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Habit Outweighs Planning in Grasp Selection for Object Manipulation

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Abstract

Object-directed grasping movements are adapted to intended interactions with an object. We address whether adjusting the grasp for object manipulation is controlled habitually, based on past experiences, or by goal-directed planning, based on an evaluation of the expected action outcomes. Therefore, we asked participants to grasp and rotate a dial. In such tasks, participants typically grasp the dial with an excursed, uncomfortable arm posture, which then allows to complete the dial rotation in a comfortable end-state. We extended this task by manipulating the contingency between the orientation of the grasp and the resulting end-state of the arm. A one-step (control) group rotated the dial to a single target. A two-step group rotated the dial to an initial target and then in the opposite direction. A three-step group rotated the dial to the initial target, then in the opposite direction, and then back to the initial target. During practice, the two-step and three-step groups reduced the excursion of their grasps, thus avoiding overly excursed arm postures after the second rotation. When the two-step and three-step groups were asked to execute one-step rotations, their grasps resembled those that were acquired during the two-step and three-step rotations, respectively. However, the carry-over was not complete. This suggests that adjusting grasps for forthcoming object manipulations is controlled by a mixture of habitual and goal-directed processes. In the present experiment, the former contributed approximately twice as much to grasp selection than the latter.

Keywords: planning, goal-directed processes, habitual processes, grasping, object manipulation

1. Introduction

When we plan an action, we often have subsequent actions in mind. This becomes evident as the way we execute initial actions depends on the actions that follow (Ansuini, Santello, Massaccesi, & Castiello, 2006; Cohen & Rosenbaum, 2004; Gentilucci, Negrotti, & Gangitano, 1997; Marteniuk, Mackenzie, Jeannerod, Athenes & Dugas, 1987; Rosenbaum et al., 1990; Sartori, Straulino, & Castiello, 2011). Such anticipatory behavior is particularly important for grasping a to-be-manipulated object because most object manipulations are best executed with a particular grasp. For example, a person who wants to rotate a door-knob in a clockwise direction will rotate the arm counterclockwise before grasping it and vice versa. This maintains the arm posture in a neutral medial range during the object manipulation and increases its' speed and accuracy (Herbort, 2015; Rosenbaum, van Heugten, & Caldwell, 1996; Short & Cauraugh, 1999).

Before an object can be grasped, the grasping movement must be planned. This process includes several aspects, such as specifying the direction of the movement, shaping the fingers, or determining the force with which the object will be grasped. Here, we focus on the following specific – but central – aspect of this planning process: selecting how to place the fingers on an object based on the intended object manipulation (“grasp selection for object manipulation”). Although grasp selection for object manipulation has extensively been studied (for recent reviews, see Rosenbaum, Chapman, Weigelt, Weiss, & van der Wel, 2012; Wunsch, Henning, Aschersleben, & Weigelt, 2013), little is known about the underlying mechanisms. There are two different perspectives that correspond to a dichotomy between goal-directed and habitual action selection (Dickinson, 1985; Dolan & Dayan, 2013). According to one approach, grasp selection for object manipulation is primarily a goal-directed planning process that is based on the anticipated action outcomes (Cohen & Rosenbaum, 2004; Johnson, 2000; Wunsch & Weigelt, 2016). This notion is goal-directed as

grasp selection depends on the expected consequences of a grasp (e.g., the resulting arm posture) and matching these consequences to an individual's motivations (e.g., assuming a comfortable posture). According to the other approach, grasp selection is primarily habitual and is based on learned object manipulation task – grasp associations (Herbort, Butz, & Kunde, 2014; van Swieten et al., 2010). This is habitual because it assumes that grasps are selected because they proved useful in the past for manipulating objects in comparable ways, regardless of the expected requirements for the upcoming task. However, there is no compelling evidence for either perspective. In the remainder of the introduction, we present arguments for both views and outline the experimental procedure used to test between them.

1.1. Arguments in favor of the goal-directed view

According to the *goal-directed view* of grasp selection, anticipating the arm movement that is necessary to manipulate an object is used to select a grasp that allows for fast, accurate, or comfortable object manipulations (Cohen & Rosenbaum, 2004; Johnson, 2000; Stöckel, Hughes, & Schack, 2012; Wunsch & Weigelt, 2016). Thereby, the arm posture at the end of the object manipulation (end posture) and the arm posture when the object is grasped (initial posture) seem to play a pivotal role. Notably, this view includes the possibility that planning may only be necessary when a grasp is selected for a specific task for the first time. When a task is repeated, grasp selections may rely on recalling previous instances (Cohen & Rosenbaum, 2004; Weigelt, Cohen, & Rosenbaum, 2007).

There are mainly two observations that support the goal-directed view; however, they are not conclusive per se. First, at least some of the cognitive requisites for selecting grasps based on anticipated end postures are met. For example, to plan grasps that are based on the resulting end-states, it is necessary to prospectively predict and evaluate the possible end-states. Indeed, participants can mentally simulate object manipulations (Seegelke & Hughes, 2015). Likewise, participants can predict the subjective “awkwardness” of the arm postures

(Johnson, 2000), which are a key determinant of grasp selection (Rosenbaum et al., 1992). Moreover, movement end postures appear to be represented prior to the onset of movement. For example, prospective judgments of how an object could be grasped for rotation were faster when the participant's actual arm posture was congruent to the arm posture at the end of the object manipulation (Zimmermann, Meulenbroek, & de Lange, 2012). Finally, the ability to discriminate between visual images of comfortable and awkward postures is correlated with the ability to adapt grasps for different object manipulations (Stöckel, Hughes, & Schack, 2012). However, the representation of the end postures does not imply that this information is processed during planning or that planning occurs at all (Johnson, 2000). These representations could be the result, rather than the cause, of action selection (Blakemore et al., 2002; Ziessler & Nattkemper, 2011).

Second, grasp selection often depends on the intended object manipulation from the very first trial on which the task is performed (e.g., Rosenbaum et al., 1990; Cohen & Rosenbaum, 2004). As there is no opportunity for learning, these experiment suggests that grasps are planned in goal-directed fashion (Cohen & Rosenbaum, 2004). However, because most experimental tasks are inspired by everyday actions (Rosenbaum et al., 2012), participants may have reused the task-grasp associations that were learned during daily object manipulations. In fact, in less common tasks, participants made little to no grasp adjustments for different object manipulations on the very first trial(s) and only adjusted their grasps after gaining some experience with the task (Herbort, 2012; Künzell et al., 2013).

1.2. Arguments in favor of the habitual view

There are (at least) two ways that grasp selection could depend on habitual processes. First, specific grasps may be associated with different objects, regardless of the task. As such, specific grasps may not reflect the currently intended interaction with that object. For example, humans who are asked to manipulate everyday objects tend to select grasp points or grasp

orientations that correspond to the object's prevailing use, regardless of their current object manipulation goals (Creem & Proffitt, 2001; Herbort & Butz, 2011). Likewise, grasps tend to be conserved during repeated (identical) interaction with objects (Glover & Dixon, 2013; Rosenbaum & Jorgensen, 1992). In this case, habitual processing thwarts adjusting grasps to object manipulations to some extent.

Second, specific grasps may be associated with *specific* object manipulations (i.e., a combination of object and intended object manipulations). The present article focuses on this aspect, which we refer to as the *habitual view*. This view suggests that specific grasps are selected for specific object manipulations because they have previously been used successfully for similar object manipulations (Herbort, Butz, & Kunde, 2014; van Swieten et al., 2010). Hence, grasp selections may depend on intended object manipulations because participants recollect grasps that were previously the most suitable for manipulating an object in a specific way (and not because participants anticipate, for example, the end-states that resulted from possible grasps). According to this perspective, habitual processing is the primary cause of adjusting grasps to object manipulations.

