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# Grasp Planning for Object Manipulation without Simulation of the Object Manipulation Action

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**Abstract**

When an object is grasped, the grasp is usually adapted to upcoming object manipulations. We tested the hypothesis that grasp planning for object manipulation is based on simulations of body movements that could implement intended object manipulations. The simulation of body movements requires to map the desired object movement onto body movements at some stage of the planning process. Hence, manipulating this mapping should affect simulations and ultimately grasp selections. This hypothesis was tested in five experiments, in which participants grasped a circular knob and used it to rotate a pointer to various targets. In Experiments 1-3, we selectively manipulated the pointer-to-hand-rotation mapping with a "virtual rotation" procedure. During these virtual rotations, participants were exposed to an altered mapping between their hand movements and movements of the pointer. However, the exposure did not affect grasp selections in a subsequent test block. In Experiment 4, we verified that our manipulations of the mapping were sufficient to evoke substantial changes in grasp selections. In Experiment 5, we verified that adaptations in the virtual rotation procedure carried over to the test blocks, in which grasp selections were probed. In summary, participants adapted their grasps to different intended pointer rotations on a trial-to-trial bases, thus showing the end-state comfort effect. However, grasp selections were unaffected by the acquired mapping between pointer and hand movements. This suggests that anticipations of the body movements associated with specific object manipulation play no crucial role during grasp planning.

**Keywords:** grasp planning; object manipulation; end-state comfort effect; motor simulation; prehension; anticipation; motor control

**Public Significance Statement**

Many everyday actions are executed in such a way that planned subsequent actions are facilitated or enabled. For example, when we grasp to-be-manipulated objects we usually select grasps that make the intended object manipulations faster and more accurate. It has been suggested that this anticipatory mode of acting is based on internal simulations of possible object manipulation actions. We tested this hypothesis in five experiments. Participants learned that specific rotations of an object either required relatively far or short rotations of the hand. In contrast to the hypothesis, the anticipation of either a far or a short hand rotation did not affect how participants grasped the object. Thus, when we select a specific grasp for a specific object manipulation, the simulation of object manipulation actions does not play a crucial role. By contrast, apparently sophisticated anticipatory action planning seems to be mostly based on trial-and-error learning during object manipulations.

## Grasp Planning for Object Manipulation without Simulation of the Object Manipulation Action

We use tools and handle objects every day. Thereby, the selection of a specific grasp sets the stage for subsequent tool use actions or object manipulations. Whereas a clever grasp choice can facilitate a subsequent object manipulation, an inappropriate grasp choice may hinder it or even render it impossible. An example is overturning an inverted glass. The glass could be lifted with a comfortable initial grip (base of thumb points up). But this would result in a twisted, uncomfortable arm posture after the rotation, which makes it difficult to carefully put the glass on the table again. Alternatively, the glass could be lifted with an uncomfortable initial grip (base of thumb points down) and placed down in a relaxed, comfortable arm posture, allowing fine control over the placing movement. Hence, it is important to adjust the grasp to upcoming object manipulations and participants consistently do so in a variety of object manipulation or tool use tasks (Cohen & Rosenbaum, 2011; Fischman, 1998; Herbort, 2012, 2015; Olafsdottir, Tsandilas, & Appert, 2014; Rosenbaum, van Heugten, & Caldwell, 1996; Short & Cauraugh, 1999; Weigelt, Kunde, & Prinz, 2006; for a review see Rosenbaum, Chapman, Weigelt, Weiss, & van der Wel, 2012).

### Grasp planning based on anticipated body movements

Although numerous experiments on grasp selection for object manipulation have been conducted over the last decades, the mechanisms underlying grasp selection for object manipulation remain poorly understood. Nevertheless, it is often assumed that the selection of a specific grasp is based on the simulation of *body movements* that could realize the desired object manipulation (Cohen & Rosenbaum, 2004; Johnson, 2000; Osiurak & Badets, 2017; Seegelke & Hughes, 2015; Toussaint, Tahej, Thibaut, Possamai, & Badets, 2013; Wunsch & Weigelt, 2016). We refer to this hypothesis as *simulation hypothesis* of grasp selection for object manipulation. The shaded area of Figure 1 illustrates the hypothesis. The simulation hypothesis is a central constituent of various explanations of the end-state comfort effect.

According to Johnson (2000), different grasp options are evaluated based on forward simulations of the subsequent *body movements* and their awkwardness. As an example, consider a person who intends to rotate a glass by 180°. To select a grasp, the person simulates the arm movements that would follow after a comfortable and after an uncomfortable initial grasp. Then, the one grasp is selected that results in the least awkward arm posture at the end of the simulated object manipulation.

Alternatively, the posture-based motion planning theory (Rosenbaum, Meulenbroek, Vaughan, Jansen, 2001) has been referred to as an explanation of the end-state comfort effect (e.g., Short & Cauraugh, 1999; Wunsch, Henning, Aschersleben, & Weigelt, 2013). According to this view, participants first determine the end-posture at the end of the object manipulation. Then, a posture for grasping is selected that allows the object manipulation movement to end in the already defined end-posture. To compute the grasp posture, the *body movement* (in terms of arm postures) that is necessary to realize the planned object manipulation has to be anticipated. In both accounts, the grasps for object manipulations are selected based on the anticipated or simulated body movements that are necessary to bring the object manipulation about.

To simulate the body movement required for an object manipulation, the desired object movement (e.g., encoded in 3D space) has to be translated into corresponding body movements (e.g., encoded in joint space) at some stage of the planning process. Thus, this translation is implied by the simulation hypothesis. This translation is not trivial. For example, the rotation of an object usually involves rotations of the shoulder, pro- or supination of the forearm, and movements of the wrist and fingers (Herbort & Butz, 2010; Lardy, Beurier, & Wang, 2012; van der Vaart, 1995). Modules that realize such translations are termed *internal models* (Jordan & Wolpert, 1999; Sabes, 2000; Shadmehr, Smith, & Krakauer, 2010). Importantly for the present purpose, the simulation hypothesis predicts that a change in the internal model should change the simulations of body movements that are considered during planning and consequently change grasp selections.

To our knowledge, the simulation hypothesis has not been directly tested. The best indirect evidence in its favor is provided by developmental studies showing that the ability to adjust one's grasp to upcoming object manipulations is correlated with motor imagery abilities (Fuelscher, Williams, Wilmut, Enticott, & Hyde, 2016; Toussaint et al., 2013; cf. Stöckel, Hughes, & Schack, 2012). One possible interpretation of these studies is that motor imagery is involved in grasp planning for object manipulations.

Additional support for the simulation hypothesis comes from the plausibility of its constituents. First, a vast literature on sensorimotor adaptation (e.g., Bock, 2013; Krakauer & Mazzoni, 2011) has shown that participants acquire *internal models*, which allow to translate desired object movements into body movements. Thus, the body movements during an object manipulation can be simulated (cf. Seegelke & Hughes, 2015). Second, participants can judge the comfort of various grasps prospectively (Johnson, 2000). This implies that simulated body movements can be faithfully converted into a metric – such as comfort – that could be used for deciding between alternative grasps.

However, other findings cast doubt on the involvement of simulations in grasp planning. For example, when participants are asked to execute mildly uncommon object manipulations, such as forth-and-back rotations of an object, they typically do not adapt their grasps to the object manipulations from the first trial on (Herbort, Mathew, & Kunde, 2017; Mathew, Kunde, & Herbort, 2017; c.f. Künzell et al., 2013). Although the involved body movements should be fairly easy to simulate, participants only adapted their grasps after they gained some experience with the task.

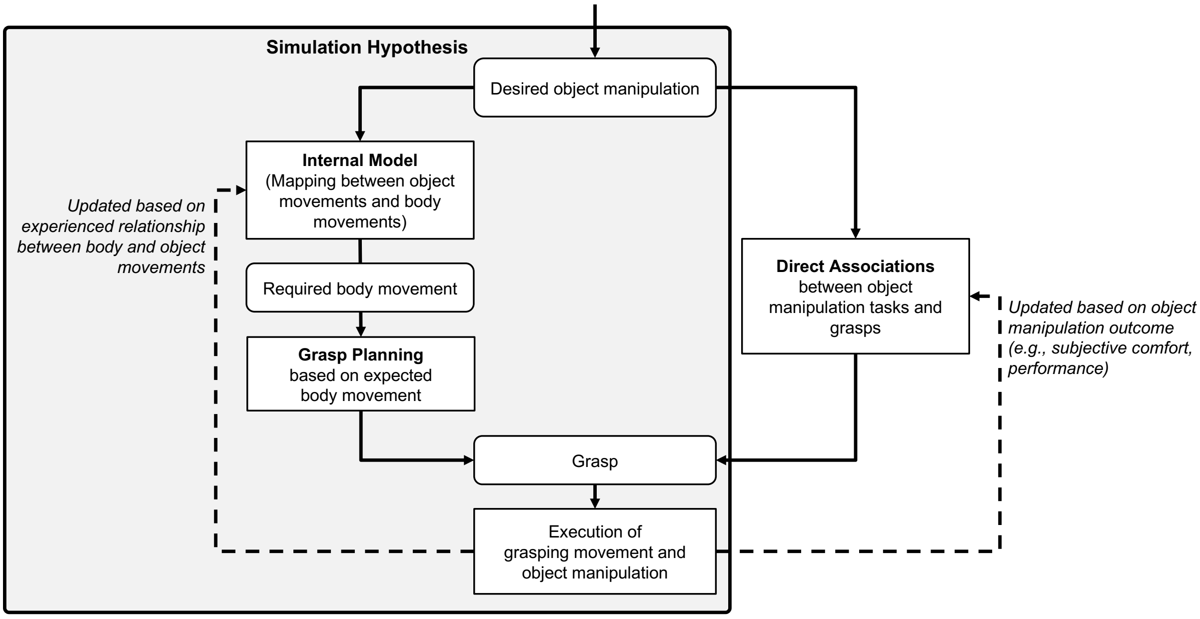


*Figure 1.* Two (possible) routes of grasp selection for object manipulation. The shaded area illustrates the simulation hypothesis of grasp selection for object manipulation: The body movement that is required to realize the desired object manipulation is computed and then used to plan a suitable grasp. Grasp selections are expected to change when the mapping between object and body movements is modified (dashed line). Additionally, a second process contributes to grasp selection for object manipulation in parallel. Desired object manipulations are directly mapped onto specific grasps. These direct associations are updated based on the outcomes of executed object manipulations (dashed line).

## Aim of the article

In this article, we want to specifically test the simulation hypothesis, thus the hypothesis that grasp selection depends on predictions of the body movements that are necessary to realize an intended object manipulation. To test the hypothesis, we aim to manipulate the relationship between object and body movements (i.e., the internal model). As argued above, according to the simulation hypothesis, the manipulation of the contingencies between object and body movements should affect the simulated body movements and consequently grasp selection. If grasp selection is affected by the manipulation of these contingencies the simulation hypothesis was supported. If it remains unaffected, this can hardly be reconciled with internal simulation.

**Grasp planning without anticipation of body movements**

However, if simulations are involved in grasp selection for object manipulations, they are most likely not the only contributors to the final grasp selection. Grasps could also be adapted to object manipulations via a second process that does not require simulated body movements (Herbort & Butz, 2012; van Swieten et al., 2010; cf. McCarty, Clifton, & Collard, 1999). This process directly associates the goal to grasp an object for a specific object manipulation with a specific grasp. This *direct association* process is depicted on the right side of Figure 1. These associations are updated based on experienced action outcomes (e.g. perceived comfort after an object manipulation). As an example, consider a person who has the compound goal to grasp and invert a glass. The person might initially grasp the glass with a comfortable posture and therefore might experience difficulties during the subsequent execution of the object manipulation. Hence, the associations between the goal to grasp an object for rotation and the comfortable grasp might be weakened. Thus, an uncomfortable initial grasp may be chosen the next time. The resulting ease of the object manipulation with an uncomfortable grasp may then result in a further strengthening of the associations between the grasp-and-rotate task and the uncomfortable initial grasp. Such learning experiences might reinforce direct associations between object manipulation tasks and the most suitable grasps. Hence, grasps could be selected without simulating the object manipulation action during grasp planning.

Evidence for the involvement of this more habitual mode of planning was provided in a recent experiment (Herbort et al., 2017). Participants preferably selected grasps for object manipulations that were useful in previous trials although other grasps might have been more effective under the current, changed task constraints – which were known to the participant. This suggests that grasps were to a large extent based on habitual task-grasp associations.

The simulation hypothesis and direct associations could – in principle – explain grasp selections in typical object manipulation task on their own. However, the direct association account differs from the simulation hypothesis with respect to the grasp selection process and to the type of information that is extracted from executed object manipulations. According to the simulation hypothesis, the grasp posture is selected by first translating intended object movements into body movements and then computing a grasp posture based on the anticipated body movements. As the translation process (realized by the internal model) reflects experienced contingencies between object and body movement, grasp selections are expected to change when participants register a change in the *relationship between object and body movements* when executing the object manipulation.

