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Hand selection for object grasping is influenced by recent motor history

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Abstract

Action selection processes such as those that underlie decisions about which hand to use for upcoming actions are fundamental to adaptive motor behavior. Previous research has shown that people grasp objects in ways that reflect anticipated task demands as well as recent movement experience. However, very few studies have addressed the possible influence of recent motor history on hand selection. In the current study, participants grasped and placed objects using either their left or right hands. The results showed faster response times to initiate successive actions when hand was repeated, even when those actions involved distinct grasp postures and object placement movements to distinct locations. Conversely, no such planning advantage was observed for repeated grasps for successive actions made with opposite hands. The findings are consistent with the idea that choices about which hand to use in the present are influenced by which hand was used in the recent past. When the same hand can be used for successive actions, planning is made more efficient, presumably because the motor parameters that specify which hand to use can be recalled from recent memory rather than formulated anew. The findings indicate that hand selection is sensitive to recent movement experience and provide novel support for computational efficiency accounts of motor history effects.

Keywords

hand selection; grasping; motor history; priming; action selection; action planning; end-state comfort; motor programming; sensorimotor control

1. Introduction

Action selection is fundamental to adaptive sensorimotor control, and can be influenced by a variety of sources of information, including past experiences and anticipated task demands. Previous research has shown that people grasp objects in ways that reflect predictions about the future demands of their intended actions, as well as their recent movement history (for review, see Rosenbaum, Chapman, Weigelt, Weiss, & van der Wel, 2012). As evidence for the role of predicted future factors, people tend to adopt relatively awkward initial hand/arm postures for grasping in favor of ending their movements comfortably, a phenomenon known as the end-state comfort effect (Rosenbaum & Jorgensen, 1992). Ending actions comfortably, in the middle of one's range of motion, allows for better, more precise control of movements, as well as greater possibilities for future actions. Grasp selection is also affected by recently executed movements (e.g., Rosenbaum & Jorgensen, 1992). The standard explanation for such history effects (hysteresis) is that the recycling of recently

executed motor parameters is computationally more efficient than is specifying those parameters anew.

Choosing which hand to use to perform actions is one of the most commonplace decisions we make as humans, and yet very little is understood about how these choices are resolved. In contrast to the work on grasp selection, surprisingly few studies have addressed the possible influence of recent motor history on hand selection. To our knowledge, only two previous studies have been carried out, and neither involved adult humans. Rostoft et al. (2002) used a ball catching task with 4 year-old children and showed hysteresis for hand selection; which hand was used for catching was sensitive to the direction in which balls were delivered (leftward or rightward), biased in favor of using the same hand according to recent history. Likewise, Weiss and Wark (2009) studied cotton-top tamarins and showed hysteresis for hand selection according to the progressive direction of presentation of food items for grasping. Gaining a better understanding of the potential impact of recent motor history on hand selection may have important implications for advancing evidence-based rehabilitation programs for patients with movement problems as a result of brain or bodily injury.

In the current study we investigate the potential influence of recent motor history on both hand and grasp selection in the same task. While the majority of previous research has focused entirely on changes in selection tendencies, here we also consider the influence of recent motor history on response times (RTs) to initiate actions. Consideration of RTs is of critical importance for evaluating computational efficiency accounts of motor history effects. Previous work indicates that actions are planned prior to movement onsets (Pellegrino, Klatzky, & McCloskey, 1989; Stelmach, Castiello, & Jeannerod, 1994). If history effects reflect more efficient planning, then RTs should be reduced when recall of recent motor plans is possible. Here, we test this hypothesis by manipulating whether or not successive actions involve repeated hand and/or grasps. Additionally, the majority of previous evidence for hysteresis for either hand or grasp selection has been based on sequential response tasks where successive actions are predictable. That is, previous studies showing motor history effects have tended to involve successive actions directed at spatial locations presented in an orderly, predictable sequence, from left-to-right, high-to-low, or from predefined 'home'-to-'target' locations, or vice-versa. It is possible that history effects are dampened or abolished when successive actions are not predictable. In the current study we evaluate this possibility by testing for the influence of recent motor history for pairs of actions that in a predictive sense are statistically unrelated. We introduce a novel paradigm whereby second actions within trials are equally likely to involve the same (repeated) or different (changed) hands and/or grasps compared with first actions.