This approach may be considered goal-oriented because it assumes a certain intended goal state prior to executing an action. However, it is habitual because it assumes that these goal states invoke “dumb” recollections of actions that were previously helpful for reaching the same end goal, rather than assuming “clever” planning processes that bridge current states and intended end states. Although it may appear counterintuitive, goal-directed control processes have been shown to trigger one or more actions that were under habitual control (Dayan, 2009; Dezfouli, & Balleine, 2013; Dezfouli, Lingawi & Balleine, 2014). For example, the goal-directed decision to cycle to the office or go to the supermarket will trigger different action sequences. However, the individual actions in the sequences (e.g., taking specific turns at intersections depending on the ultimate goal) might be driven by habit because the route

that is chosen is based on past experiences and not on the evaluation of the outcomes that are associated with each individual option. Likewise, the *habitual view* posits that the intent to conduct an object manipulation may trigger a specific habitually controlled grasp selection.

To our knowledge, there is no direct evidence for the habitual view, but these processes may theoretically account for anticipatory grasp selection. For example, one computational model of grasp selection for object manipulation in continuous tasks accurately explains the empirical data without predicting the potential action outcomes (Herbort, 2013; Herbort & Butz, 2012). Hence, goal-directed planning does not seem necessary to explain grasp selection for object manipulation.

1.3. Testing the goal-directed vs. the habitual approaches

In summary, it is not possible to determine how a grasp is selected when planning a grasping movement because there are no conclusive findings for the goal-directed or habitual approaches. Thus, in this article, we directly compare both approaches. We focus on the contributions of goal-directed or habitual processes on grasp selection, without claiming that other parts of movement planning will equally be habitual or goal-directed.

One way to test these hypotheses is to create a situation in which participants' expectancies about the consequences of selecting a specific grasp in the next trial differ from the actual consequences that were experienced in previous trials. If grasp selection is goal-directed, grasps should depend on the *expected* relationship between grasps and their consequences. That is, if participants know the changed relationship between the grasps and their consequences, they should immediately or quickly adapt their grasps to the changed consequences. In contrast, current grasps should depend on the consequences of *previous* grasp selections if they are under habitual control. That is, even when participants know the changed relationship between the grasps and their consequences, they should continue to use the grasps that were suitable in previous trials.

The present experiment is based on this rationale. We manipulated the consequences of grasp selection with a multi-step object manipulation task. Participants were asked to grasp a knob that was attached to a pointer, and rotate it to various targets (Figure 1a). Three independent groups of participants experienced different relationships between their grasp selections and action outcomes during *learning blocks*. In these blocks, the one-step group rotated the pointer to a target and then released the dial. The two-step group rotated the dial to a target and then immediately rotated the pointer to a target that was in the exact opposite position without releasing the dial between both rotation steps (two-step rotations; c.f. Figure 1b). Thus, grasps that resulted in a comfortable posture when reaching the first target ultimately resulted in an uncomfortable end posture. The three-step group rotated the dial to the target, then immediately to a target at the opposite position, and then immediately back to the position of the initial target (three-step rotations). Because each initial target was followed by a specific second (and third) target, the target sequences were fully predictable (c.f. Figure 1b). Importantly, participants benefit less from adapting their grasp to the initial rotation segment in the two-step and three-step rotations because a comfortable posture after the first (and third) rotation implies that there is an uncomfortable posture after the second rotation. Hence, it is expected that grasp selection will change during the learning blocks for the two- and three-step groups.

Although the three groups differed on the required learning block tasks, all participants executed one-step rotations from time to time in *transfer blocks*. The central question is how participants grasp the dial in the transfer blocks. If grasp selection is under habitual control, the grasps that were selected for rotation with a specific initial target in the preceding learning blocks should be used for one-step rotations with the same initial target in a subsequent transfer block. Because grasp selections are expected to differ between the one-step and the other groups in learning blocks, the habitual hypotheses suggest that grasp selections will also

differ between the groups in transfer blocks. In contrast, there should be no difference between grasp selections for learning trials and transfer trials in each group.

If grasp selection is goal-directed, the grasps that are selected for the one-step rotations in the transfer blocks should not differ between groups because the relationship between the grasps and their consequences are the same in the transfer blocks regardless of group. In contrast, the grasps that are selected for rotations with a specific initial target in the learning blocks should differ from the grasps for rotations with the same initial target in the transfer blocks for the two- and three-step groups. In the one-step group, the learning and transfer block trials do not differ; thus, there should be no differences.¹

Several measures were taken to ensure that goal-directed planning was possible in the transfer blocks, in which participants only executed one-step rotations. First, transfer trials were administered blockwise, and the type of block was announced prior to the start of the block (one-step vs. two-step vs. three-step). Hence, it is unlikely that participants did not register the task for the upcoming trial. Second, one-step rotations were used in transfer blocks because participants were expected to be most familiar with this task (and the data will suggest that this was the case). Thus, if participants engaged in goal-directed planning, they didn't have to acquire a new mapping between grasps and their consequences to be able to plan the critical transfer trials. Third, the two- and three-step rotations always contained the one-step rotation as the initial part of the overall object manipulation, which allowed

¹ Additionally, goal-directed planning could be indicated by higher reaction times for more complex object manipulations. However, because reaction times are prone to alternative explanations in the current context and participants were not asked to respond quickly, we focus on grasp selections as the primary dependent variable in the current experiment.

participants to maintain previously acquired knowledge from the one-step rotations during the learning blocks.

2. Method

2.1. Participants

Thirty participants were recruited from the Würzburg area and were tested after providing informed consent (22 females, 8 males, mean age 27 years, $sd = 7$). All participants were right-handed (Lateral Preference Inventory, Coren 1993).

2.2. Stimulus and Apparatus

Figure 1a shows the experimental layout. Participants were seated in front of a table, on which there was a start button and a dial. The start button (3 cm x 4 cm x 2.5 cm) was located between the participant and the dial (distance from dial: 35 cm). The dial consisted of a circular knob (diameter 8 cm) with an attached plastic pointer that protruded 14.5 cm from the dial's axis of rotation. Green LEDs (5 mm) were installed on a circular panel behind the knob. The LEDs were arranged on an imaginary circle (diameter 30 cm) that were located at 0° , $\pm 5^\circ$, $\pm 10^\circ$, $\pm 15^\circ$, $\pm 30^\circ$, $\pm 45^\circ$, $\pm 90^\circ$, and $\pm 135^\circ$ relative to the 12 o'clock position (not all LEDs were used in the current experiment). The knob and pointer were constantly pulled to the 12 o'clock position with a low torque. This allowed the pointer to reset after the participants released the knob and prevented participants from readjusting their grasps during rotation.

2.3. Procedure and Design

The trials differed in the numbers of targets that had to be reached (one-step, two-step, three-step trials) and the initial target (Figure 1b). The initial target could be located at -90° , -

45°, 45°, and 90°. The second target in the two- and three-step trials was always opposite from the first target, and the third target in the three-step trials was always identical to the first.

A trial started when the participant grasped the start button. Once the start button was held for 1 s, the target LED was lit and there was a short click (1760 Hz for 25 ms). When the target was not the last in the trial, it was considered hit when the pointer was within 2.5° of the target for 100 ms. Once this occurred, the current target LED switched off, the next target LED was lit, and there was another click. The final target was considered hit when the pointer remained within 2.5° of the target for 1000 ms. Once this occurred, the target LED flashed three times to indicate that the trial was successfully completed. Participants were instructed to always use their right hands, to firmly grasp the knob without readjusting their grasps and to release the knob once the trial was completed. Before the experiment, participants were informed about the different block types and the structure of the target sequences.