By contrast, the direct associations process translates the intended object manipulation into a specific grasp without invoking simulations of the body movements during the object manipulation. Which grasps are activated depends on the experienced outcomes of object manipulations (in terms of comfort, control, or other variables). Thus, the grasps associated with specific object manipulations are updated when the relationship *between grasps and object manipulation outcomes* changes. In summary, the simulation hypothesis reflects a planned, model-based mode of grasp selection, whereas the direct associations process reflects a more habitual, model-free mode of grasp selection.

**Object manipulation task**

The aim of the present article is to test whether the process implied by the simulation hypothesis contributes to grasp selection for object manipulation, irrespective of the (possible) additional involvement of a direct associations. To this end, we run experiments in which we aim to (1) specifically manipulate the relationship between object and body movements, which plays a critical role in the simulation hypothesis, and (2) prevent any updating of direct associations between object manipulation tasks and specific grasps.

The following general procedure was used in our experiments. Participants grasped a rotary control – comparable to the volume control on a stereo – and rotated it to move a pointer to different targets. In such a setting, grasps are reliably affected by the direction and extent of the object manipulation. For clockwise rotations, the arm is rotated counter-clockwise before grasping and vice versa. Importantly, the further the rotation, the more excursed is the orientation of the hand when grasping the dial (e.g., Herbort, 2015; Herbort & Butz, 2010; van der Vaart, 1995). In pre-test and post-test trials of our experiments, the movement of the pointer corresponded to that of the hand and dial (gain = 1). In an adaptation phase, participants conducted *virtual rotations*, which were designed to facilitate the acquisition of an internal model while at the same time preventing the updating of direct object manipulation grasp associations. The rationale for using such virtual rotations is laid out in the next section. During the adaptation phase, the gain used to translate hand rotations (i.e. body movements) into pointer rotations was either increased (requiring shorter hand rotations) or decreased (requiring further hand rotations). We then compared how strongly the grasps depended on the instructed pointer rotations after exposure to a high or low gain. If grasps are excursed more after adaptation to a small gain (far hand rotations) than to a larger gain (short hand rotations), the simulation hypothesis is supported.

**Virtual rotation task**

In the following, we lay out the rationale for using virtual rotations in the adaptation phase. The virtual rotation task was developed to (1) facilitate adaptation of an internal model to the changed gains and to (2) prevent updating of direct associations between object manipulations and grasps.

What is learned during sensorimotor adaptation is specific to the conditions of practice (Sülzenbrück, 2012). Hence, we wanted to make the conditions during adaptation as similar as possible to the conditions during grasp planning, which typically happens before grasp onset (Herbort & Butz, 2010). As no feedback of an ongoing movement is available when a grasp is planned, we likewise provided as little feedback as possible during adaptation. Visual feedback was removed by occluding the hand and removing the pointer. The pointer position was only presented after the rotation (terminal feedback), which facilitates the updating of internal models (Barra, Mégard, & Vidal, 2013; Bernier, Chua, & Franks, 2005; Heuer & Hegele, 2008a,b). Additionally, haptic feedback was removed by requiring participants to execute the rotation close to the dial but without actually grasping it.

On the one hand, the virtual rotation procedure is expected to facilitate the adaptation of an internal model of the task because it eliminates, as far as possible, the possibility to compensate the gain manipulation by reorganizing feedback-based processing. On the other hand, the virtual rotation procedure differs from the actual dial rotation procedure used in pre- and post-test block. Thus, it might be questioned if any information acquired during virtual rotations is also employed to plan actual rotations. This question is addressed in Experiment 5, which shows that adaptation to novel gains in virtual rotations carries over to actual dial rotations. Finally, it has been suggested that adaptation with terminal feedback may result in the application of explicit strategies rather than adaptation of internal models (Hinder, Tresilian, Riek, & Carson, 2008). However, this can be avoided by slowly increasing or decreasing the gain to its final level (Kagerer, Contreras-Vidal, & Stelmach, 1997; Klassen, Tong, & Flanagan, 2005; Michel, Pisella, Pralanc, Rode, & Rosetti, 2007). Hence, in the first adaptation block, we started with a gain of 1.00 in the first trial and slowly adjusted the gain trial-by-trial until the planned value was reached at the end of the first block. In summary, we aimed at creating conditions in the adaptation procedure that matched those during grasp planning and that facilitate the updating of internal models.

A second constraint of the virtual rotation task was to prevent updating of direct associations, and thus to confine potential effects of the gain manipulation on grasp selection to internal simulation alone. Direct associations are basically updated by a reinforcement learning process, in which the action outcome (e.g., level of comfort, ease of the object manipulation) serves as reward signal for the preceding grasp choice. Reinforcement learning hinges on the ability to explore new actions. In some motor tasks, high motor variability and thus a stronger tendency to explore different actions may facilitate adaptation (Wu, Miyamoto, Gonzalez Castro, Ölveczky, & Smith, 2014) and failure in a motor task increases the tendency for exploration (Pekny, Izawa, & Shadmehr, 2015). Hence, to prevent updating of direct associations, we eliminated the possibility to explore the suitability of different grasps after changing the gain by requiring participants to use predetermined grasps for dial rotations.

In summary, the virtual rotation procedure allowed participants to register the changed relationship between dial and arm rotations and update their internal model accordingly. Thereby, it prevented participants from exploring the changed relationship between grasps and action outcomes and thus prevented updating of direct associations between object manipulations and grasps.

In the following, five experiments are reported. Experiments 1-3 show no effect of the gain manipulation in virtual rotations on grasp selection, despite sufficient power to detect such effects. Experiment 4 shows that grasp selections are affected by the gain manipulation if participants are allowed to freely select their grasps and actually rotate the dial in the adaptation phase. Thus, the gain manipulation was sufficient to evoke substantial effects on grasp selections. Experiment 5 shows that adaptation to virtual rotations affects the extent of actual dial rotations in test blocks without feedback. Thus, adaptations to virtual rotation carry over to the dial rotations used in the test blocks. In summary, the data do not support the simulation hypothesis. The anticipated arm and hand movements involved in object manipulations do not have a measurable effect on grasp selections.

## Experiment 1

In Experiment 1, we asked participants to rotate an actual dial in pre- and post-test phases. Participants executed *virtual rotations* in an adaptation phase between pre- and post-test. During virtual rotations one group experienced that pointer rotations require relatively short hand rotations (high gain) whereas another group experienced that pointer rotations required relatively far hand rotations (low gain). If the simulation hypothesis is correct and grasp selections are based on the extent of the expected hand rotations, the excursion of the grasps should increase from pre- to post-test in the low gain group and decreases in the high gain group. Additionally, three manipulation checks were performed. First, we checked whether the manipulation of the gain during the adaptation blocks actually affected how far the hand had to be rotated during the rotations. Second, it was assured that participants did not preserve the pre-determined grasps of the adaptation phase in the post-test. Third, we tested whether an adaptation of the grasp to the internal model would have affected the comfortableness of the dial rotation by collecting comfort ratings for various postures after the experiment.

## Method

### Participants

Sixty participants were recruited from the Würzburg area (21 men, 39 women, mean age = 27). According to the handedness scale of the Lateral Preference Inventory (LPI, Coren, 1993), all were right-handed. Participants signed informed consent and received a payment of 7€ or course credit.[1]

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[1] This and the following experiments have been approved by the ethics committee of the Department of Psychology of the Julius-Maximilians-Universität Würzburg (GZ-2017-17; “Grasp planning for object manipulations without simulation of the object manipulation action”).

The sample size was selected as a compromise between the following considerations. On the one hand, a simulation of the planned experiment based on previous data (see Appendix A) showed that if the gain adaptation in virtual rotations fully carries over to the dial rotations and affects grasp choices as predicted by the simulation hypothesis, a rather high effect size could be expected ($\eta^2_p = .3427$). Effects of this size can be detected with a power of $1-\beta = 0.95$ using 30 participants. However, as other simulations have shown that our constraints for equating grasp selections of the high- and low-gain group in the pre-tests benefits from a greater sample size and as the effect size was only estimated from a simulation, we collected 60 participants. This allows to detect the expected effect with a power of $1-\beta = 0.9997$ and an effect with 50% of the computed size with a power of $1-\beta = 0.93$.

**Apparatus and Stimuli**

Figure 2a shows the experimental setup. Participants were seated in front of a table in a dimly lit room. A back-projection screen (80 cm x 50 cm) was placed 50 cm from the front edge of the table. A dial (diameter 8 cm) was placed 6 cm before the projection screen and 17 cm above the table. A start block (3.2 cm x 4.8 cm x 2.6 cm) was fixed on the table at a distance of 15 cm from the edge at an angle of 45°. A button was fixed 40 cm to the left of the block. In virtual rotation trials, vision was blocked with a screen (40 cm x 83 cm) that was positioned 30 cm above the table surface.

Stimuli were presented on a black background. In the top half of the screen, a circle (diameter 12.5 cm) of white tick marks (length 1.3 cm, spacing 15°) was presented. A white line originating in the center of the dial served as pointer. The target angle of the pointer rotation was displayed by coloring the tick mark at the target position green and by connecting the inner ends of the target tick mark and 12 o'clock tick mark with a green arc.

In the virtual rotation trials, a *hand position indicator* stimulus was used to allow participants to navigate their hand to the position of the virtual dial. The actual and target hand orientation and position was visualized by two lines. The orientation of the lines corresponded to the actual and required orientation of the line from thumb to index finger in the screen plane. The thumb side of the line was colored red and the index finger side was colored blue. There was a small gap between the red and blue part (10% of line length). The target line was presented in the center of the tick mark circle (length 6.3 cm). The displacement of the line indicating the actual hand position (defined as the position in the middle between the index finger and thumb sensor) from the target line corresponded to the displacement of the hand position from the center of the dial in the screen plane. The line's length reflected the longitudinal hand position. That is, the further the hand was away from the participant, the longer was the line. The length of both lines were identical when the hand position was 6 cm in front of the dial. The target line was painted in darker tones of red and blue than the line indicating the actual hand position. The latter line turned white, when the x-, y-, and z-components of the actual hand position were within 3 cm of the respective components of the target and when the actual grasp orientation was within 5° of the target grasp orientation.

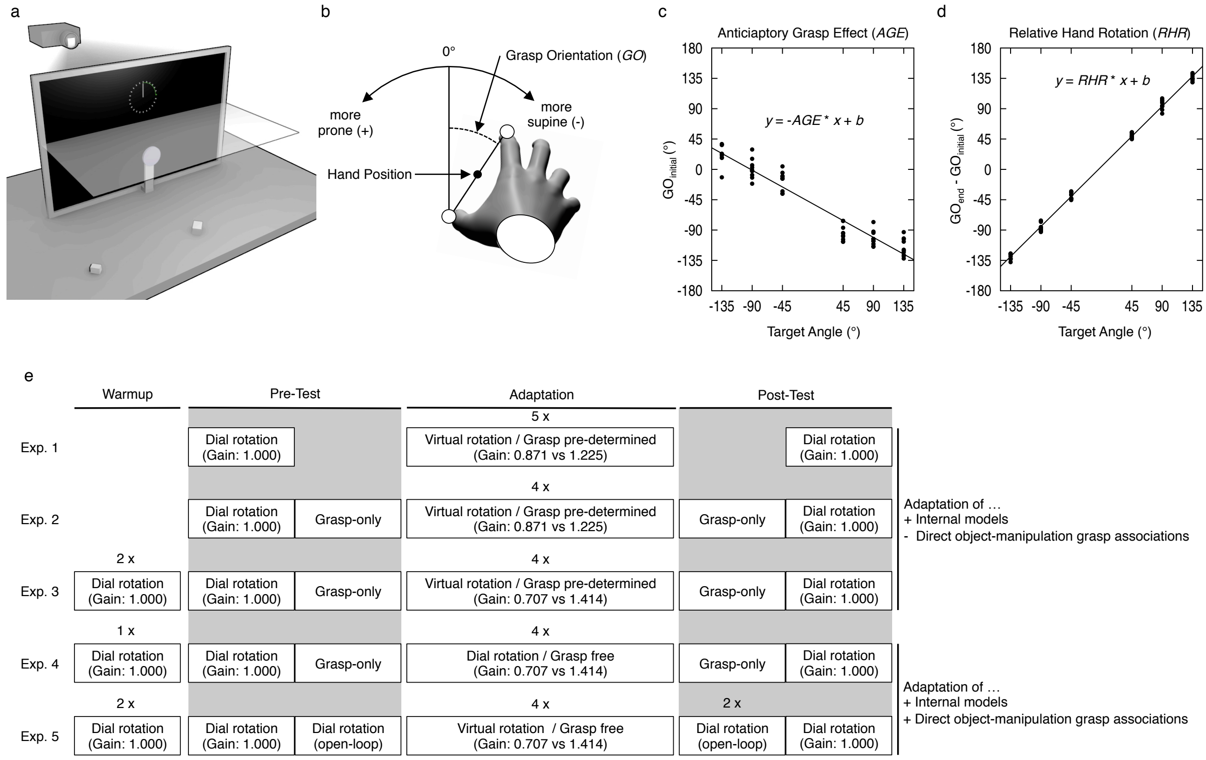


*Figure 2.* a) Apparatus, including the dial, the start element (center) and the response key (left). b) Sensor placement (white circles) and extraction of grasp orientation GO. c) Exemplary data illustrating how the anticipatory grasp effect (AGE) was computed from the grasp orientations for rotations to different targets. The value of AGE reflects how strongly the grasp is adjusted to subsequent dial rotations d) Exemplary data illustrating how the relative hand rotation (RHR) was computed from the hand rotations during dial rotations of various extents. The RHR indicates how far the hand is rotated during the dial rotation e) The sequence of blocks for Experiments 1-5. Experiments 1-3 but not 4 and 5 suppressed the updating of direct object-manipulation grasp associations during the adaptation phase. The updating of internal models that negotiate between object manipulations and grasps were possible in the adaptation phases of all experiments.