Novel tools were presented centrally with their handles oriented vertically, parallel to participants' midlines. According to arbitrary rules defined by the shape of tools, participants grasped and placed tools in one of four locations: either to the left or right side of center, in either an outside or inside position (Figure 1A). Tools to be placed on the left were to be grasped with the left hand while those to be placed on the right were to be grasped with the right hand, and tools to be placed in outside positions were to be oriented with their handles facing away from center while tools to be placed in inside positions were to be oriented with their handles facing toward the center.

According to predictions about forthcoming task demands, participants were expected to grasp tools differently depending on where and in what orientation they were to be placed. Inside object placement tasks for both left and right handed actions were predicted to involve pronated hand/arm orientations – grasp postures – while outside placement tasks were predicted to involve neutral grasp postures, in the middle of the range of hand/arm

pronation-supination (Figure 1A). These predictions are in accordance with the end-state comfort effect, as discussed above. Differences in grasp postures according to tool placement requirements would indicate that grasp selection is influenced by predictions about forthcoming biomechanical factors associated with the later steps of intended actions.

Our main interest was to test for the influence of recent motor history on hand and grasp selection. Here we consider the term priming as synonymous with history effects. To address the possibility of either hand or grasp selection priming, trials involved two actions in succession, a prime and probe, separated by a variable 3-4s delay interval. Four conditions were defined by the relationship between prime and probe events: either the same actions were repeated (Identical Repeat, IR), hand was repeated but grasp was changed (Hand Repeat, HR), grasp was repeated but hand was changed (Grasp Repeat, GR), or neither hand nor grasp were repeated (No Repeat, NR) (Figure 1B). Hand selection priming was predicted to result in relatively faster RTs to initiate actions for probe events for trials that involved repeated (IR and HR) versus changed hands (GR and NR). The same logic applied for grasp selection – priming would be indicated by faster RTs for trials that involved repeated (IR and GR) versus changed grasps (HR and NR).

These predictions can be conceptualized as either computational gains associated with the reuse of aspects of recent motor plans (repeat hands and/or grasps) or costs associated with the need to adjust and/or newly formulate aspects of recent motor plans (change hands and/or grasps). Since the IR condition involves repetition of the same tools and tool-associated action rules, it is difficult to interpret comparisons of this condition with other conditions; priming effects could be attributable to repeated hand, grasp, and/or the processes underlying object recognition and associative rule retrieval. Conversely, comparisons between HR and NR, and GR and NR conditions allow for straightforward interpretations not confounded by the repetition of tools and tool-based action rules. Faster RTs for HR versus NR conditions would provide evidence of hand selection priming for actions involving distinct grasps, while faster RTs for GR versus NR conditions would provide evidence of grasp selection priming for actions involving opposite hands. Notably, the latter potential findings would suggest that grasp plans can be specified independent of hand; that aspects of grasp plans can be shared for both hands.

In addition to RTs, if participants were found to persist with the use of the same hand when task instructions required switching hands this would also provide evidence for the influence of recent motor history on hand selection. Such findings could be interpreted as the sensorimotor system being primed to reuse the same hand to an extent that overruled task instructions.

The same kind of logic can be applied for grasp behavior, however, it should be appreciated that while hand choices were defined by task rules, grasps were freely chosen by participants, predicted to conform with end-state comfort effects. Grasp switch conditions (HR, NR) can be thought of as situations where recent grasp history is in conflict with prospective factors known to influence grasp selection based on predictions about forthcoming task constraints. For the HR condition, reuse of the same grasp postures for probe actions as recently implemented for prime actions would come at the cost of ending actions uncomfortably, in violation of end-state comfort principles. Notice that these effects would indicate the influence of grasp history on grasp selection involving the same hand. Conversely, a tendency to reuse grasp postures for the NR condition would indicate effects of recent grasp selection history *between* hands, and would thus provide evidence of hand-independent levels of grasp planning.

2. Methods

2.1 Participants

Sixteen individuals (5 female, mean age = 21 +/- 4 years, age range = 17-37) from the University of Missouri participated in the experiment. All participants were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971), had normal or corrected-to-normal vision, and provided informed consent in accordance with the local IRB and the Declaration of Helsinki. The experiment took approximately 1 hour to complete and participants received course credits for their participation.

2.2 Experimental setup and materials

Four novel tools were used, made up of simple 3D shapes – sphere, cube, triangle, plus-sign – affixed to 6.5 (length) × 2.5 (width) × 1.7 (depth) cm handles (Figure 1A). Duplicates of each tool were included in the set so that even when identity was repeated within trials tools were exchanged by the experimenter.