The central independent variables were the between-subject factor of learning group (one-step, two-step, three-step group) and the within-subject factor of block type (learning block, transfer block). In the learning blocks, the one-step group only performed one-step trials, the two-step group only two-step trials, and the three-step group only three-step trials. Each learning block consisted of 64 trials (16 repetitions for each target sequence). In the transfer blocks, participants in both groups only received one-step trials. Each transfer block consisted of 32 trials (8 repetitions for each target).

The data were collected in four experimental sessions that were separated by 1.4 days on average ($sd = 0.8$). Ten blocks were administered in each of the first three sessions. The 1st, 4th, 7th, and 10th blocks were transfer blocks, and the remaining blocks were learning blocks. The 4th session consisted of four transfer blocks that tested for longer lasting effects for the learning conditions and for extinguishing these effects. The blocks in each session were separated by short self-paced breaks in which participants remained seated.

Participants required an average of 50 minutes for each of the first three sessions (512 trials each) and 10 minutes for the fourth sessions (128 trials). At the beginning of each block, the illumination of one (at 0°), two (at $-5^\circ, 5^\circ$) or three (at $-5^\circ, 0^\circ, 5^\circ$) LEDs indicated whether the block consisted of one-step, two-step, or three-step trials. The trial order within the blocks and the assignment of participants to the different groups were random.

2.4. Data Recording and Analysis

Participant's arm movements were recorded with an electromagnetic motion tracker (Ascension trakSTAR, Ascension Technology Corp, Shelburne, VT, USA) at a sample rate of 100 Hz. Sensors were attached to the thumb and index finger nails, the forearm close to the wrist, and the dial axis. The data were smoothed with a bidirectional second order Butterworth filter that had a cut-off frequency of 20 Hz. The positions for the index finger and thumb sensors in the dial plane were used to compute grasp orientation (GO, Figure 1c). The 0° position was defined as a grasp, in which the index finger was directly above the thumb. A positive GO denotes pronations of the hand and forearm. The forearm sensor data was used to disambiguate finger configurations that could have resulted from either an extreme pronation or supination. The grasp orientation was extracted at the beginning of the first dial rotation segment, when the dial rotation rate first exceeded $10^\circ/\text{s}$. Except for two trials, in which data was not completely recorded, all trials were used in the analysis.

To simplify the analyses, we computed the *anticipatory grasp effect (AGE)* for each block and participant. The AGE is defined as the negative slope of the linear regression of GO on the initial target angle (Figure 1d). That is, AGE reflects the number of degrees that the GO is rotated against the direction of the initial dial rotation for each degree of the initial dial rotation. A value of 0 indicates that there are identical GOs regardless of the initial rotation angle. That is, participants do not show the end-state comfort effect. A value of 1 indicates that the GOs fully compensate the initial rotation. That is, GOs are selected that result in

identical postures after the initial rotation, regardless of their direction and extent. We used this simplification because we expected that learning group and block type affected the effects of the initial target angles on GO, but did not expect that these conditions would result in a general change in GO (i.e., generally more prone or supine grasps). The GOs are reported in supplemental Figure 1. Finally, as an indicator for differences in the grasp selection process, we also recorded reaction time (RT), which was defined as the interval between the onset of the first target LED and the release of the start button.

3. Results

3.1. Manipulation Check: The effect of the learning condition on AGE in the learning blocks

The experiment hinges on the assumption that grasp selections differ between groups in learning blocks after the learning occurs. This assumption is asserted as follows. The connected lines in Figure 2 show that the AGE did not change in the one-step group but decreased in the two- and three-step groups. A split-plot ANOVA² on AGE with the within-subject factor of learning block and the between-subject factor of learning group revealed a main effect for block, $F(17,459) = 3.55, p = .011, \eta^2_p = .116$, group, $F(2,27) = 11.76, p < .001, \eta^2_p = .466$, and an interaction between the two, $F(34,459) = 2.73, p = .011, \eta^2_p = .168$.

To examine the interaction, the one-step group was compared to each of the remaining groups with split-plot ANOVAs with a within-subject factor of learning block and a between-subject factor of learning group. The AGE for the one-step was generally larger than for the two-step group, $F(1,18) = 14.69, p = .001, \eta^2_p = .449$. This difference increased over blocks,

² We report Greenhouse-Geisser corrected p-values but uncorrected dfs.

$F(17,306) = 3.92, p = .010, \eta^2_p = .179$. Although two-sided t-tests ($\alpha = .05$) revealed no significant differences between the groups for the first two learning blocks, both groups differed for all remaining learning blocks. Likewise, the AGE for the one-step group was generally larger than for the three-step group, $F(1,18) = 13.56, p = .002, \eta^2_p = .430$. This difference also increased over blocks, $F(17,306) = 3.20, p = .018, \eta^2_p = .151$. Two-sided t-tests ($\alpha = .05$) revealed no significant differences between the groups for the first learning block with significant differences for all subsequent learning blocks. In summary, this manipulation check revealed that participants adapted their grasps to the requirements of the two-step or three-step rotations.

Finally, we examined whether there were group differences prior to the experiment. An ANOVA on the AGE in the first block with a between-subject factor of group did not have a significant effect, $F(2,27) = 1.92, p = .165, \eta^2_p = .125$.

3.2. The effect of the learning condition on AGE in the transfer blocks

First, we tested whether grasp selection in the transfer blocks differed between groups (as predicted by the habitual hypothesis and opposed by the goal-directed hypothesis). Figure 2 shows that the AGE in transfer blocks differed between groups. For this analysis, we averaged the AGE of the transfer blocks for the second and third sessions (Table 1). The average AGE of the transfer blocks was examined in a split-plot ANOVA with a between-subject factor of learning group and a within-subject factor of session (2, 3). The AGE differed between groups, $F(2,27) = 5.84, p = .008, \eta^2_p = .302$. There was no significant effect for session, $F(1,27) = 0.273, p = .606, \eta^2_p = .010$. Likewise, there was no significant interaction, $F(2,27) = 0.77, p = .474, \eta^2_p = .054$.

Post hoc ANOVAS revealed that the AGE in the transfer blocks was smaller for the two-step group than the one-step group, $F(1,187) = 6.55, p = .020, \eta^2_p = .267$. Neither session

($F[1,18] = 0.01, p = .914, \eta^2_p = .001$) nor the interaction was significant, $F(1,18) = 0.52, p = .479, \eta^2_p = .028$. A similar ANOVA that compared the one-step and three-step groups revealed that the AGE was smaller for the three-step group than the two-step group, $F(1,18) = 8.32, p = .010, \eta^2_p = .316$. Neither session ($F[1,18] = 0.07, p = .796, \eta^2_p = .004$) nor the interaction was significant, $F(1,18) = 0.30, p = .303, \eta^2_p = .059$. In summary, how participants grasped the dial for a one-step rotation in transfer block depended on the kind of rotation executed in learning blocks.

3.3. Comparisons of AGE in the learning conditions and transfer blocks

Second, we examined whether there were differences in the AGE for the transfer and learning blocks in the second and third sessions (as predicted by the goal-directed hypothesis and opposed by the habitual hypothesis). A split-plot ANOVA with within-subject factors of block type (learning vs. transfer) and session (2, 3) and a between-subject factor of learning group (one-, two-, three-step group) demonstrated the following results (Table 1 reports the means and standard deviations). The AGE was lower in the learning blocks than in the transfer blocks, ($F[1,27] = 18.68, p < .001, \eta^2_p = .409$). The AGE depended on the group, $F(2,27) = 9.58, p = .001, \eta^2_p = .415$. Importantly, there was an interaction between group and block type, $F(2,27) = 5.77, p = .008, \eta^2_p = .300$. There were no main effects for session or other interactions, all $ps \geq .583$.