## Procedure

Two different trial types were presented during the experiment. In dial rotation trials, the hand could be always seen (Figure 3a). The back-projection screen initially showed the tick marks and the pointer at the 12 o'clock position. If participants didn't grasp the start block within 2 s, a message prompted them to grasp the start block ("Legostein greifen", German for: "Grasp lego brick"; the start block was made of Lego). Once the hand position was continuously within 3 cm of the start block center, the pointer target was displayed and a short beep (1760 Hz for 25 ms) was played. Upon this signal, participants grasped the dial and used it to rotate the pointer to the target. When the pointer was within 2° of the target for 250 ms, a click sound was played and the message "Gut gemacht!" (German for "Well done!") was displayed for 500 ms. Then, the next trial started. Participants were instructed to firmly grasp the dial with the right hand, to grasp the dial with a stretched arm, to not release the dial or readjust the grasp during the rotation, and to move at a comfortable speed.

In virtual rotation trials, vision of the hand was blocked by a screen parallel to the table surface (Figure 3b). Virtual rotation trials were identical to the dial trials until the point at which participants grasped the start block for 1 s. Then, the pointer was removed and the hand position indicator stimulus was displayed. Participants then moved their hand to a position in front of the real dial. Once the participants held their hand for 500 ms in the designated position and orientation (for criteria see above), the hand position indicator was removed, the pointer target was presented, and a beep was played. Participants then rotated their hand as if they were using the dial to rotate the pointer. To indicate that they finished the virtual dial rotation, they pressed a key on their left with the left hand. Then, the pointer reappeared. Its position was computed by multiplying the change of the hand orientation during the virtual rotation (from target onset to button press) with a gain factor. When the pointer was within 5° of the target angle, the text “Treffer” (German for “hit”) was displayed for 500 ms. Otherwise, the texts “zu kurz” or “zu weit” (German for “too short” and “too far”) were presented for 500 ms. In virtual rotation blocks, participants were asked to move as if they were rotating the actual dial, without touching it, to move as if they would turn the dial without releasing it during the rotation, to move at a comfortable speed, and to move the pointer as accurate as possible to the target.

Two independent groups of participants were tested. In the low-gain group, the gain in virtual rotation was 0.817. In the high-gain group, the gain was set to 1.225. Thus, participants in the low-gain group had to rotate the hand 1.5 times further than participants in the high-gain group to rotate the pointer to the same target.

The experiment consisted of a pre-test dial rotation block, followed by five virtual rotation blocks, and a post-test dial rotation block (Figure 2e). Each dial rotation block consisted of ten subblocks in which rotations to -135°, -90°, -45°, 45°, 90°, and 135° were presented in random order. Each virtual rotation block consisted of three repetitions of rotations to -135°, -120°, …, -30°, 30°, 45°, …, 135°, which were presented in random order (48 trials per block in total). In virtual rotation blocks, participants had to assume a grasp orientation of 10° for clockwise rotations and -70° for counterclockwise rotations (cf. Figure 2b). These values correspond to the grasps that participants used for comparable dial rotations in previous experiments of our lab. Before the start of the virtual rotation blocks, participants could practice the virtual task without the screen that occluded vision of the hand (8 trials). In the practice trials, the gain was set to 1.0 and participants were encouraged to check that their hand rotation properly translated into pointer movements. In the first virtual rotation block, the gain was linearly ramped down or up from 1.0 to its final value (0.817 or 1.225). In the remaining four virtual rotation blocks, the gain remained constant. After the last block, we collected comfort ratings. Participants were asked to grasp the dial and assume various grasp orientations. Then, they rate the comfort of the arm posture on a scale from 1 (very uncomfortable) to 9 (very comfortable). The to-be-rated arm postures (-180°, -135°, …, 135) were presented three times in random order.

Participants show considerable variability in how they adjust their grasp to upcoming object manipulation in comparable tasks. Hence, we tried to match both groups with respect to this variable in the pre-test blocks with the following procedure. For simplicity, we used an approximation of the variable that would eventually be used for data analysis. We computed the difference $D$ between the mean forearm orientations for clockwise and counterclockwise rotations in the pre-test block from the second subblock on. The first twenty participants were randomly assigned to the different groups (ten each). The remaining participants were assigned in such a way that the difference between the average $D$ values of both groups remained as low as possible. Once one group reached the planned number of participants, the other group was filled up with the remaining participants.

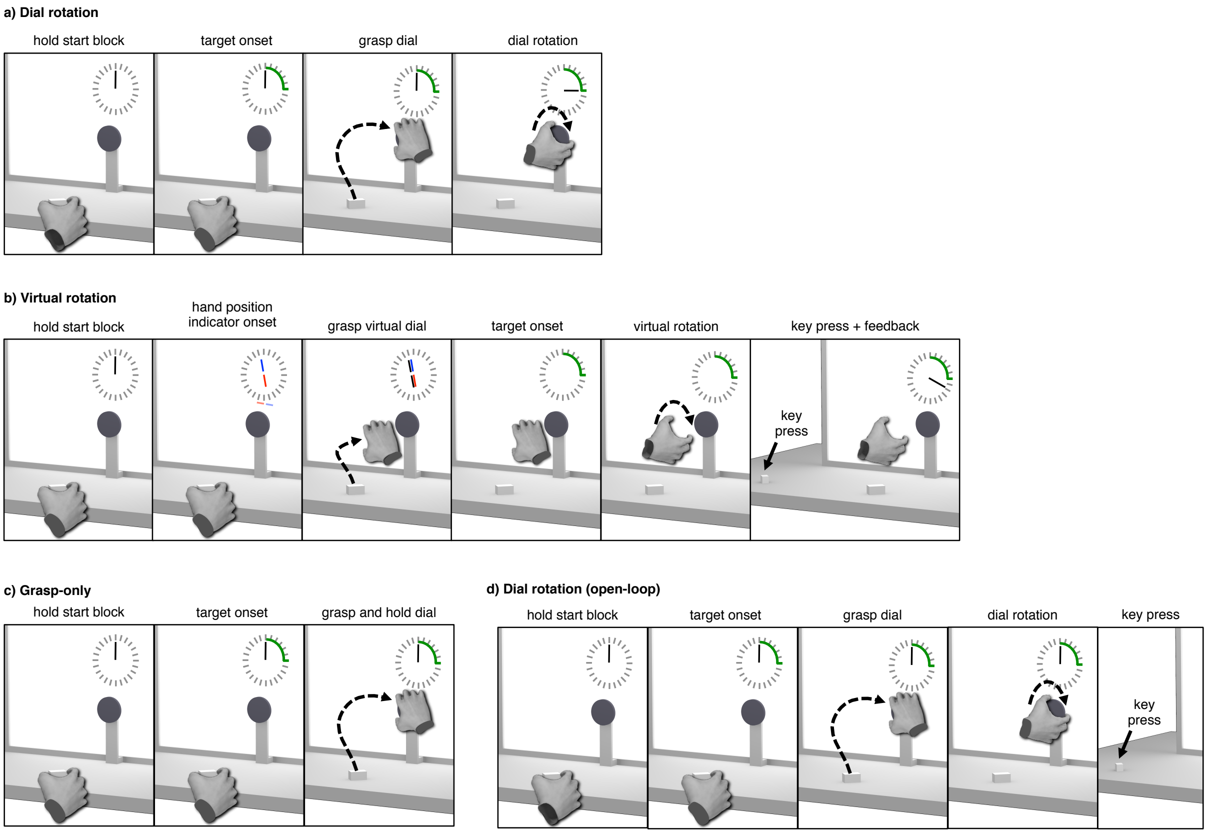


*Figure 3.* Sequence of events in the different trial types. The screen blocking the view of the hand in virtual rotation trials is not shown.

### Data Collection and Analysis

Movements were recorded with an Ascension Trakstar motion tracker at 100Hz. Sensors were attached to the index finger nail, thumb nail, to the distal end of the forearm, and to the dial (Figure 2b). For offline analysis, the data was resampled to 1000Hz using linear interpolation and smoothed with a bidirectional low-pass filter (second-order Butterworth-Filter with cutoff of 20Hz). The grasp orientation (GO) was defined as the angle between thumb and index finger in the screen plane. The forearm sensor was used to disambiguate finger configurations that could either result from extreme pronation or supination. The *GO* was extracted at the initiation and end of rotations. In dial rotation trials, $GO_{initial}$ was defined as the *GO* at the local minimum of the dial rotation rate preceding the first peak of the dial rotation rate (> 30°/s). $GO_{end}$ was defined as the *GO* when the target was considered hit. In virtual rotation trials, $GO_{initial}$ was defined as the *GO* when the target was displayed. $GO_{end}$ was defined as the $GO$ when the button was pressed. To simplify the analysis, we computed the *anticipatory grasp effect* (AGE) and the *relative hand rotation* (RHR). The AGE expresses how strongly the initial grasp orientation is adapted to the upcoming dial rotation (Figure 2c). It is operationalized as the negative slope of the linear regression from $GO_{initial}$ on the target angle (cf., Herbort et al., 2017, Seegelke, Hughes, Knoblauch, & Schack, 2015). An AGE of zero implies that participants use the same grasp regardless of the upcoming dial rotation (i.e., no end-state comfort effect). The higher the AGE, the stronger the grasp is adjusted to the upcoming dial rotation. A value of 1.0 would indicate that grasps fully compensate the subsequent dial rotation so that all dial rotations end in the same arm posture. The RHR (Figure 2d) is the slope of the linear regression from the difference between $GO_{end}$ and $GO_{initial}$ on the target angle. It expresses how far the hand is rotated relative to the resulting pointer rotation. Trials were excluded from the analysis, when the motion tracker data could not be segmented (0.1%) or when participants took more than 10 s to complete the task (1.7%). The second and third comfort rating of each posture was used for analysis.

**Results**

The AGE and RHR were averaged for each participant and each block of the experiment (Figure 4a,b). As expected, the data show positive AGE values for the population (Figure 2a) and each individual participant (Figure 2c). This means that all participants adjusted the orientation of their grasp to the instructed pointer rotation: Clockwise-oriented grasps were selected for counterclockwise dial rotations and counterclockwise-oriented grasps were selected for clockwise dial rotations (a statistical analysis of the effect of the target angle on the initial grasp orientation is provided in ESM 1).

Next, we checked whether this adjustment was further modulated by the gain manipulation. A split-plot ANOVA on the mean AGE with a within-participant factor of block (pre vs. post) and a between-participant factor of gain revealed the following results. The AGE increased from the pre-test to the post-test, $F(1,58) = 5.209$, $p = .026$, $\eta^2_p = .082$. There was no significant effect of gain, $F(1,58) = 1.128$, $p = .293$, $\eta^2_p = .019$. Most importantly, there was no significant interaction, $F(1,58) = 1.625$, $p = .207$, $\eta^2_p = .027$. Numerically, the AGE increased more in the high than in the low gain condition – opposite to the prediction of the simulation hypothesis. To test whether a more nuanced analysis yields different results, $GO_{initial}$ was subjected to a split-plot ANOVA with factors of block, gain, and target angle (-135°, -90°, … , 135°). The results mirrored the analyses of the AGE. Statistics and charts for this analysis are reported in as supplemental material (ESM1).

As a manipulation check, we computed whether the gain actually influenced the extent of the hand rotations during the object manipulation. For each block, the RHR was compared between the high and low gain group, using independent sample t-tests. As expected, RHR was larger in the low gain group from the first adaptation block on, all $t(58)$s $\geq 9.206$, all $p$s $\leq .001$, all $d_s \geq 2.377$. The ratio between the extents of the hand rotations in the low gain and high gain groups was 1.47 in the final adaptation block. Thus, even though participants in the low gain group rotated the hand 47% further during the object manipulation, this did not affect grasp selections.

In the virtual rotation blocks, participants had to use specific grasps. It is hence possible that these predetermined grasps carried over to the post-test blocks and shrouded any effect of the gain. However, this was not the case. Figure 4c plots the AGE in the pre-test against the AGE in the post-test for each participant. The horizontal line shows the AGE during the final virtual rotation blocks ($m = 0.416$, $sd = 0.006$). If grasps carried over from virtual rotation to dial rotation blocks, data points should flock around this line. The scatter plots reveals a high correlation of pre-test and post-test AGE ($r = .741$) and almost identical variability at the pre-test ($SD = 0.18$) and post-test ($SD = 0.19$). Hence, the instruction to use specific grasp during adaptation did not constrain grasp selections in the post-test.

