of the knob-turn when planning the grasp. Finally, the cognitive load imposed by the task might have impaired motor planning. In either case, it might be an adequate strategy to rotate the forearm in the direction contrary to the forthcoming knob-turn by an amount that enables comfortable grasping of the knob but also provides play to turn the knob to various targets without assuming awkward postures.

Planning process

A second aim of the current study was to investigate whether the opportunity for the participants to plan specific segments of the movement sequence well in advance of the choice reaction signal affects the kinematics of anticipatory forearm rotations. Advance information did not affect movement kinematics but had strong effects on RT and MT_{GRASP}, suggesting that the CNS forms an integrated movement plan in which critical and non-critical parameters are specified before movement onset. As advance information about both, the knob location and the turn angle, facilitated motor planning, the forearm orientation and the hand transport could be specified independently. However, as movement kinematics was not affected by advance information, it is likely that movement planning resulted in the same motor program in all advance information conditions. Thus, movements were not initialized before all movement parameters were specified. It is interesting to note that this was even the case when the target angle was ±45° and thus the knob-turn could be easily executed without adopting a specific hand orientation at grasping. This hypothesis finds further support in the very early onset of knob-turn direction dependent anticipatory forearm rotations during the grasping movement. The comparatively late onset of angle-dependent anticipatory forearm rotations cannot provide further insight because these anticipatory rotations might only be detected later due to their modest size. The conclusion that movements could not be initiated before both the hand location and forearm orientation—and thus the end-posture—were specified supports the hypothesis that movement planning includes the determination of the movement's end-posture (Aflalo and Graziano 2006; Butz et al. 2007, Elsinger and Rosenbaum 2003; Fan et al. 2006; Herbort and Butz 2007; Rosenbaum et al. 2001).

Grasping and turning

Interaction between control of the grasp and planning for the Knob-Turn

In the previous sections, we discussed the implication of the present data for the planning of the grasping segment. Now, we turn to the scheduling of the preparation of the motor program for the knob-turning segment. MT_{GRASP} exhibits a compatibility effect between knob location and knob-turn direction (with left-counterclockwise and right-clockwise as compatible). The compatibility effect might be partially based on features of the movement itself. For example the amplitude of SUP_{GRASP} is generally lower in compatible than in incompatible trials and it might be more natural to continue a rightward hand movement with a clockwise rotation of the hand than otherwise. However, as the compatibility effect is reduced in the precue-angle condition, it cannot be solely caused by the motoric properties of the movement but has to result partially from differences in the movement planning processes between the advance information conditions. The online programming hypothesis, according to which a plan for a forthcoming movement may be generated and implemented during an ongoing movement may account for the three-way interaction (Chamberlin and Magill 1989, Rosenbaum et al. 1987). On the one side, in the precue-knob and precue-angle condition, participants were not able to plan any part of the motor program for the knob-turn before the onset of the choice reaction signal. In this case, the participants might have adopted an online programming strategy and planned the knob-turn during the grasping segment. As the preparation and control of movements that require achievement of multiple sub-goals are facilitated if the sub-goals are compatible (Kunde and Weigelt 2005, Mechsner et al. 2001) and as the implementation of a movement during the execution of another causes interference (Adam et al. 2000), the overlap of the goals of the grasping and knob-turning segment may have facilitated the preparation of the knob-turn during the control of the grasp in compatible trials and impaired it in incompatible trials. On the other side, in the precue-angle condition the influence of preparatory processes of the knob-turn on the execution of the grasp might have been reduced because the knob-turn might have been prepared already before the onset of the choice reaction signal. This interpretation is in line with data that suggest that late segments of a sequential movement can be prepared partially independently of earlier segments (Fischer et al. 1997; Herbort and Butz 2007; Herbort and Butz in press).

Control of hand orientation and transport

Desmurget et al. (1996) reported that in prehension hand orientation and hand transport are controlled interdependently. The present results add further evidence for the interdependence between a transport component and forearm rotations that adjust the hand orientation grasping. First, participants only initiated the grasp once the movement parameters for the hand transport and the hand orientation were specified, suggesting that target location and desired hand orientation at the grasp were integrated in a common, effectively posture-based movement plan. Second, the forearm angle at grasping was not only determined by the target of the knob-turn but also strongly depended on the location of the knob and hence the target of the hand-transportation movement. This suggests a strong interdependence between the transport and orientation component in grasping movements.

Contribution of forearm and fingers to Knob-Turning

The comparison of SUP_{GRASP} and SUP_{TURN} for each target angle reveals that the forearm rotations that were exerted by the participants covered just about 50% of the totally necessary rotation. When requested to turn the knob by 45°, 90°, or 135°, participants made on average (SD in parenthesis) forearm rotations of 23.5° (4.9°), 47.3° (10.9°), and 71.8° (16.6°), respectively. As the participants were seated so that they had to grasp the knob with an almost stretched arm and thus upper arm adduction or abduction could not contribute much to the knob rotation, we conclude by process of elimination that the remaining 50% of the knob rotation were achieved by movements of the fingers.[4] While there was some variance between the participants' ratio of forearm and finger movements in general, this ratio was independent of the extent of the knob-turn for each participant. This is evident as a subject-wise linear regression of target angle on average forearm rotations ($\mathrm{SUP}_{\mathrm{TURN}}$–$\mathrm{SUP}_{\mathrm{GRASP}}$) yielded average R^2s of 0.9962 (SD = 0.00453). This is important to note because it shows that the forearm orientation, which was recorded in this experiment, is a good predictor for the actual grasp orientation. Finally, this complements previous data of a prehension task in which the forearm and the fingers also contributed equally to the final grasp orientation and in which the ratio of forearm and finger contribution was also independent of the grasp orientation (Marotta et al. 2003).

Conclusion

We examined planning and execution of anticipatory forearm rotations in a knob-grasping and—turning task. The results clearly reveal that humans adjust their movements to intended future actions. However, even if the shape of the knob did not constrain grasp selection on the pronation-supination dimension, participants adjusted the forearm angle at grasping mostly to the direction of the upcoming knob-turn. The extent of the knob-turn only slightly affected grasp selection. This suggests that constraints imposed by future actions were coarsely integrated into the motor program for immediate movements. It remains an open question, by which criteria the CNS selects grasping and manipulation movements and how neural and cognitive mechanisms achieve the effective and often beautiful integration of different movement segments of human actions.

Acknowledgments The authors acknowledge funding from the Emmy Noether program of the German Research Foundation (grant BU1335/3-1) and thank Georg Schüssler for technical support.

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[4] We inferred the finger movements from the movements of the control knobs because finger movements have not been directly recorded.

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