The result was followed up within-subject ANOVAs with block type and session as factors for each individual group. Not surprisingly, the AGE for the one step group was not affected by block type, session, or their interaction, all $ps \geq .422$. In the two-step group, the AGE was smaller for the learning trials compared to the transfer trials, $F(1,9) = 8.51, p = .017, \eta^2_p = .486$. There was no significant effect for session ($p = .425$) and no significant interaction ($p = .909$). In the three-step group, the AGE was smaller for the learning trials compared to

the transfer trials, $F(1,9) = 16.66, p = .003, \eta^2_p = .649$. There was no significant effect for session ($p = .105$) and no significant interaction ($p = .620$). Thus, grasp selections differed between the learning and transfer blocks for the two-step and three-step groups. There was no change in the difference between both trial types between sessions 2 and 3.

3.4. Detailed Analyses for the Transfer Blocks

The previous analyses revealed that the AGE for the multi-step rotations carried over to the one-step rotations, but that this carry-over was not complete. As such, we tested two possible post hoc explanations, which are referenced in the discussion. First, it is possible that the carry-over was incomplete in the transfer blocks because participants slowly adjusted the AGE to the demands of the one-step rotations in these blocks. Second, participants may have used a goal-directed strategy in some trials and a habitual strategy on others.

3.4.1. Changes of AGE within blocks.

To analyze adaptations of the AGE within blocks, we pooled the data from all but the first transfer blocks for the second and third sessions. Next, we computed the AGE based on all trials that occurred at positions 1-4 in the transfer blocks, for all trials that occurred at positions 5-8, etc. Aggregating the data was necessary because data from several trials are needed to compute the AGE.

Figure 3 shows the within-block adaptations in the transfer blocks. A split-plot ANOVA with a within-subject factor of trial position (first four: 1-4, 5-8, ..., 29-32) and a between-subject factor of learning group (one-step vs. two-step group vs. three-step) revealed significant effects for trial position, $F(7,189) = 4.15, p = .002, \eta^2_p = .133$, and learning group, $F(2,27) = 6.49, p = .005, \eta^2_p = .325$. Importantly, there was a significant interaction, which suggests that the AGE increases during the transfer blocks for the two-step and three-step

groups but not the one-step group, $F(14,186) = 1.99$, $p = .046$, $\eta^2_p = .128$. To confirm this interpretation, a t-test was conducted to compare trials 1-4, 5-8, etc. with trials 29-32 for each individual group. In the one-step group, the AGE at positions 13-16 were significantly smaller than the AGE at positions 29-32, $t(9) = 2.43$, $p = .038$, $g = 0.77$. There were no additional significant differences, all $ps \geq .068$. In the two-step group, the AGE for the first trials (1-4) was significantly smaller than for the final trials, $t(9) = 2.74$, $p = .025$, $g = 0.87$, all other $ps \geq .137$. In the three-step group, the AGE for the trials at positions 1-4, 5-8, 9-12, 17-20, and 21-24 were significantly smaller than the AGE for the trials at positions 29-32, all $t(9)s \geq 2.29$, all $ps \leq .048$, all $gs \geq 0.72$, all other $ps \geq .082$. Thus, in the transfer blocks for the two-step and three-step groups, the AGE slowly re-adapts toward the one-step rotation requirements, while it remained constant in the one-step group.

3.4.2. The distribution of GO on the transfer trials.

It is possible that participants selected grasps in goal-directed fashion in some trials and habitually in others. If this was the case, the distributions of GO should be bimodal in the transfer blocks. To test this assumption, we split the data for the transfer blocks in the second and third sessions by participant and the initial target angle to conduct dip-tests (Hartigan & Hartigan, 1985) on GO. The dip-test examines multimodality and is based on the maximum difference between an empirical data distribution and a fitted unimodal distribution function. The distributions of the GOs did not significantly deviate from unimodality for participant or initial target angle in the two-step, all $dips \leq .034$, all $ps \geq .242$ or the three-step group, all $dips \leq .036$, all $ps \geq .108$. Hence, the AGE on transfer trials most likely did not reflect a trial-by-trial mixture of grasps, which were under habitual control in some trials and goal-directed control in others.

3.5. Session four

The fourth session was conducted to test the persistence of the grasp choices that were acquired during the two-step and three-step rotations. Hence, the session consisted of four blocks of one-step rotations. This test was administered at least one day after the third session ($m = 1.4$, $sd = 0.9$). A split-plot ANOVA with a within-subject factor of block (1, 2, 3, 4) and a between subject factor of learning group revealed a significant effect for block, which indicated that the AGE increased during session 4, $F(3,81) = 5.61$, $p = .004$, $\eta^2_p = .172$. The interaction between block and learning group was marginally significant, $F(6,81) = 2.15$, $p = .077$, $\eta^2_p = .137$. The main effect for learning group was marginally significant, $F(2,27) = 2.57$, $p = .095$, $\eta^2_p = .160$. Although the interaction was only marginally significant, we conducted t-tests to compare the one-step group with the other groups for the first block of session 4. The AGE for the one-step group was marginally larger than the two-step group ($t[18] = 2.1$, $p = .051$, $g = 0.933$), and significantly larger than the three-step group during the first block of session 4, $t(18) = 2.5$, $p = .022$, $g = 1.119$. Additionally, we conducted repeated measures ANOVAs with a within-subject factor of block (1, 2, 3, 4) for each group. There was no significant effect for the one-step group, $F(3,27) = 0.57$, $p = .640$, $\eta^2_p = .060$. In this analysis, the mean AGE was .677 in the first block and .666 in the fourth block. The AGE increased from .429 to .492 in the two-step group, $F(3,27) = 9.66$, $p < .001$, $\eta^2_p = .518$. The AGE marginally increased from .415 to .474 in the three-step group, $F(3,27) = 3.56$, $p = .054$, $\eta^2_p = .284$.

Additionally, we tested whether the responses in session 4 reflected a trial-by-trial mix of goal-directed and habitual processing (as in subsection 3.4.2.). Individual dip-tests were computed on the GOs for each participant and each target angle in session 4. Again, the GOs did not deviate from unimodality in the two-step, all $dips \leq .079$, all $ps \geq .112$ or three-step groups, all $dips \leq .077$, all $ps \geq .126$.

In summary, the grasp selection that was acquired during the learning blocks tended to persist in the first blocks of the fourth session, which was administered approximately 1.4 days after the third session. The two-step and three-step groups then slowly converged back toward the AGE of the one-step group. However, given several marginally significant effects in the session 4 data, these results should be interpreted with caution.

3.6. Reaction time

The average reaction time for the transfer and training blocks (Table 1) was examined in a split-plot ANOVA with the within-subject factors of block type (learning vs. transfer) and session (2, 3) and the between-subject factor of learning group (one-, two-, three-step groups). Reaction times decreased from session 2 to session 3, $F(1,27) = 7.16, p = .013, \eta^2_p = .209$. Reaction times were marginally significantly faster in the learning blocks compared to the transfer blocks, $F(1,27) = 4.00, p = .056, \eta^2_p = .129$. This difference decreased from the second to the third sessions, $F(1,27) = 5.12, p = .032, \eta^2_p = .159$. There was no significant difference between groups, $F(2,27) = 0.62, p = .544, \eta^2_p = .044$ and no additional significant interactions, all $ps \geq .090$. In summary, the reaction times do not support goal-directed planning processes. The group that performed two- or three-step reactions reacted as fast (numerically somewhat faster) as the group that only executed one-step rotations. Likewise, participants initiated their grasping movements slightly faster in the multi-step rotations in the learning blocks than in the one-step rotations in the transfer blocks.