Finally, although the end-postures may have differed between gain conditions, the associated level of comfort might have been similar. Consequently, an adaptation of the grasp to the gain might not have been beneficial. To address this issue, we collected comfort ratings for various postures (Figure 4d). Paired t-tests revealed that the comfort rating of each adjacent pairs of probed arm-postures differed, with the exception of the -45° and 0° posture, $t(59)\text{s} = 1.858$, $p =$ 068, $d_s = 0.240$; all other $t(59)\text{s} \geq 2.815$, all $ps \leq .007$, all $d_s \geq 0.369$. As already relatively small differences between postures affected comfort, adapting the grasps to the different gain conditions would most likely have been beneficial for the participants.

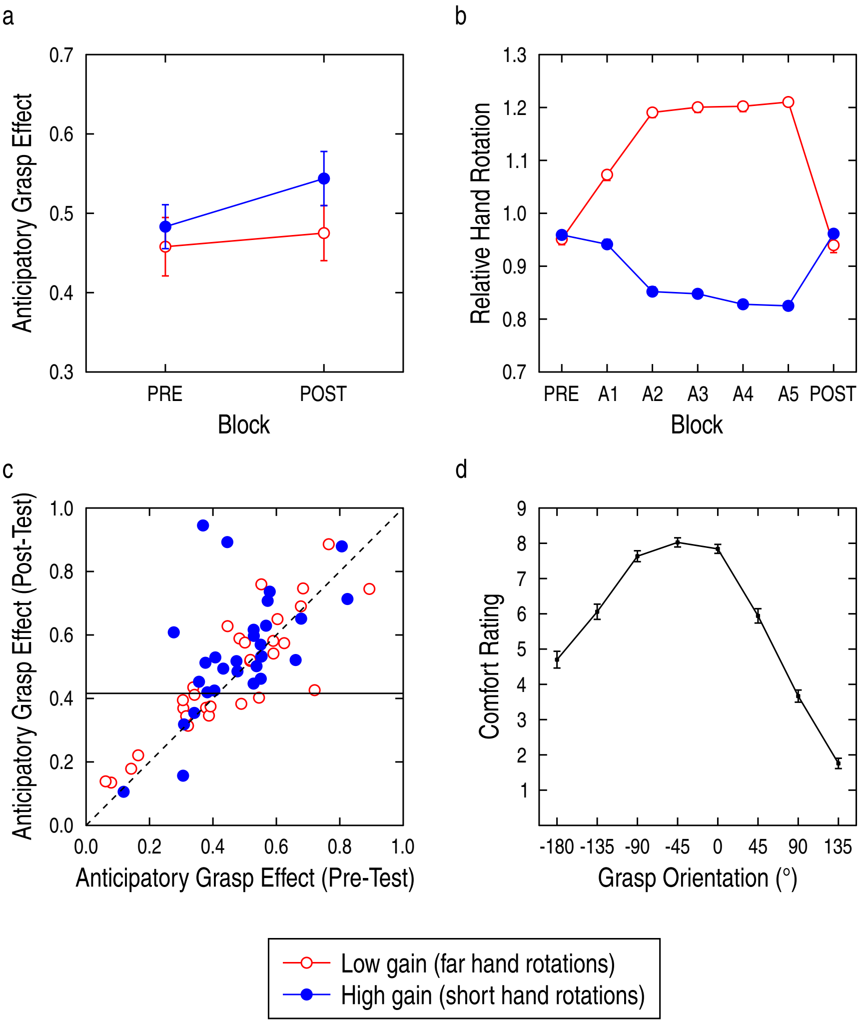


*Figure 4.* Results of Experiment 1. a) Anticipatory grasp effect (AGE) in the pre- and post-test for both gain conditions. b) Relative hand rotation (RHR) by block (A1-A4 = adaptation blocks 1-4) and gain condition c) AGE in pre-tests plotted against AGE in post-tests. d) Average comfort ratings for various arm postures. High values indicate a high level of comfort (9 = very comfortable, 1 = very uncomfortable). Error bars show 1 s.e.m. in all plots.

**Short Discussion**

In Experiment 1, we tested whether the modification of an internal model that translates object movements into body movements affects grasp selections. No such effects were observed. Descriptively the effect was even reversed: Larger expected hand rotations (low gain) resulted in a descriptively smaller adjustment of the grasp to the instructed dial rotation (AGE) in the post-test. Manipulation checks showed that the gain manipulation affected the required hand movements as intended, that the necessity to select specific grasps in the pre-test did not clamp grasp selections in the post-test, and that even small changes in arm posture result in substantial changes in subjective comfort. Together, these findings suggest that manipulating the internal model – and thus subsequent simulations of the object manipulation action – did not affect grasp selections in a meaningful way.

## Experiment 2

Experiment 1 provided evidence against the simulation hypothesis. However, the re-exposure to the gain of 1.0 in the post-test block could have led to a rapid recalibration of the internal model in Experiment 1. If this was the case, no measurable differences between the different gain groups could be expected (Experiment 4 eventually showed that this was not the case). In Experiment 2, we aimed to rule out this possibility by introducing a condition that aimed at measuring grasp selections without providing feedback from the object manipulation. In this additional condition, participants were asked to grasp the dial for rotation to a specific target without actually executing the rotation. We expected that grasp selections in this condition are correlated with grasp selections for actual dial rotations, because also prospective judgments of grasp selections for object manipulation have been found to be closely correlated to grasp selection for actual object manipulations (Zimmermann, Meulenbroek, de Lange, 2012). Note that we learned from Experiment 4 that contrary to our expectations this task may not be sensitive to the gain manipulation and that the results of the new *grasp-only* blocks should hence be viewed with caution. As we included this condition in the following experiments (and as the regular dial rotation blocks, which were also administered in the following experiments, will be shown to be informative by Experiment 4), we nevertheless report the data. Additionally, we switched from a between-participant to a within-participant design.

## Method

### Participants

Thirty-two volunteers from the Würzburg area participated for payment (14€) or course credit after signing informed consent (10 men, 22 women, mean age = 25). According to the handedness scale of the LPI, 30 were right-handed and two showed no hand preference.

We again used a simulation (Appendix A) to estimate the size of the interaction effect ($d_z = 3.3466$). As we had no good estimate for the within-participant variability in the grasp-only condition, we aimed for a power of $1-\beta = 0.95$ to detect an effect with a size of 25% of the expected value ($n = 21$). In case that not all participants could handle the grasp-only condition and to enable counterbalancing, 32 participants were collected in total.

### Stimulus, apparatus and Procedure

Stimuli, apparatus and the procedures in dial rotation trials and virtual rotation trials were identical to Experiment 1. In grasp-only trials (Figure 3c), the procedure was identical to the dial rotation trials, up to the point where the pointer rotation target was displayed. After target onset, participants grasped but did not rotate it. Once the longitudinal component of the hand position was within 1 cm of the dial and once the velocity of this component remained under 15cm/s for 750 ms, a click was played. After that, participants moved their hand back to the start block and the next trial was initiated. Participants were instructed to imagine that they wanted to rotate the dial to the target, grasp the dial, and hold it until the click sound without rotating it. They were further instructed to grasp the dial firmly with the stretched right arm, to imagine that they should not release the dial during rotation, and to move at a comfortable speed. Each grasp-only block and each dial-rotation block consisted of eight subblocks, in which the different target angles (-135°, -90°, -45°, 45°, 90°, 135°) were presented in random order.

Participants were invited to two experimental sessions, which were separated by at least seven days. On one session, participants were exposed to the high gain condition, in the other session, participants were exposed to the low gain condition. Which condition was presented first was counterbalanced and randomized over participants. The block order is depicted in Figure 2e.

### Data Analysis

Trials were excluded from the analysis, when the motion tracker data could not be segmented (0.01%) or when participants took more than 10 s to complete the task (0.4%). Moreover, six participants did not show a positive correlation between the grasp orientations in the dial rotation and grasp-only task in the pre-test of at least one session. These participants were excluded from the analysis of the grasp-only trials. For the remaining participants, the average correlations between grasps orientations in both conditions was .981 ($SD$ = .023).

## Results and Discussion

Figure 5 shows the results. A repeated measures ANOVA on the mean AGE in the dial rotation trials with within-participant factors of block (pre vs. post) and of gain (low vs. high) revealed the following results. The AGE increased from the pre-test to the post-test, $F(1,31) = 10.582$, $p = .003$, $\eta^2_p = .254$. The AGE was marginally higher in the low gain condition, $F(1,31) = 3.810$, $p = .060$, $\eta^2_p = .109$. Again, there was no significant interaction, $F(1,31) = 0.967$, $p = .333$, $\eta^2_p = .030$. A similar ANOVA on the AGE in grasp-only trials revealed no significant effect of block, $F(1,25) = 0.256$, $p = .618$, $\eta^2_p = .010$. The AGE tended to be generally higher in the low gain condition, $F(1,25) = 3.988$, $p = .057$, $\eta^2_p = .138$. Again, there was no significant interaction, $F(1,25) = 2.042$, $p = .165$, $\eta^2_p = .076$. An analysis of the initial grasp orientations revealed the same pattern of results (ESM1).

As expected RHR was larger in the low gain group from the first adaptation block on, all $t(31)\text{s} \geq 9.121$, all $ps \leq .001$, all $d_z \geq 1.612$. In the final adaptation block, the ratio between the RHRs of the hand rotations in the low gain and high gain condition was 1.43.

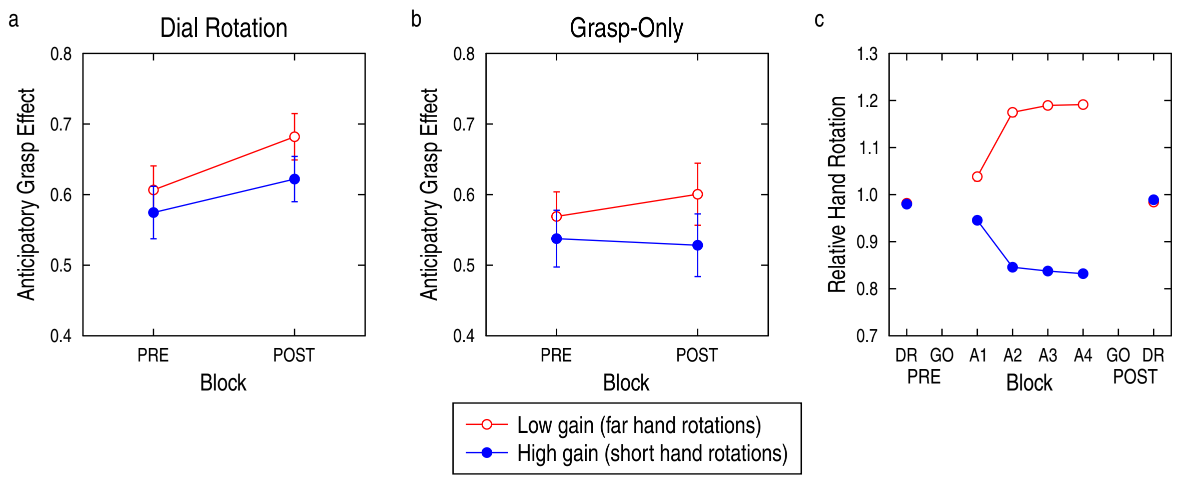


*Figure 5.* Results of Experiment 2. a) AGE in the dial rotation pre- and post-test by gain conditions. b) AGE in the grasp-only pre- and post-test by gain conditions. c) RHR over the course of the experiment. DR = Dial rotation, GO = Grasp Only, A1 … A4 = adaptation block 1 … 4. Error bars show 1 s.e.m. in all plots.

Experiment 2 replicated Experiment 1. Even though participants had to rotate the arm 43% further in the low gain condition than in the high gain condition to realize a given pointer movement, this did not affect grasp selections. In addition to the actual rotation condition, we asked participants to grasp the dial without rotating it. Thus, participants had to execute several grasps without the possibility to recalibrate the mapping from pointer movement to hand movement. Also, in this condition, the adaptation of the internal model did not affect grasp selections. However, we refrain from making strong inferences from this null-effect as we could not validate this task with Experiment 4.

## Experiment 3

It might have been possible that the differences in the hand rotations required in the low and high gain conditions of Experiments 1 and 2 were too small to affect grasp selections in a meaningful way. Hence, in Experiment 3 we increased the gain difference. Now participants had to rotate their hands in the low gain condition twice as far as in the high gain condition. Additionally, we introduced two warm-up blocks before the pre-test to give participants more time to adapt to the experiment.

### Method

#### Participants

Twenty-one participants from the Würzburg area participated for payment (14€) or course credit after signing informed consent (7 men, 14 women, mean age = 28). According to the handedness scale of the LPI, 20 were right-handed and one showed no hand preference.