Participants were seated at a 64.5 × 130cm table with a 16.1 × 24.1cm button-box positioned directly in front of them, centered with respect to their mid-sagittal plane (Figure 1A). In the start position, participants held down two 1.9 × 3.8cm buttons, one button to the left of midline held down with the left hand and one button to the right of midline held down with the right hand. The distance between left and right hand start buttons was 8.8cm, on center. Tools were presented on a 24.2 × 19.5cm presentation platform positioned directly in front of the button box with their handles vertically aligned with participants' midline, specified by a set of vertically oriented hash marks centered and aligned with the leading edge of the platform. Two 28 × 25.5cm placement platforms flanked left and right of the start position. Each of the placement platforms had a cross-hair that specified the middle point and two horizontally-oriented sets of hash marks to the left and right that specified inside and outside placement positions. The central start location and target placement locations were all comfortably within reach of participants while seated, for either left- or right-handed actions.

Vision was controlled using PLATO goggles (Translucent Technologies, Toronto, Canada). An Intel-based Macintosh desktop computer was used to control the experiment using Superlab Pro version 4.5. Experiments were video recorded using a Logitech Webcam C310 (www.logitech.com) and QuickTime 7 software.

2.3 Procedure

The experiment began with completion of consent forms and the Edinburgh Handedness Inventory followed by an instruction period in which the task and sequence of events within trials were explained. Tool-placement rules were provided visually using both a simple depiction of the setup showing the target location and handle orientation rules for each tool as well as an explicit demonstration of each of the tool-placement actions by the experimenter. The experimenter demonstrated each action using predicted grasp postures according to the end-state comfort effect. However, it was not suggested that participants copy movements as demonstrated by the experimenter, but rather it was said that participants should perform actions as they choose, in ways that were most comfortable for them.

Trials began with participants in the start position holding down both the left and right hand start buttons with the goggles in the closed position so that no vision was available. The experimenter placed one of the four tools on the presentation platform and initiated the trial sequence with a key press on the computer. First, a 400ms duration tone was played by the

computer which served to cue participants that a new trial had been initiated. Second, the goggles opened to reveal the tool that had been placed on the presentation platform. This was the signal for participants to perform the correct grasping and placement task for that tool. The goggles remained open for 4s so that participants had visual feedback of their actions. A variable 3-4s delay interval followed, onset by the return of the goggles to the closed position, during which time the experimenter removed the prime and placed down the probe tool while vision remained unavailable to participants. Finally, re-opening of the goggles signaled the probe event whereby participants were to again perform the correct placement task according to the identity of the tool present. As with the prime event, the goggles remained open for 4s. Participants were told to perform actions at a speed that was comfortable.

Following initial instructions, a training period was implemented whereby participants completed a block of 16 trials with the purpose of learning tool-placement rules and the timing of different aspects of the task. All 16 possible prime-probe combinations were included. Feedback about whether responses were correct for both prime and probe actions was provided. If errors were made, the depiction showing tool-placement rules was again shown to participants and correct responses per tool were confirmed. A one minute break was introduced after completion of training. The rest of the experiment was organized as two blocks of 64 trials separated by a two minute break period. Each block took approximately 22-25 minutes to complete and participants were notified at the 15min point, to simply provide them with an approximate indication about how much time remained.

A custom Matlab (R2011b) script was used to create trial sequences for both the experimental and training blocks whereby trial history (N-1) was balanced according to the type of probe action performed, and successive repetitions of conditions were limited to a maximum of two. In each experimental block, 4 repetitions of all 16 possible prime-probe combinations were included. Thus, equal proportions of trials were included for each of the four conditions – i.e., prime events held no predictive value. Two coding schemes defined tool-placement rules, counterbalanced across participants. Coding schemes were such that pairs of tools assigned to either the left or right hand, inside or outside placement positions, were switched for either scheme.

2.4 Dependent measures and analyses

2.4.1 Response times—The time from the opening of the goggles in the probe phase until the release of (left/right hand) start buttons was used to calculate response times (RTs; i.e., times-to-movement onset). Outlier analyses involved removal of trials more than two standard deviations above or below the mean, performed separately for each individual. Data from training trials were not included in the analyses.