4. Discussion

We examined whether grasp selection for object manipulation is primarily based on goal-directed or habitual planning. To test our hypotheses, the postures that resulted from selecting a specific grasp were varied between three groups. In the one-step group, grasp

selections did not change across four sessions, which suggests that the grasps were tuned to the tasks from the onset of the experiment. In the two-step and three-step groups, grasps were initially comparable to the one-step group but adapted to the task demands of the two-step and three-step rotations over the course of the experiment. Participants transferred the grasps that were used for the two-step or three-step rotations with a specific initial target to the one-step rotations that had the same initial target. However, the transfer was not complete. Thus, the data do not fully support either of our initial hypotheses. In the following discussion, we review the results with respect to the planning mode, implications for learning processes and grasp selection for sequential object manipulations.

4.1. Goal-directed planning vs. habitual control

When participants in the two-step and three-step groups executed one step rotations, their grasps were in between the grasps of the one-step group and the grasps that they used for the two-step or three-step rotations. This result matches neither of our original hypotheses. The hypotheses that planning is fully goal-directed can be rejected because it cannot explain why grasp choices for identical one-step object manipulations differ between groups. Moreover, because the required movements were highly predictable, a goal-directed process would have instantaneously or within a few trials adapted to the two-step and three-step rotations. However, grasps were adapted over the course of several blocks. Finally, the reaction time data did not suggest a goal-directed planning process because reaction times were not longer for multi-step than one-step rotations (neither between groups nor within groups).

Likewise, at first glance, the data appear incompatible with the habitual hypothesis because the AGE in the learning blocks and transfer blocks differed within the same participant groups. However, the habitual hypothesis cannot immediately be rejected because partial transfer may have been an artifact of aggregating data for all the transfer block trials.

Just as the AGE decreased during the multi-step rotations in the learning blocks, the AGE again increased during the training blocks (Figure 3). Even if the AGE at the beginning of a transfer block was identical to the AGE at the end of the previous learning block, this might be obscured by the (necessary) aggregation of multiple trials to compute the AGE in transfer blocks. Finally, the slow and gradual learning process can be interpreted as a sign of the involvement of the habitual system (Bayley, Frascino, & Squire, 2005).

Third, it could be possible that the data represent a combination of goal-directed and habitual grasp selection. A mix of both strategies could be implemented in three ways. First, it is possible that some participant's only employed goal-directed while others employed habitual strategies. Closer inspection of the data does not support this hypothesis because almost all (18 out of 20) participants in the two-step and three-step groups demonstrated a (numerically) partial transfer from the learning to the transfer blocks. Second, participants may have used a goal-directed strategy on a subset of trials and a habitual strategy on other trials. This possibility was not supported by the data because the grasp orientation distributions were unimodal in the transfer blocks (including those from the fourth session). Third, it could be possible that the grasp selections in the individual trials resulted from blending the grasps that were favored by the goal-directed and habitual systems. Currently, we cannot provide additional data to support or reject this possibility.

4.2. Comparisons between habitual and hybrid models

To provide additional resources for deciding between the latter two hypotheses, we tested simple formal models for the hypothesis that grasp selection is entirely habitual (model H) and that it is a hybrid of goal-directed and habitual processes (model GH). We briefly outline our approach here and provide the model specifications in the appendix. Each model generates grasp selections in terms of the AGEs for each block of the experiment.

According to habitual model H, only the habitual system specifies the grasp. After the object manipulation, the habitual grasp is adapted to the requirements of the trial. Thus, the grasp converges toward a grasp that is best used to execute the task that is presented in a specific block. According to this model, the AGE should decrease during the learning blocks and increase during the transfer blocks. Because the model is purely habitual, the grasp that is selected does not depend on the type of the upcoming trial. The model parameters were the AGEs, toward which the model converges during the learning and transfer blocks. Another parameter specified the learning rate. Additionally, we included a parameter to reflect the standard deviation of the probability distribution of the model outcomes to allow us to use the Bayesian Information Criterion (BIC, see below) for model comparisons.

According to the hybrid model GH, the executed grasp was a weighted mean of the grasps that were favored by the habitual and goal-directed systems. The goal-directed system was assumed to favor a specific grasp for the one-step rotations, another for the two-step rotations, and a third for the three-step rotations. For simplicity, these values were assumed to be constant throughout the experiment. Likewise, a parameter w , which specified the relative contribution of the goal-directed and habitual systems for grasp selection, was assumed to be constant. Although the goal-directed grasps did not change, the habitual grasps were continuously shifted toward the grasp that was actually used in each trial. The model parameters were the AGEs that were favored by the goal-directed system in the learning and transfer blocks, the learning rate of the habitual system, the relative weight of both systems, and the standard deviation of the probability distribution of the model predictions.

In both models, the AGEs were adapted with the delta rule. Both models assume that the habitual system is initially tuned to one-step rotations. We compared both models with the Bayesian information criterion (BIC) because it discounts the greater flexibility of model GH and allows one to compute the relative likelihood of both models (Lewandowsky and Farrell,

2010).³ To compute the BIC, Bayesian versions of both models were constructed by assuming that the probability distributions of the model predictions were normally distributed around the predicted AGE values with a constant standard deviation. Because the model predictions were identical for the one-step group, the maximum likelihood estimates for both models were fitted to the averaged data for the two-step and three-step groups.

Figure 4 shows the fit (R^2) and parameter estimates for the models. The differences between the BIC ($BIC_{\text{model H}} - BIC_{\text{model GH}}$) for the two-step group and three-step group were 81 and 24. As small BIC scores indicate better fit, comparing the BIC values favor model GH. From the BIC, the Bayes factor can be derived, which indicates the relative likelihood of the models after accounting for the number of parameters. For both groups, the Bayes factor is .000, which indicates that model H is less likely to have produced the observed data than model GH. These values provide strong evidence for model GH (Wasserman, 2000). In summary, the hybrid model provides a better fit than the habitual model. The finding that the estimates of the learning rate and the weighting of the system in model GH are rather consistent for both groups lends further credibility to the model.

Given the data and the model comparisons, we suggest that grasp selection for object manipulation is a hybrid process, in which the output of the goal-directed and habitual systems contribute to grasp selection in a single trial. Model GH contains the parameter w ,

³ BIC scores are computed as follows: $BIC = -2\ln(L) + K*\ln(N)$, where L is the likelihood of the model, N is the number of data points (34 in the present cases), and K is the number of model parameters. Differences in the BIC scores (ΔBIC) can be interpreted as the logarithm of the Bayes factor, which is the ratio of the likelihoods for the two models. Because the likelihood is multiplied by -2 in the BIC term, Bayes factor B can be computed as $B = \exp(-0.5\Delta BIC)$.

which directly reflects the relative contribution of the goal-directed and the habitual systems. According to this estimate, the relative contribution of the habitual system (72% and 67% for the two-step and three-step groups) to grasp selection was approximately twice as large as that of the goal-directed system in the current experiment.

The data suggest that participants use goal-directed and habitual strategies and combine the outputs of both to select a grasp. Interestingly, even though goal-directed processing is important, participants did not exclusively rely on this strategy. This may be because participants opportunistically used both processes, according to their usefulness in a specific situation. Goal-directed planning has the advantage that grasps can be quickly adapted to a changed context but is limited because the plans might not always operate as expected. Habitual grasp selection is based on experience and may reflect factors that are not easily captured by a planning process. When the context does not change, a habitual system can result in close-to-optimal grasp selections. However, a limitation is that habitual grasps may be inadequate when there are changes in the environment. Because both modes of grasp selections have advantages and disadvantages, combining them may be a good strategy. Partially relying on the habitual system prevents planning errors from causing wildly inappropriate grasp selections. Partially relying on the goal-directed system modifies previously optimal grasps in the direction of the current task demands.