We estimated the effects of the interaction between block and gain for the dial rotation condition ($d_z = 2.208$) and the grasp-only condition ($d_z = 2.420$, see Appendix A). To detect an effect size that is 50% that of the lower value with a power of $1\text{-}\beta = 0.95$, a sample size of 13 is necessary. To allow for the exclusion of participants that show low correlation between dial rotation and grasp-only trials from the analysis of the grasp-only condition, we collected 21 participants.

#### Stimulus, apparatus and Procedure

Stimuli, apparatus and the procedures in dial rotation trials, grasp-only trials, and virtual rotation trials were identical to Experiment 2, with the following exceptions. First, to increase the magnitude of possible effects, the low gain was reduced to 0.707 and the high gain was increased to 1.414. Thus, in the low gain condition, the hand rotation had to be twice as far as in the high gain condition to accomplish the same pointer rotation. Second, we included two warm-up blocks to give participants time to accommodate to the experiment before the pre-test was administered. The warm-up blocks were identical to the pre- and post-test dial rotation blocks but not analyzed. Figure 2e shows the block sequence in each session.

### Data Analysis

Trials were excluded from the analysis, when the motion tracker data could not be segmented (0.1%) or when participants took more than 10 s to complete the task (0.4%). Moreover, three participants did not show a high, positive correlation ($r < .2$) between the grasp orientations in the dial rotation and grasp-only task in the pre-test of at least one session. These participants were excluded from the analysis of the grasp-only trials. For the remaining participants, the average correlations between grasps orientations in both conditions was .961 (SD = .053).

## Results and Discussion

Figure 6 shows the results of Experiment 3. A repeated measures ANOVA on the mean AGE in the dial rotation trials with within-participant factors of block (pre vs. post) and of gain revealed the following results. The AGE did not change significantly from pre- to post-test, $F(1,20) = 1.908$, $p = .182$, $\eta^2_p = .087$, neither was it affected by the gain, $F(1,20) = 0.011$, $p = .917$, $\eta^2_p = .001$. There was no significant interaction, $F(1,20) = 0.756$, $p = .395$, $\eta^2_p = .036$. A similar ANOVA on the AGE in grasp-only trials revealed no significant effect of block, $F(1,17) = 0.253$, $p = .621$, $\eta^2_p = .015$, or gain, $F(1,17) = 1.449$, $p = .245$, $\eta^2_p = .079$. There was a marginal interaction, $F(1,17) = 3.895$, $p = .065$, $\eta^2_p = .186$. The AGE of the low gain condition tended to increase while the gain of the high gain condition decreased, as predicted by the simulation hypothesis. An analysis of the initial grasp orientations revealed a comparable pattern of results (ESM1).

Again, RHR was larger in the low gain group from the first adaptation block on, all $t(20)\text{s} \geq 12.439$, all $ps \leq .001$, all $d_z \geq 2.714$. Participants had to rotate their hands on average 1.87 times further in the low gain condition than in the high gain condition in the final adaptation block. Nevertheless, grasp selections did not reflect these differences. However, there was a small tendency toward the expected interaction, but only in the grasp-only trials. In summary, Experiment 3 replicated Experiments 1 and 2.

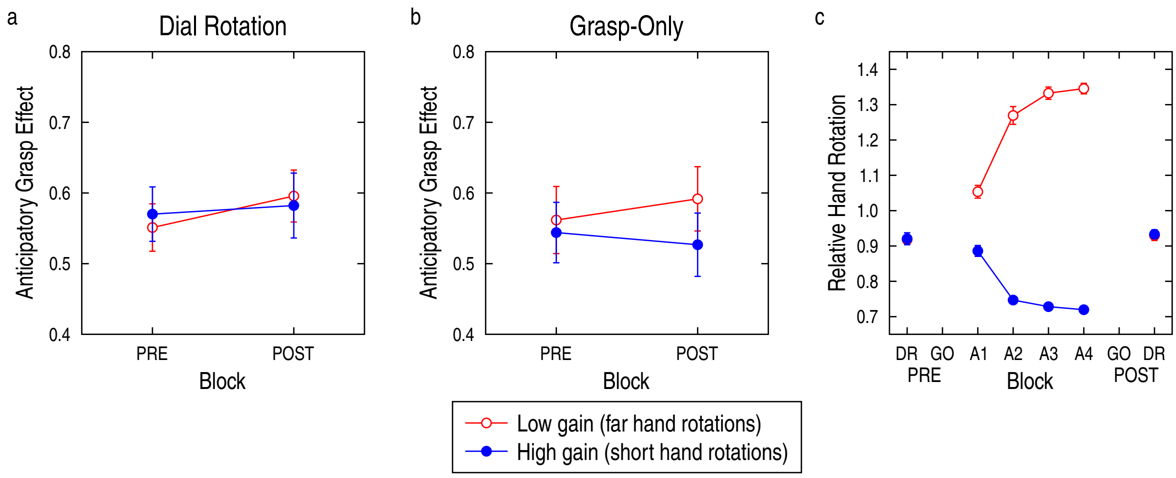


*Figure 6.* Results of Experiment 3. a) AGE in the dial rotation pre- and post-test by gain conditions. b) AGE in the grasp-only pre- and post-test by gain conditions. c) RHR over the course of the experiment. DR = Dial rotation, GO = Grasp Only, A1 … A4 = adaptation block 1 … 4. Error bars show 1 s.e.m. in all plots.

## Experiment 4

Experiment 1-3 revealed that the gain manipulation during adaptation blocks did not affect grasp selections. These experiments departed from the assumption that a) the manipulation of the gain would affect the AGE and b) that the adaptation to the high or low gain would be preserved long enough in the post-test to reveal an effect of the gain on AGE. If these assumptions turned out as incorrect, no effect of the gain on the AGE should have been expected in Experiments 1-3 in the first place. Experiment 4 asserts the validity of these assumptions. In Experiment 4, we replaced the virtual rotations in the adaptation blocks by trials with actual dial rotations and tested the effect of the gain manipulation on the AGE in post-tests. If the null effects of Experiments 1-3 resulted because the gain manipulation was not sufficient to evoke detectable changes in the AGE in post-test blocks then also adaptation to actual dial rotations should not affect the AGE in the post-test. On the other hand, if the above-mentioned assumptions were valid, an effect of the AGE on grasp selections can be expected. In this case, the null effect of Experiments 1-3 would speak against the simulation hypothesis.

## Method

### Participants

Eight women and four men from the Würzburg area participated after signing informed consent (mean age = 25, all right handed). They received a payment (14€) or course credit. We estimated the effects of the interaction between block and gain for the dial rotation condition ($d_z = 2.167$) and the grasp-only condition ($d_z = 2.760$, see Appendix A). We collected 12 participants, which allows to detect an interaction between gain and effect which is 50% of the size of the expected effect in dial rotation condition with a power of $1-\beta = .926$.

### Stimulus, apparatus and Procedure

Stimuli, apparatus and the procedures in dial rotation trials and grasp-only trials were identical to Experiment 3. The key difference between Experiment 3 and Experiment 4 are that the dial rotation task was performed in the adaptation blocks. The procedure of these dial rotations was identical to the pre- and post-test dial rotation trials, except that the relationship between dial position and pointer position was manipulated by a gain factor, which was ramped down (low-gain condition) to 0.707 or up (high-gain condition) to 1.414 in the first adaptation block. The targets of the rotations during the adaptation blocks were identical to Experiments 1-3. Before the pre-test dial-rotation block, a warm-up dial-rotation block was administered but not analyzed. Figure 2e shows the block sequence in each session.

### Data Analysis

Trials were excluded from the analysis, when the motion tracker data could not be segmented (0.2%) or when participants took more than 10 s to complete the task (0.02%). Moreover, two participants did not show positive correlations between the grasp orientations in the dial rotation and grasp-only task in the pre-test of at least one session and were thus excluded from the analysis of the grasp-only trials. For the remaining participants, the average correlations between grasps orientations in both conditions was .957 ($SD$ = .046).

## Results and Discussion

Figure 7 shows the results. A repeated measures ANOVA on the mean AGE in the dial-rotation trials with factors of block (pre vs. post) and of gain revealed the following results. The AGE did not change significantly from pre- to post-test, $F(1,11) = 3.349$, $p = .094$, $\eta^2_p = .233$. AGE was not affected by gain, $F(1,11) = 0.327$, $p = .579$, $\eta^2_p = .029$. Most importantly, there was a significant interaction, $F(1,11) = 21.905$, $p = .001$, $\eta^2_p = .666$. The AGE increased from pretest to posttest when participants had to rotate the arm further (low gain condition) and decreased when they had to rotate the arm less far (high gain condition) to hit a specific target.

An ANOVA on the AGE in grasp-only trials with factors block and gain revealed no significant effect of block, $F(1,9) = 0.651$, $p = .441$, $\eta^2_p = .067$, or gain, $F(1,9) = 0.414$, $p = .536$, $\eta^2_p = .044$. There was no significant interaction, $F(1,9) = 0.371$, $p = .558$, $\eta^2_p = .040$. A more detailed analysis of $GO_{init}$ yielded similar results (ESM1). Figure 7c shows that the AGE increased in the low gain condition, $t(11) = 3.910$, $p = .002$, $d_z = 1.129$, and decreased in the high gain condition, $t(11) = -2.322$, $p = .040$, $d_z = 0.670$. Paired sample t-tests revealed no difference between AGE in the first adaptation block, $t(11) = -0.258$, $p = .801$, $d_z = 0.074$, but all subsequent adaptation blocks, $t(11) \geq 3.686$, $p \leq .004$, $d_z \geq 1.064$. The difference also persisted in the post-test dial-rotation block, $t(11) = 2.967$, $p = .013$, $d_z = 0.856$.

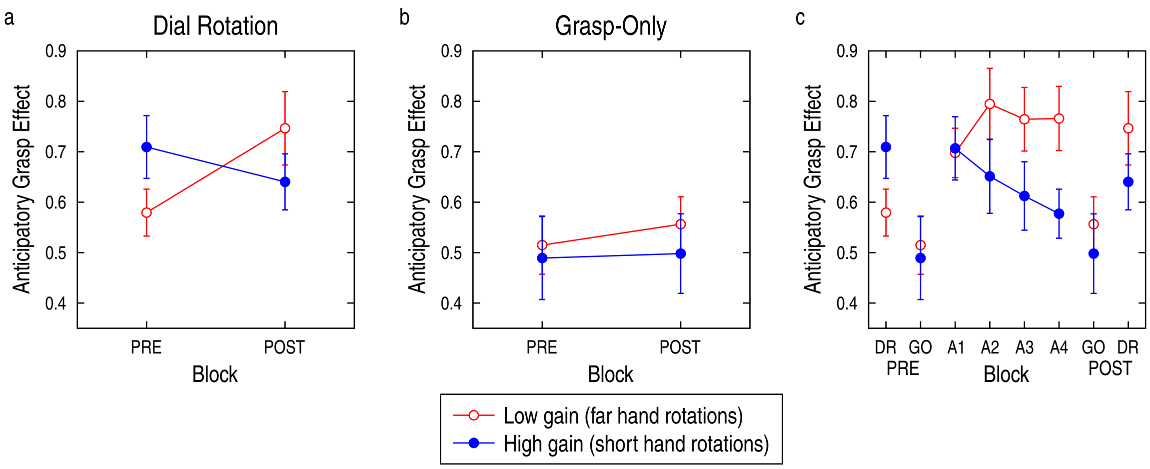


*Figure 7.* Results of Experiment 4. a) AGE in the dial rotation pre- and post-test by gain conditions. b) AGE in the grasp-only pre- and post-test by gain conditions. c) AGE over the course of the experiment, including the pre- and post-test blocks. DR = Dial rotation, GO = Grasp Only, A1 … A4 = adaptation block 1 … 4. Error bars show 1 s.e.m. in all plots.

Experiment 4 asserted that the adaptation to actually experienced gain changes clearly affects grasp selections and that this effect persists during subsequent post-test blocks, in which the gain is reset to 1.00. This corresponds to previous reports suggesting that task-dependent grasp selections are preserved even if the task changes (Herbort et al., 2017). Thus, if an internal model was involved in grasp selection for object manipulation and if this internal model was updated in the virtual rotation trials, an effect of the gain manipulation on the AGE should have been visible in the dial rotation post-tests of Experiments 1-3.

Unexpectedly, the grasp-only post-test was not affected by the gain manipulation. This implies that the null effects in the grasp-only block (but not in the dial rotation blocks) of Experiments 2 and 3 cannot be considered evidence against the simulation hypothesis. The insensitivity of the grasp-only task comes as a surprise for two reasons. First, grasp selections in the grasp-only pre-tests correlated highly with grasp selections in dial-rotation pre-tests in the vast majority of participants. Second, previous research has shown high correlations between prospective judgments of grasp selections and actual grasp selection (Johnson, 2000; Zimmermann et al., 2012). If participants are able to indicate how they would grasp an object for an object manipulation via key presses, one could have expected that they are also able to indicate this with an actual grasp. Obviously, this was not the case in the grasp-only trials. At the moment, we cannot provide an explanation for this insensitivity of the grasp-only measure.

## Experiment 5

We introduced the virtual rotation task to match the conditions of grasp planning and sensorimotor adaptation as far as possible. However, different internal models could be involved in the virtual rotation and the dial rotation task. If this was the case, no transfer of the adaptation to the different gains in virtual rotations to grasp selections in dial rotations could be expected. The primary goal of Experiment 5 was to rule out this possibility by assessing whether the gain manipulation in virtual rotations affects the extent of actual dial rotations. In the experiment, participants adapted to virtual rotations. In pre- and post-test blocks, they executed rotations both with and without feedback or knowledge of result (Figure 3d). If adaptation to virtual rotations carries over to actual dial rotations, we expect the following pattern of results: Participants rotate the actual dial further after adapting to low-gain virtual rotations and less far after adapting to high-gain virtual rotations when no online feedback about the pointer position is provided. If, however, both tasks are encoded in independent internal models, the gain manipulation in the virtual rotations cannot be expected to affect the extent of dial rotations.

A secondary goal of Experiment 5 was to test whether grasp selections in the dial rotation task would be affected when the virtual rotations allow the updating of direct links between object manipulations and grasps based on object manipulation outcomes. Hence, in Experiment 5, we did not require participants to select specific predetermined grasps in the virtual rotation task. As Experiments 1-3 did not reveal effects of the gain manipulation on grasp selections, any such effects in Experiment 5 can be attributed to the updating of direct associations between object manipulations and grasps.

## Method

### Participants

Nine women and three men from the Würzburg area participated after signing informed consent (mean age = 28, all right handed). They received a payment (14€) or course credit.

The effect size of the interaction between gain and block in the dial rotation trials was $d_z = 1.292$ in Experiment 4. If such an effect was driven by the anticipated extents of the hand rotations, a similar or larger effect size should be expected for the effect of the gain on the extent of dial rotations in open-loop trials. Hence, data of 12 participants were collected, which allow to detect effects ($d_z = 1.292$) with a power of $1\text{-}\beta = .982$.

### Stimulus, apparatus and Procedure

Experiment 5 was comparable to Experiment 3 with the following changes. First, the grasp-only blocks were replaced by open-loop dial rotation blocks (Figure 3d). As in Experiment 3, (closed-loop) dial rotation blocks were administered at the beginning and the end of each session. The procedure of open-loop dial-rotation trials were identical to the closed-loop dial-rotation trials in the other experiments. However, upon presentation of the target, the pointer was extinguished. Moreover, participants indicated the end of the dial rotation by pressing the button with the left hand. No feedback of the final pointer position was provided. The structure of the open-loop dial rotation blocks were identical to the pre- and post-test dial-rotation blocks (i.e. eight rotations to each of the target angles -135°, -90°, -45°, 45°, 90°, 135°). For these trials, $GO_{end}$ was extracted when the button was pressed. Figure 2e shows the block sequence of Experiment 5.

Second, participants were not required any more to assume specific hand orientations before beginning the virtual rotations. Hence, the hand-position indicator stimulus was replaced by two circles, with a fixed dark blue circle in the center of the tick mark circle indicating the target hand position and a light blue circle, which moved and changed size contingent on the participants hand movement.

### Data Analysis

Trials were excluded from the analysis, when the motion tracker data could not be segmented (0.01%) or when participants took more than 10 s to complete the task (0.4%).

## Results

A repeated measures ANOVA on the mean AGE in the closed-loop dial rotation trials with factors of block (pre vs. post) and of gain revealed the following results (Figure 8a). The AGE did not change significantly from pre- to post-test, $F(1,11) = 0.055$, $p = .819$, $\eta^2_p = .005$, neither was it affected by the gain, $F(1,11) = 0.109$, $p = .747$, $\eta^2_p = .010$. There was no significant interaction, $F(1,11) = 0.220$, $p = .648$, $\eta^2_p = .020$. A similar ANOVA for the open-loop trials revealed no significant effects of block, $F(1,11) = 1.834$, $p = .203$, $\eta^2_p = .143$, of gain, $F(1,11) = 1.079$, $p = .321$, $\eta^2_p = .089$, or the interaction, $F(1,11) = 1.373$, $p = .266$, $\eta^2_p = .111$. A more detailed analysis of the initial grasp orientations confirmed these results (ESM1). Even though grasps got descriptively more excursed when adapting to the low gain, no significant differences between gains could be detected in any of the training blocks, all $t(11) \leq 2.050$, all $p$s $\geq .065$, all $d_z$s $\leq 0.592$.

To test whether the gains affected the extent of open-loop dial rotations, RHR of the pre- and post-test open-loop blocks was subjected to a repeated measures ANOVA with factors of block and of gain (Figure 8b). There was a marginal effect of block, $F(1,11) = 4.543$, $p = .056$, $\eta^2_p = .292$. The value of RHR was generally higher in the low gain condition, $F(1,11) = 10.396$, $p = .008$, $\eta^2_p = .486$. Most importantly, the effect of gain increased from the pre- to the post-test, $F(1,11) = 25.509$, $p < .001$, $\eta^2_p = .699$. Paired sample t-tests revealed higher RHR in the low-gain condition from the first adaptation block on, all $t(11) \geq 6.971$, $p$

≤ .001, $d_z \geq 2.012$. The difference also persisted in the post-test open-loop block, $t(11) = 8.017$, $p < .001$, $d_z = 2.314$.

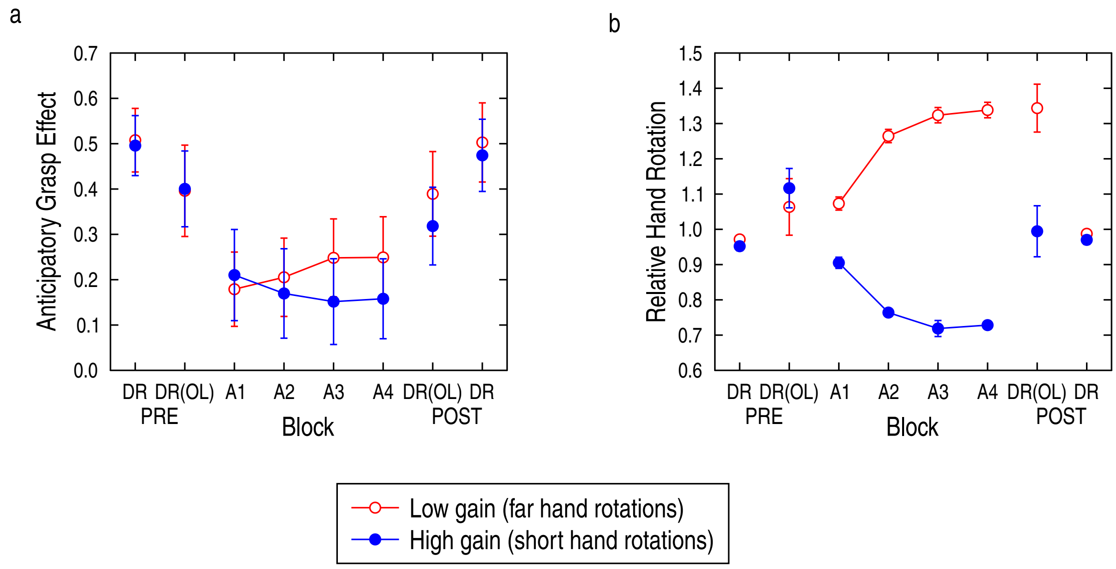


*Figure 8.* Results of Experiment 5. a) AGE by block and gain conditions. b) RHR by block and gain conditions. DR = Dial rotation, DR(OL) = Dial rotation (open-loop), A1 … A4 = adaptation block 1 … 4. Error bars show 1 s.e.m. in both plots.

The primary finding of Experiment 5 was that the adaptation to the gain in the virtual object rotation task did carry over to the dial rotation task. When participants had just experienced a low gain in the virtual rotation blocks they rotated the actual dial further when the pointer was not visible. When they just experienced high gain virtual rotations, they rotated the actual dial less far. This indicates that the internal model acquired during virtual rotations is also used to control actual dial rotations – in this case the extent of these dial rotations. Hence, the null effects of Experiments 1-3 cannot be attributed to distinct internal models for the virtual rotation and dial rotation task.

The secondary aim of the study was to test whether allowing the updating of direct object manipulation – grasp links based on object manipulation outcome affects grasp selections in the dial rotation task. Unfortunately, no significant effect of gain on grasp selections emerged during the virtual rotations (although a numerical trend can be seen in 8a).

Consequently, no effect of the gain manipulation on grasp selections could be expected in the dial rotation task.

An unexpected finding was that the AGE was rather low in the virtual rotation blocks, somewhat higher in the open loop dial rotations and highest in the actual dial rotations.[2] These differences may have emerged because grasp selections lead to comfortable arm postures in the phase of the movement with the highest control requirements (Künzell et al., 2013; Rosenbaum et al., 1996). Participants may have found it more difficult to move their hand to the start position of the virtual rotation than to actually grasp the dial. Hence, they may have deviated slightly from a preferred posture when assuming the start position for the virtual rotations, which then results in a low AGE. In the actual dial rotations, the control requirements at the end of the movement were presumably lower in the open-loop trials because precise corrections at the end of the movement were neither necessary nor possible. For this reason, the AGE in open-loop trials might have been lower than in the dial rotations with continuous feedback.

**Between Experiment Comparison**

Finally, we tested whether the interaction between block and gain in the dial rotation task was larger in Experiment 4, in which the adaptation was realized with actual dial rotations, than in the other experiments. To this end, we computed the interaction effects of the AGE between block and gain for each experiment.[3] Two interaction effects were computed. One was based on all trials of the pre- and post-tests and corresponds to the values reported so far. To check for possible effects of a rapid re-adaptation of the AGE during post-

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[2] This trend was confirmed post-hoc by paired t-tests comparing the average AGE of all adaption blocks with the average AGE of all open-loop dial rotation blocks, $t(11) = 4.835$, $p = .001$ and a likewise comparison of open-loop dial rotation blocks with closed-loop dial rotation blocks, $t(11) = 3.434$, $p = .006$.

[3] The interaction effect was computed as follows: $IA = (AGE_{low,post} - AGE_{low,pre}) - (AGE_{high,post} - AGE_{high,pre})$.

tests, we computed another interaction effect based on the last six trials of the pre-test and the first six trials of the post-text.[4] Each of these six trials included rotations to all possible targets. Figure 9 shows the size of the interactions (the simulation hypothesis predicts positive values).

The interaction computed from all pre- and post-test trials differed between Experiments 2 and 4, $t(42) = 3.742$, $p = .001$, $d_s = 1.267$, between Experiments 3 and 4, $t(31) = 3.270$, $p = .003$, $d_s = 1.183$, and between Experiments 4 and 5 (closed-loop condition), $t(22) = 3.571$, $p = .002$, $d_s = 1.458$. The interaction of the open-loop condition of Experiment 5 was marginally smaller than that of Experiment 4, $t(22) = 1.969$, $p = .062$, $d_s = 0.804$. The interaction computed from the last pre-test and first post-test trials differed between Experiments 2 and 4, $t(42) = 3.227$, $p = .002$, $d_s = 1.091$, between Experiments 3 and 4, $t(31) = 2.737$, $p = .010$, $d_s = 0.990$, and between Experiments 4 and 5 (closed-loop condition), $t(22) = 2.951$, $p = .007$, $d_s = 1.205$. The interaction of the open-loop condition of Experiment 5 did not differ significantly from the interaction of Experiment 4, $t(22) = 1.607$, $p = .122$, $d_s = 0.656$.

Finally, we tested whether a significant gain x block interaction emerges by pooling the interactions effects of the AGEs of the dial rotation blocks of Experiments 2 and 3. This was neither the case for the interaction of the AGE based on all trials, $t(52) = 1.326$, $p = .191$, $d_z = 0.182$, nor for the AGE interaction computed from the last pre-test and first post-test trials, $t(52) = 0.460$, $p = .647$, $d_z = 0.063$. The pooled data allowed to detect medium effect sizes ($d_z = 0.505$) with a power of $1-\beta = 0.95$ ($\alpha = .05$).

In summary, we did not find any effect of the adaptation to different gains with the virtual rotation task on grasp orientations. Thus, any effects of simulation-based grasp planning were considerably smaller than the effect of adapting to the gain with an actual dial

[4] We thank a reviewer for suggesting this analysis.

rotation task, in which adaptation of the AGE could be alternatively explained by the updating of direct associations. The largest effect was observed in the open-loop trials of Experiment 5. As participants could freely adjust their grasps during the adaptation phase (a constraint imposed to hinder the updating of direct associations between object manipulations and grasps) as in Experiment 4, this effect cannot be exclusively attributed to the simulation hypothesis. The interaction effects in experiments that suppressed the updating of such direct associations were considerably smaller.