4.3. Implications for interpreting the end-state comfort effects

In summary, the above finding has important implications for interpreting the end-state comfort effect. The finding that participants grasp the same object in different ways, depending on the intended use, has been taken as evidence that grasps are adjusted to forthcoming object manipulations based on the anticipated arm posture at the end of the object manipulation (i.e. end-state, e.g., Cohen & Rosenbaum, 2004). The present experiment qualifies such conclusions in two ways. First, the experiment showed that how grasps were

adjusted to different object manipulation depended largely on habitual processes. This demonstrates that an effect of an upcoming object manipulation on grasp selections could – in theory – result from habitual processing and does not necessarily imply goal-directed planning.

Second, our experiment created situations, in which goal-directed and habitual grasp selections could be disentangled. The data suggest that goal-directed processing indeed contributed to grasp selection, even if it is outweighed by habitual processing. From this perspective, the present data provide the currently most direct evidence for the involvement of goal-directed planning processes in the adjustment of the grasp to intended object manipulations.

4.4. Explanations for habitual processing involvement

According to the parameter estimates from the best fitting model (GH), grasps were adapted mostly habitually to forthcoming object manipulations. In this section, we try to explain the comparable small influence of goal-directed processes.

One explanation for the partial reliance on habitual processing is that goal-directed planning for object manipulations may not have been possible or may have been difficult in our experimental task. We do not believe that this was the case. First, the data suggest that goal-directed planning is partially involved and, hence, it was possible to apply this strategy in the current experiment. Second, the experimental task was designed to allow for goal-directed processing in the critical transfer blocks (see Section 1.3). For example, the object manipulation task was simple and predictable. Moreover, participants had extensive prior experience because the task was common in everyday life (e.g., rotary controls, door knobs, jar lids), and the participants in the one-step group did not demonstrate signs of (further) learning. Additionally, participants were informed about the nature of the task beforehand and transfer trials were presented blockwise, making it unlikely that participants were surprised by

the one-step trials. Finally, the one-step rotations were always a part of the two-step and three-step rotations, so that learning blocks provided the necessary information to predict action outcomes on transfer trials. In sum, the one-step dial rotations required in transfer blocks were among those object manipulations, for which goal-directed planning should be most easily possible.

One aspect of our experiment that may have biased participants toward a habitual mode of grasp selection was the length of the experiment (Tricomi, Balleine, & O'Doherty, 2009). However, at least for the two-step group, grasps in the first and second transfer blocks clearly differed, which suggests that grasp selection was (partially) under habitual control early in the experiment, AGE .66 vs. .51, $t(9) = 2.33$, $p = .045$, $g = 0.74$. In conclusion, if goal-directed processing is feasible for selecting grasps in object manipulations, it should have also been possible in our experiment.

Another potential explanation for the strong habitual component in our data is that the facilitation of the object manipulation that resulted from goal-directed planning did not justify the associated cognitive efforts that were required in the present task. Because we cannot quantify the subjective costs of planning and object manipulations that are executed with different grasps, it is difficult to discuss this possibility. Several arguments suggest that goal-directed planning may be worthwhile. Research has shown that grasp selections affect the performance of object manipulations in different tasks (Herbort, 2012; 2015; Rosenbaum et al., 1996; Short & Cauraugh, 1999), which determine grasp selections. Moreover, the requirements for an upcoming object manipulation impose central constraints on movement planning. This constraint outweighs several factors, such as hand preference (Coelho, Studenka, & Rosenbaum, 2013). Likewise, participants adapted their grasps to the upcoming object manipulations even when it was not necessary and prolonged their response times in a reaction time task (Herbort & Butz, 2010). These findings suggest that participants care about

the grasps that they select and that they are motivated to select a suitable grasp even in comparably mundane tasks. Likewise, participants adapted their grasps in the two-step and three-step groups over the course of the experiment and re-adapted within the transfer blocks, which indicates that they could process that grasp selections affected the efficiency of the object manipulations and that different grasps were most suitable for different tasks.

That said, it is possible that the benefits of selecting a task-adequate grasp instead of a habitual grasp may have been too small to invoke planning in the transfer trials. For example, participants may have considered the required cognitive effort required for quickly adapting to the transfer trials as larger than the expected benefits for executing the rotations (c.f. Cohen & Rosenbaum, 2011). From this perspective, the cognitive effort for planning may have been traded off with the physical effort for moving, which could have minimized some overall effort. Second, participants might only begin to plan once the experienced effort of moving or the awkwardness of the required postures exceeds a limit (Rosenbaum & Jorgensen, 1992). Thus, it is possible that participants could have relied more on planning, when the benefits of planning were larger.

Nevertheless, the one-step rotation task is comparable to many of the tasks that are used to study grasp selection for object manipulation and is also reminiscent of many everyday tasks. Thus, when the goal-directed grasp selections are too difficult or effortful compared to the potential benefits, it is possible that similar situations could arise in many (or most) other object manipulation tasks and, thus, constrain the mode of planning in general. This would suggest that habitual processes – not planning – is the default mode for selecting a grasp for object manipulation.

4.5. Learning to select grasps for object manipulation

We further discuss the role of learning in grasp selection for object manipulation, as it has received little attention. Thus far, grasp selection has primarily been viewed as a function

of the task requirements (c.f. Ansuini et al., 2006; Künzell et al., 2013; Rosenbaum et al., 2012), properties of the to-be-grasped object (Rosenbaum et al., 1992; Herbort & Butz, 2011; Sartori et al., 2011), or biases that result from task framing (Herbort & Butz, 2012; Herbort et al., 2014; Huhn III, Potts & Rosenbaum, 2016). Moreover, grasp selections did not change or changed little during previous experiments (Seegelke, Hughes, Knoblauch, & Schack, 2013, Herbort, 2015; Herbort et al., 2014; for an exception, see Hossner, Klostermann & Spinnler, 2011).

Only small learning effects can be observed in tasks that use one-step rotations (e.g., Herbort, 2015) because these tasks may probe a highly overlearned skill. Likewise, grasp selections in the one-step group did not change over the course of the present experiment. In tasks that required two-step object manipulations, the presence of learning effects may have depended on the contingency between the first and second object manipulation steps. In experiments in which the first manipulation step was contingently followed by a specific second manipulation step, grasps were adapted to later manipulation steps (Hossner et al., 2011; present experiment). In contrast, participants relatively weakly adapted to the second object manipulation step when the first and second targets were independently varied (Seegelke et al., 2013).⁴ This suggests that adapting grasps to later manipulation steps does not result from an increase in the number of manipulation steps that are considered during planning. Rather, it suggests that task-grasp associations are updated based on the required actions that contingently follow an initial object manipulation.

Given the conclusion that grasps were updated based on contingently unfolding movement, one could ask which aspect of the unfolding movement drove adaptation in the

⁴ Alternatively, the lack of an effect could be due to the smaller number of trials in Seegelke et al.'s (2013) experiment.

current experiment. On the one hand, grasps in the two-step and three-step groups did not differ, which suggests that the range of postures that were involved in the object manipulation was a learning signal. On the other hand, even after extensive practice, grasp orientations were inversely related to the first dial rotation, which suggests that the first object manipulation had an eminent role. A possible suggestion for reconciling these findings is that later arm postures are discounted and may contribute less to the learning signal (c.f. Shadmehr, 2010; Shadmehr, Orban de Xivry, Xu-Wilson, & Shih, 2010). Moreover, it had to be assumed that the arm postures that were involved in the third rotation segment were discounted such that they only had a marginal impact on grasp selections.

4.6. Grasp selection for multi-step object manipulations

In the previous section, we discussed how learning affects grasp selections. Now, we turn to the process of selecting an appropriate grasp for an object manipulation, regardless of whether this process is goal-directed or habitual. Interestingly, participants who were used to executing two-step or three-step object manipulations did not adjust their grasps (much) when asked to conduct one-step object manipulations. This suggests that they treated one-step and multi-step object manipulations as similar. This complements previous research that shows that there is a limited ability to adjust the grasp to later object manipulation steps, even when the entire movement sequence is known in advance (for an exception, see Haggard, 1998). For example, grasp selection for sequential bar transport movements is based on the requirements of the first step in the sequence (Rosenbaum et al., 1990). When there are effects for later object manipulation steps, they are often smaller than the effects of the initial steps (Seegelke et al., 2013). This has been referred to as a “planning gradient” (Haggard, 1998). An exception to this rule are tasks, in which an initial object manipulation step does not constrain grasp selections (Hesse & Deubel, 2010; Seegelke, Hughes, Knoblauch, & Schack, 2015). In summary, the current results and previous research suggest that grasp selection is

primarily based on the first object manipulation step that provides a clear constraint on grasp selection, although later steps may affect grasp selection to some extent.

4.7. Conclusion

In the present experiment, adjusting grasps for the intended object manipulations partially depended on adjustments that were used in previous object manipulations and expectancies about the upcoming object manipulations. Hence, adjusting grasps combined habitual and goal-directed processing. The parameter estimation of a computational model suggested that the influence of the habitual system was approximately twice as strong as that of the goal-directed system in the current task. Finally, on a more abstract level, the data show that goal-directed processes, such as movement planning, may invoke habitual processes to specify subordinate components of the plan.

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Appendix

Models H and GH rely on the following parameters. AGE_H is the habitual AGE and is the only component in the model that changes throughout the simulated experiment. In model H, AGE_L and AGE_T define the values to which AGE_H converges during the learning and transfer blocks, respectively. In model GH, AGE_L and AGE_T correspond to the AGE that would be assumed if only goal-directed planning determined grasp selection in learning and transfer blocks, respectively. At the onset of the experiment, AGE_H is assumed to be identical to AGE_T . This reflects the assumption that anticipatory grasps are tuned into one-step rotations at the onset of the experiment. This assumption is justified by the constant AGE of participants in the one-step group. The learning rate α determines the speed of adaptation in both models. In model GH, the parameter w describes the relative contribution of the habitual AGE to the selected AGE. To compute the BIC, it was assumed that the probability distribution of the model predictions were normally distributed with a constant standard deviation sd . Except for the value of AGE_H , all parameters are assumed to be constant throughout the experiment.

For each trial in the experiment, the models generated a grasp (corresponding to an AGE value) and updated the habitual AGE_H . In the habitual model H, the selected AGE on trial i was set to AGE_H and the value for AGE_H was updated afterwards:

$$AGE_i := AGE_H$$

$$AGE_H := \begin{cases} AGE_H + \alpha(AGE_L - AGE_H), & \text{in learning blocks} \\ AGE_H + \alpha(AGE_T - AGE_H), & \text{in transfer blocks} \end{cases}$$

In the hybrid model GH, the selected AGE on trial i was computed from AGE_H and the outcome of the goal-directed process, which depends on the block type. Then, the value for AGE_H was updated.

$$AGE_i := \begin{cases} wAGE_H + (1 - w)(AGE_L), & \text{in learning blocks} \\ wAGE_H + (1 - w)(AGE_T), & \text{in transfer blocks} \end{cases}$$

$$AGE_H := AGE_H + \alpha(AGE_i - AGE_H),$$

The AGEs for the trials from each block were averaged, which resulted in 34 AGE values. The probability distribution for the model predictions was assumed to be a normal distribution with a constant standard deviation (sd). The free parameters were then fit, maximizing the model likelihood given the average data of the two-step and three-step groups. The parameter estimates are shown in Figure 4.

Table 1. AGE and reaction times

Group	Session	AGE				RT			
		transfer blocks		learning blocks		transfer blocks		learning blocks	
		mean	sd	mean	sd	Mean	sd	mean	sd
one-step group	2	.68	.30	.69	.32	320	85	316	85
	3	.70	.25	.70	.25	306	100	298	95
two-step group	2	.43	.19	.31	.14	291	63	274	66
	3	.42	.19	.29	.18	277	82	275	82
three-step group	2	.44	.10	.34	.11	294	93	276	77
	3	.41	.14	.32	.13	259	89	261	67

Figure 1. Setup, design, and dependent variables. a) The figure shows the setup of the experiment. b) The table lists the target sequences by block type for each learning group. c) The figure shows how the grasp orientation (GO) was computed. The white squares represent the positions of the index finger and thumb sensors. d) The figure shows how the anticipatory grasp effect (AGE) was computed for a particular block from one exemplar participant. The AGE was defined as the negative slope of the regression line from GO on the initial target angle.

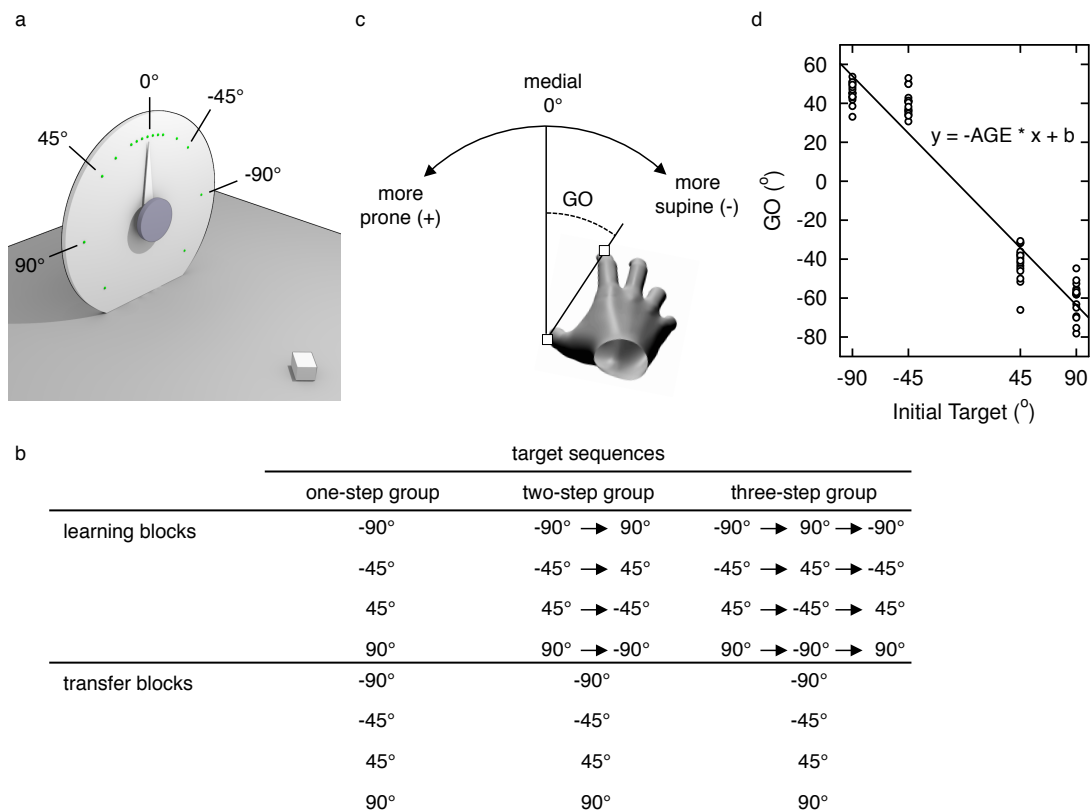


Figure 2. The anticipatory grasp effect (AGE) across blocks. The figure shows the AGE for the three groups and the learning (L, white area) and transfer (T, gray area) blocks. Error bars were ± 1 s.e.m.