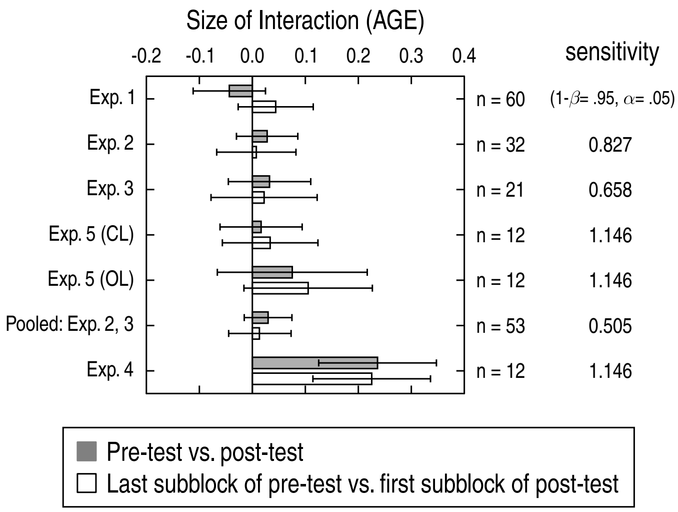


*Figure 9.* Interaction effects (block x gain) of AGE and sensitivity of Experiments 1-5. Error bars show 95% CIs.

## General Discussion

When someone grasps an object, the grasp usually depends on the intended object manipulation. For example, before turning a dial clockwise, the hand is moved to a relatively counter-clockwise orientation for grasping and vice versa. In five experiments, we addressed whether such adaptations of the grasp to planned object manipulations are affected by the anticipation of the bodily movements required to implement the object manipulation (e.g., Johnson, 2000). If this was the case, a selective manipulation of the internal model that maps object movements onto body movements should affect the anticipated body movements and hence grasp selections. In Experiments 1-3, we used a virtual rotation task to modify participants' internal models while preventing updating of direct associations between object manipulations and grasps, which typically also contribute to grasp selections. These experiments revealed no systematic effect of the gain manipulation on grasp selections. Experiment 4 showed that the gain manipulation can have a substantial effect on grasp selection for dial rotation and that this effect was preserved in subsequent post-tests, in which the dial-to-pointer gain was reset to 1.0. Experiment 5 showed that adaptation to gain manipulations during virtual rotations carried over to actual dial rotations. Hence, if the simulation hypothesis was correct, one could have expected that adaptations of the internal model to different gains was reflected in the grasp selections in our post-tests. However, this was not the case. Despite sufficient power, no significant effects of the gain manipulations could be found in Experiments 1-3. Even though the average effects pointed numerically in the right direction in Experiments 2-3, they were considerably lower than the effects that could have been expected from Experiment 4. The numerically largest effect of the adaptation to virtual rotations on grasp selections were observed in the open-loop trials of Experiment 5. However, Experiment 5 (as Experiment 4) did not suppress updating of direct associations between object manipulations and grasps and thus effects in this experiment do not provide critical support for the simulation hypothesis. In summary, the data do not support the simulation hypothesis.

**Relation to previous studies**

In general, the experiments replicate the findings that grasps are aligned to upcoming object manipulations (Rosenbaum et al., 1990, 2012). Throughout the dial-rotation trials of five experiments, consistently positive AGEs were observed. Thus, participants rotated the hand against the direction of the upcoming object manipulation before grasping the object.

AGE values typically flocked around .5 in the pre-tests, showing that the initial grasps compensated the upcoming object manipulation movement only partially. This can be described as a trade-off between the arm excursion or comfort between the initial- and end-state (cf., Herbort, 2015; Herbort & Butz, 2012; Lardy et al., 2012; Seegelke et al. 2015; van der Vaart, 1996). In summary, the data once more show that intended future actions are an important constraint on grasp selection.

Recent studies have reported correlation between the ability to adapt grasps to future actions and motor imagery (Fuelscher et al., 2016; Toussaint et al., 2013) or the ability to categorize the grasps by postural comfort (Stöckel et al., 2012). This correlation could be explained by a grasp planning process that involves a representation of the object manipulation movement. By contrast, the present study found no evidence for the involvement for such representations. Numerous differences between the previous studies and the current experiments could account for the discrepancies. Here, we want to offer one possible explanation. McCarty et al., (1999) proposed that during the development of grasp selection for tool-use actions, a "fully-planned" strategy is used at some point. This strategy allows children for the first time during development to consistently adjust their grasp task-dependently. Eventually, this strategy is replaced by a "habitual solution", which results in identical grasp selections but does not involve more elaborate planning processes during grasp selection. It is reasonable to assume that motor imagery may be related to the fully-planned strategy but not to the habitual strategy. The correlational studies focused on children, whose grasp selections may depend on whether or not they already reached the fully-planned stage. Hence, correlations between grasp selections and motor imagery may have emerged. By contrast, our experiments focused on adults, who have already transitioned to the habitual stage. Consequently, no evidence for an involvement of anticipated body movements in grasp planning could be found. However, there are certainly other ways to reconcile these findings and it might not be necessary that children actually move through a "fully-planned strategy" stage during development (van Swieten et al., 2010). Nevertheless, the data support McCarty et al., (1999) proposal that the development of grasp planning ultimately leads to a habitual strategy.

**Rapid re-adaptation and limited between-task transfer**

In the following, we address two potential caveats related to our procedure.[5] First, participants may have re-adapted their grasp to the gain of 1.0 in the post-tests of our experiments so rapidly that no effects could be detected. However, several observations speak against this possibility. First, the effects of the gain manipulation in Experiment 4 remained clearly detectable even when all pre-test and post-test trials were entered into the analysis. Second, the interaction effect computed from the last pre-test trials and the first post-test trials were comparable to the effects computed from all pre- and post-test trials. Third, adaptation of the AGE continued after the first block of the adaptation phase in Experiment 4 and 5. Hence, also re-adaptation can be expected to operate on a similar, relatively slow time-scale (c.f., Herbort et al. & 2017). In conclusion, although some degree of re-adaptation has to be (necessarily) expected in the post-tests, re-adaptation should be slow enough to allow the detection of effects of the gain manipulation.

Another concern may be that participants noted that the feedback in the virtual rotation task was not veridical and thus did not transfer their adaptations to the virtual rotation task to the actual rotations in post-tests. However, the following points speak against this possibility. First, we tried to hide the non-veridicality of the virtual rotation task. For example, the gain was set to 1.0 in the practice trials of the virtual rotation task and participants were encouraged to assert its veridicality. Then the gain was ramped up or down slowly. In Experiment 1, this procedure was successful: Only 17% of participant noted the non-

[5] We thank two reviewers for point out these potential caveats.

veridicality of the pointer movements in a post-experiment questionnaire and of those, only 50% correctly judged whether the gain was increased or decreased. Second, albeit 50% of the participants of Experiment 2 and 38% of participants of Experiment 3 correctly identified the session in which the gain was high or low, this did not influence the interaction effect. If anything, the interaction effect (and thus transfer between tasks) was higher for the participants who correctly identified the gain manipulation (see ESM1 for details). Third, Experiment 5 showed that adaptation to different gains in the virtual rotation task transferred to the extent of open-loop dial rotations but not to grasp selections. These considerations suggest that transfer from the virtual rotation task was possible. This notion is also in line with the finding that virtual training of sensorimotor skills transfers to real-world tasks (Gray, 2017; Rose et al., 2000; Tirp, Steingröver, Wattie, Baker, & Schorer, 2015).

**Methodological considerations**

We based the present experiments on the expectation that the virtual rotation procedure affects the mapping between dial rotations and body movements. One might object that the differences between the tasks may have prevented transfer from virtual rotations to physical dial rotations. However, even when identical tasks were employed in test and adaptation blocks, an updating of the mapping between dial and body movements would not have been guaranteed. For example, the continuous feedback from the manipulated dial might have limited the updating of an internal model (Bernier et al., 2005). For this reason, we aimed for conditions that facilitate the acquisition of internal models although this implied introducing differences between tasks. This approach seemed justified as the task differences did not hinder transfer between the virtual and physical dial rotation task as indicated by Experiment 5.

To prevent updating of direct associations between object manipulations and grasps, participants were required to use pre-determined grasps. We reasoned that this procedure prevents participants from discovering more suitable grasps for the different dial rotations once the gain had been manipulated. The pattern of results indicates that this method worked as expected. Participants did not change grasp selections in Experiments 1-3, suggesting that neither an internal model nor direct associations between object manipulations grasps were affected by the gain manipulation. Participants could freely select the grasp in Experiments 4 and 5. In Experiment 4, participants adapted the grasp to the different gains indicating updating of direct associations. In Experiment 5, only a numerical trend was found, which however can be attributed to high accuracy demands of the virtual grasps.

**Conclusion**

Finally, the question arises how grasps are adjusted to different object manipulations if grasp selection is not planned based on simulated body movements. An alternative mechanism could be direct associations between object manipulation tasks and the associated grasps, which are updated based on feedback from object manipulations (Herbort, Butz, & Kunde, 2014; Herbort et al., 2017). The role of such a mechanism has not been explicitly tested in the present series of experiments but it is at least in line with our findings. In Experiments 1-3, we specifically suppressed the exploration of the contingencies between grasps and object manipulation outcomes. In these experiments, no effects of the gain on grasp selections were found. In Experiment 4, exploration and updating of direct object manipulation-grasp associations was possible. Here adaptations of the grasps to the different gains were observed. This was also possible in Experiment 5, but the gain modulation did not lead to significant modulations of the grasp. Consequently, also no significant effects of gain on the AGE could have been expected in the post-test. These findings replicate previous research showing that experience of object manipulation outcomes is often a prerequisite for task-dependent grasp selection (Herbort, 2012; Künzell et al., 2013; Mathew, Kunde, & Herbort, 2017).

In summary, a series of five experiments provided no evidence for the hypothesis that simulations of planned object manipulation actions are involved in adult grasp planning in a common object manipulation task. Whether such simulations are invoked in other task or under other circumstances still needs to be elucidated.

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## Appendix A: Estimation of effect sizes

To estimate the size of the effect of the gain manipulation on the grasp selections – assuming that the anticipated hand rotation during the object manipulation determines grasp selection – it is necessary to know how the anticipated hand rotations translate into grasp choices. That is, we need a function *GO* = f(x), which takes a hand rotation extent *x* as input and returns a grasp orientation (*GO*). For simplicity, we assume that the pointer rotation and hand rotation are identical when the gain is not manipulated (i.e., gain = 1). This simplification is justified, because before introducing a gain, the values of RHR were close to 1. In the low or high gain (gains: 0.82; 1.22) conditions, we assume that participants select grasps orientations for specific targets *as if* they had to rotate the pointer further or less far, respectively, than actually necessary. For example, to rotate the pointer by 90° in the low gain condition, they select the grasp that they would use for a 110.2° (= 90°/0.82) rotation because they have to rotate the hand this far. In the high gain condition, they would use the grasp that they normally use for a 73.5° (=90°/1.22) rotation.

To predict the effect size of experiment 1, we used data from a previous experiment (Herbort, 2015, Exp. 1), in which twelve participants had to grasp and rotate a comparable dial to various angles (from ±5° to ± 270°).[6] For each participant, we constructed the following functions. The function $f_{pre}(x)$ and $f_{post}(x)$ results from the linear interpolation of the function from target angle to grasp orientations in blocks 1-3 and 8-10, respectively, of each individual participant of the earlier experiment. These function correspond to grasp selection in pre- and post-test. We used data of the first and last blocks to account for within-participant variability over the course of an experiment. To estimate the effect of the gains, we defined $f_{0.82} = f_{post}(x/0.82)$ and $f_{1.22} = f_{post}(x/1.22)$. Thus $f_{pre}$ represents grasp choices in the pre-test and $f_{0.82}$ and $f_{1.22}$ in the post-test after adaptation. These function were used to compute average grasp orientations for the target angles ±45, ±90, and ±135 and subsequently the AGE. Thus, for each participant *i* of the original study, we computed a pre-test $AGE_{i,pre}$, a post-test $AGE_{i,post,low}$ for the low gain condition and a post-test $AGE_{i,post,high}$ for the high gain condition. From these values, “virtual” data sets were constructed in which half of the participants were assigned to the low-gain group (with data points [‘low’, $AGE_{i,pre}$, $AGE_{i,post,low}$]) and half were assigned to the high gain group (with data points [‘high’, $AGE_{i,pre}$, $AGE_{i,post,high}$]). All 924 possible datasets were constructed and used to compute the effect size of the interaction between gain (low vs. high) and test phase (pre vs. post). The average $\eta^2_p$was .343 (*SD* = .183). The expected magnitude of the interaction was 0.211 (*SD* = 0.083).

Experiment 2 has a within-subject design. We used the above AGE values ($AGE_{i,pre}$, $AGE_{i,post,low}$, $AGE_{i,post,high}$) to simulate a within-subject experiment and compute the expected interaction values ([$AGE_{i,post,low}$ - $AGE_{i,pre}$] - [$AGE_{i,post,high}$ - $AGE_{i,pre}$]). The effect size of the expected interaction was $d_z = 3.346$. To compute the predicted effect size for Experiment 3, we conducted a similar analyses to estimate the expected numerical size of the interaction (0.353). We used the standard deviation of the interaction terms from Experiment 2 (dial

[6] The paper reports forearm orientations. Here we use the grasp orientations, which were recorded but not reported in Herbort (2015).

rotation: *SD* = 0.160, grasp-only: *SD* = 0.146) to derive the expected effect sizes (dial rotation: $d_z$ =2.208; grasp-only: $d_z$ = 2.420). For Experiment 4, we repeated the procedure but used the joint standard deviations of Experiments 2 and 3 (dial rotation: *SD* = 0.163, grasp-only: *SD* = 0.128). This results in expected effect sizes of $d_z$ = 2.167 (dial rotation) and $d_z$ = 2.760 (grasp-only).