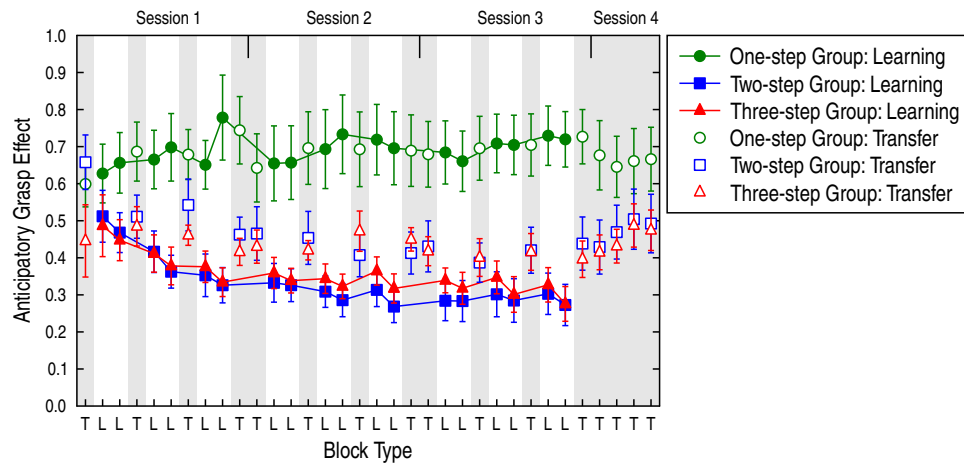
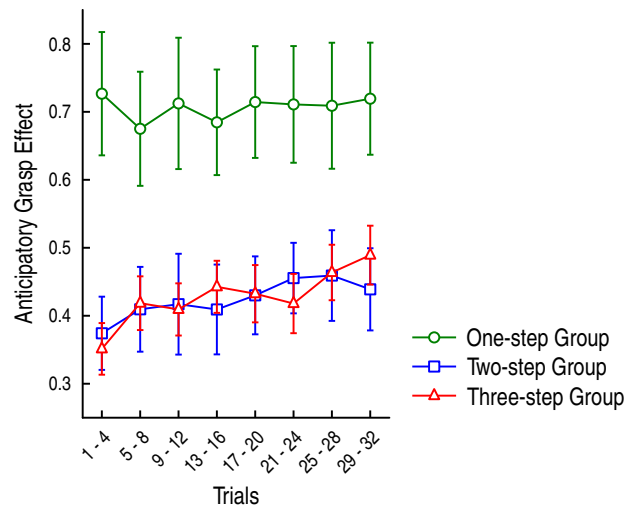
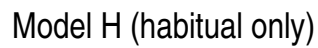
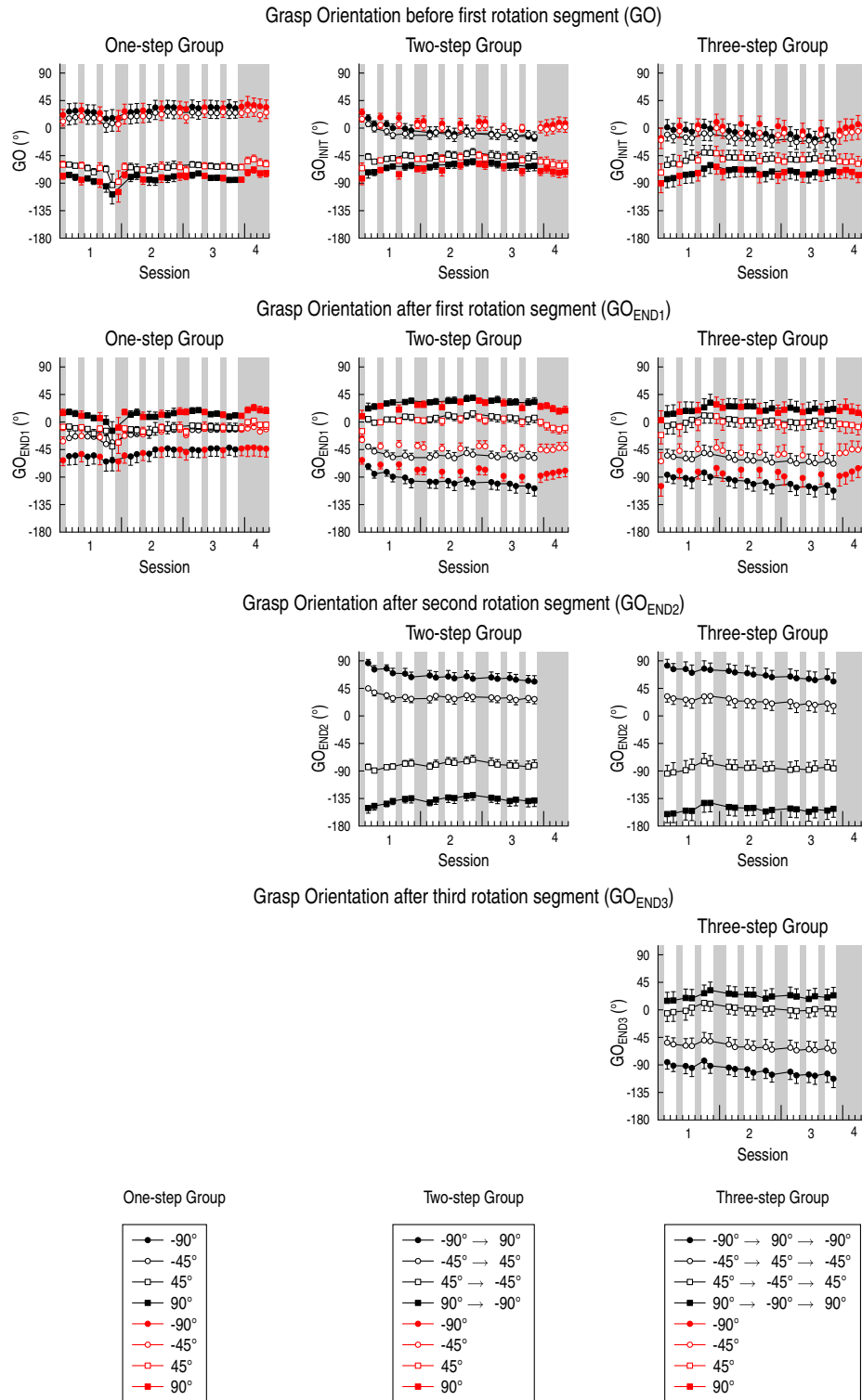


Figure 3. The anticipatory grasp effect (AGE) within the transfer blocks. The figure shows the AGE in the transfer blocks by trial position. Error bars are ± 1 s.e.m.



Model GH (goal-directed + habitual)





Supplemental Figure 1. The effects of learning and initial target angle on postures during object manipulation. The figure shows the GO by initial target angle for all blocks (first row). Rows two through four show the grasp orientation at the end of the first, second, and third rotation segments (GO_{END1} , GO_{END2} , GO_{END3}), which were recorded when the dial rotation rate exceeded 10°/s for the last time in a specific segment. Data from the learning blocks (L) are plotted with black markers on a white area, data from the transfer blocks (T) are plotted with red markers on gray areas. Error bars are ± 1 s.e.m.