**Electronic Supplemental Material to:**

**Grasp Planning for Object Manipulation without Simulation of the Object Manipulation Action**

**Oliver Herbort, Wladimir Kirsch, & Wilfried Kunde**

## Analysis by block, gain, and target angle

In the main manuscripts, the aggregate measures AGE and RHR were reported, which characterized the effect of the target angle on the initial grasp orientation (AGE) and the hand rotation during the object manipulation (RHR). In the supplemental material, grasp selections and hand rotations are reported as a function of the target orientation, gain, and block. Figures 1-5 report initial grasp orientations ($GO_{initial}$) for the different pre- and post-test blocks by target angle and gain. Figure 5 additionally reports the difference between the initial and final grasp orientation (*ΔGrasp Orientation* = $GO_{end} - GO_{initial}$) in the open-loop dial rotation trials of Experiment 5.

Tables 1 and 2 report the statistics of ANOVAS (Exp. 1: split-plot ANOVA, Exp. 2-4 repeated measures ANOVAS) on $GO_{initial}$ with factors of target angle (-135°, -90°, -45°, 45°, 90°, 135°), of block (pre- vs. post-test), and of gain (high vs. low). In these ANOVAs, two effects are of special interest. First, a main effect of target angle implies that participants adjust the grasp to different dial rotations (i.e. participants show the end-state comfort effect). This main effect was found in every experiment. Second, a significant three-way interaction implies that the gain manipulation affects how grasp selections change from pre-test to post-test. A significant effect is only found in Experiment 4 and rather low effect sizes a reported for all other experiments.

Table 3 reports a likewise repeated measures ANOVA on *ΔGrasp Orientation* in the open-loop dial rotation blocks of Experiment 4. The main effect of target angle shows that the extent of the hand rotation depended on the target angle, as expected. The three-way interaction verifies that the gain manipulation affected the change of the effect of target angle from pre- to post test: *ΔGrasp Orientations* in both gain conditions were similar in the pre-test but in the post-test, further rotations were executed in the low gain condition.

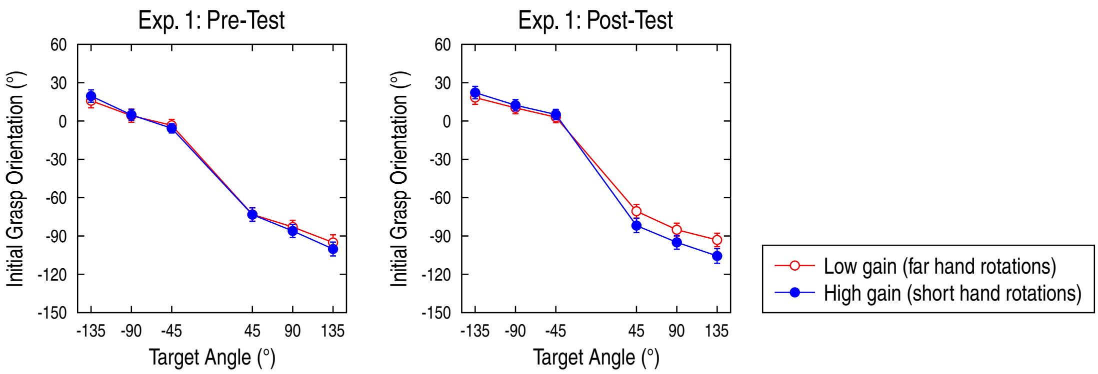

*Figure ESM1*. Effect of target angle on initial grasp orientation (GOinitial) by block and gain in Experiment 1. Error bars show 1 s.e.m.

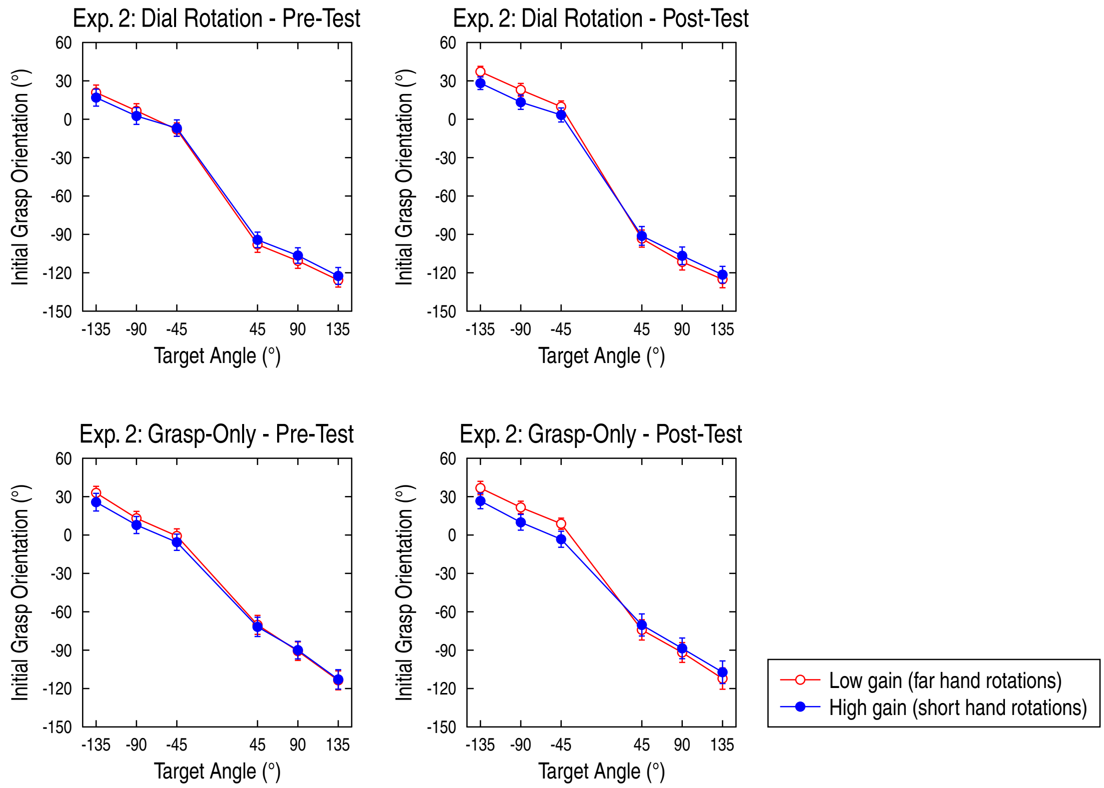


*Figure ESM2*. Effect of target angle on initial grasp orientation ($GO_{initial}$) by block and gain for the dial rotation and grasp-only blocks in Experiment 2. Error bars show 1 s.e.m.

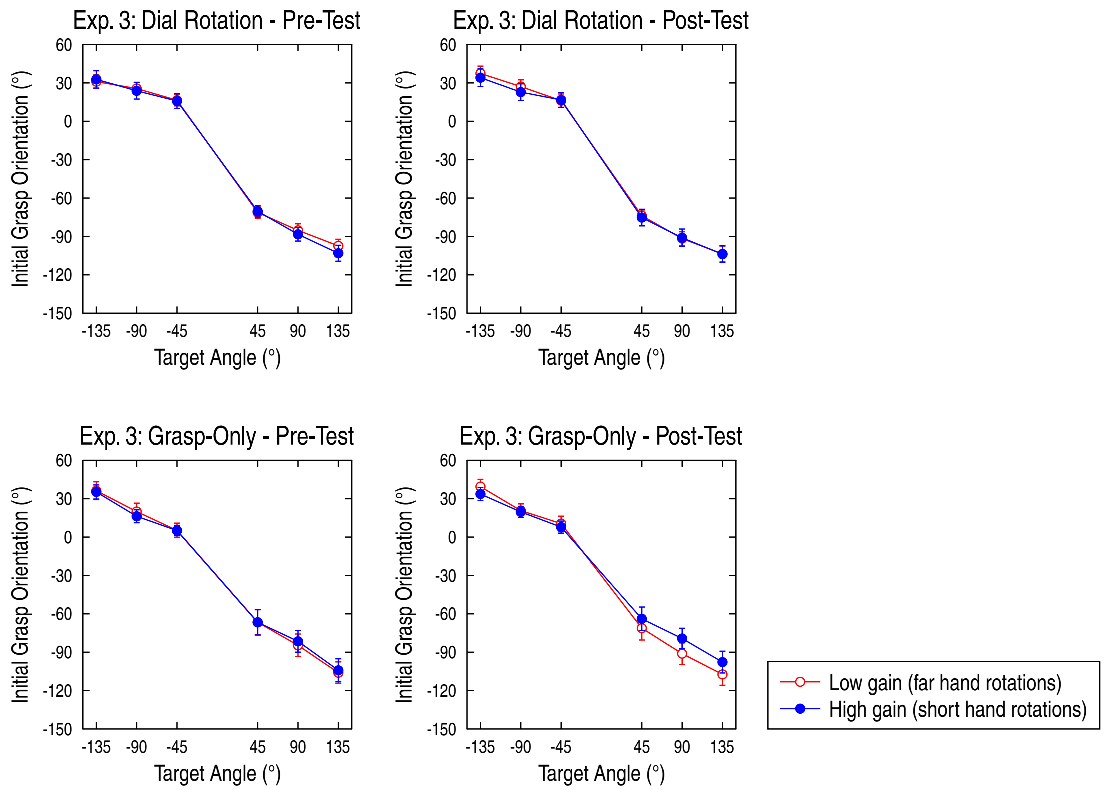

*Figure ESM3.* Effect of target angle on initial grasp orientation ($GO_{initial}$) by block and gain for the dial rotation and grasp-only blocks in Experiment 3. Error bars show 1 s.e.m.

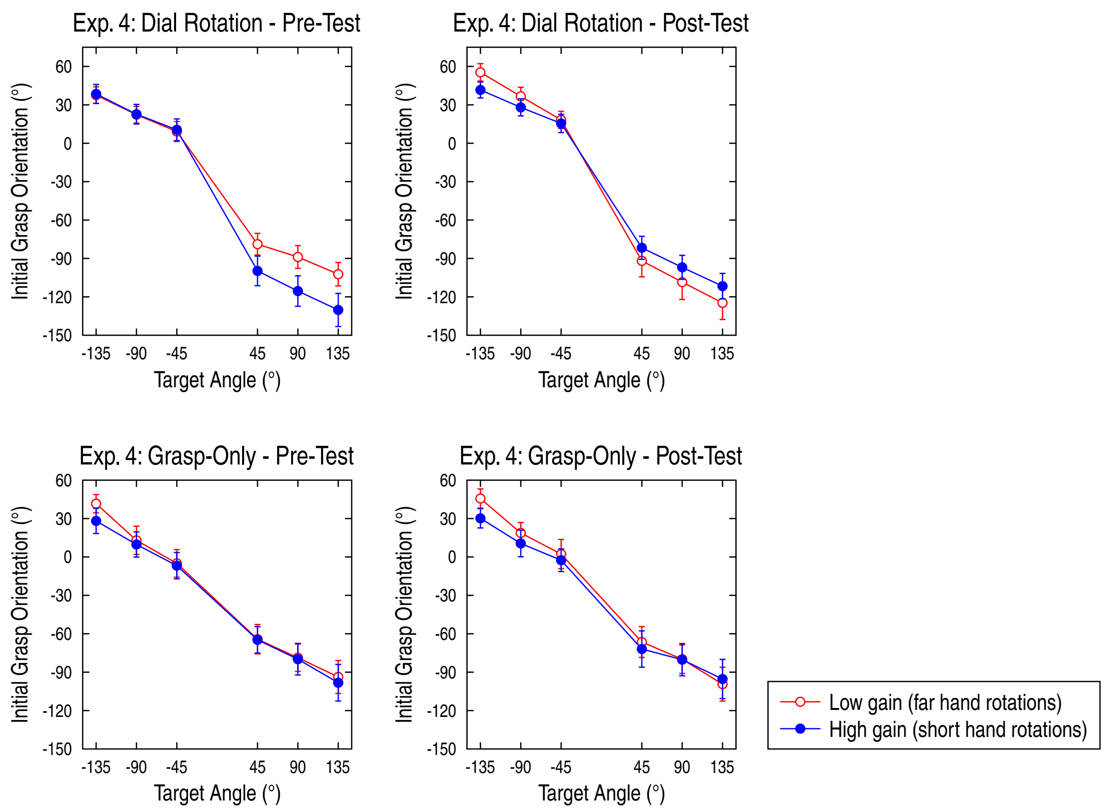


*Figure ESM4.* Effect of target angle on initial grasp orientation ($GO_{initial}$) by block and gain for the dial rotation and grasp-only blocks in Experiment 4. Error bars show 1 s.e.m.