RTs were entered into a three-factor Hand (two levels) $\times$ Grasp (two levels) $\times$ Condition (four levels) repeated measures analysis of variance (RM-ANOVA). Results applied the Greenhouse-Geisser correction for violations of the sphericity assumption, taken to be significant at $p < 0.05$. Post hoc follow-ups to significant main effects compared all possible pairwise comparisons of the most relevant factor. Bonferroni corrections for multiple comparisons were applied with a corrected $p < 0.05$ taken as significant.

2.4.2 Videos—Videos were observed offline by two independent raters instructed to evaluate and score actions with respect to the following possibilities: i) tools were placed in wrong locations and/or handle orientations, ii) movements were initiated with the wrong hand (hand errors), iii) grasp postures were inconsistent with end-state comfort effects (grasp errors¹), and/or iv) the experimenter placed down the wrong tools. For each observation type, Cohen's Kappa coefficients were computed as measures of inter-rater

reliability. The raters were otherwise naïve to the specific predictions and goals of the experiment.

We reasoned that evidence for the influence of recent motor history on hand selection would be provided if participants showed a tendency to initiate movements with the same hand even when task instructions required the use of the opposite hand. Such a pattern of behavior would be evident as a greater number of hand errors for hand changed (GR, NR) versus repeated (IR, HR) conditions. Similar logic applied for grasp postures. If recent motor history influenced grasp selection, then a greater number of grasp errors were expected for grasp changed (HR, NR) versus repeated (IR, GR) conditions. To evaluate either possibility, we compared the observed proportions of hand and grasp errors per condition with those expected based on the frequency of trials per condition using Chi-Squared tests.

Only trials where participants performed the wrong placements were excluded from RT analysis. Experimenter errors that involved presentation of the incorrect tool were recoded accordingly and included in the analysis.

3. Results

3.1. Response times

Three-factor RM-ANOVA revealed a significant main effect of Condition ($F(1.88, 28.2) = 41, p < 1.0 \times 10^{-8}$) and no significant main effects of Hand ($F(1, 15) = 0.065, p = 0.80$) or Grasp ($F(1, 15) = 2.93, p = 0.11$) (Figure 2). No two-way (p 's > 0.6) or three-way ($p = 0.15$) interactions were significant (see Supplementary Materials for all statistical outcomes). Post-hoc pairwise comparisons revealed faster RTs for IR versus all other conditions (all p 's < 0.001). Moreover, hand selection priming was evident as a RT advantage for HR versus NR conditions ($p < 0.05$; Figure 2C). Participants were faster to initiate actions for probe events when they repeated the same hand used for prime events (even though grasp was changed), consistent with the hypothesis that hand selection processes are sensitive to recent motor history. Faster RTs for HR relative to GR conditions also provided evidence for hand selection priming, however these differences did not reach significance following Bonferroni correction for multiple comparisons ($p = 0.07$).

One of the reviewers raised the possibility that hand selection priming may have been attributable to participants anticipating hand repeats prior to the onset of probe events. However, the results of two additional analyses were found to discount this alternate hypothesis, included as part of our Supplementary Materials.

In contrast to hand selection, our findings revealed no evidence for the influence of recent motor history on grasp selection. RTs for GR and NR conditions were statistically equivalent ($p = 0.92$; Figure 2C). This indicates that when successive actions involved a change in hands there were no performance gains (or costs) associated with repeating (or changing) grasps. These findings suggest that grasp plans are computed independently per hand, and support the involvement of hand- or effector-specific levels of representation for grasp selection.

Note that this interpretation of effector-specific action selection accommodates both sets of findings. First, hand selection priming suggests facilitation of planning when successive

¹For brevity, we use the term “grasp errors”, but it is important to appreciate that these behaviors were not true errors, but rather instances where grasp choices were in violation of end-state comfort effects, resulting in relatively awkward hand/arm postures to complete tasks (see Supplementary Materials for examples from video data).

actions involve the same hand. Second, failure to find a similar planning advantage for repeated grasps between hands suggests that grasps are specified for each hand separately.

3.2. Videos

Scoring and analyses of videos failed to provide any additional evidence for the influence of recent motor history on either hand or grasp selection. Very few trials were noted to involve either hand or grasp errors (Table 1). With so few of these instances noted, interpretations of their relative proportions across Conditions are problematic. Nevertheless, we report the results of these comparisons as part of our Supplementary Materials.

With respect to grasp postures, these results indicate that participants largely (> 98% of the time) conformed to predictions based on end-state comfort principles. In other words, grasps were selected according to expectations about forthcoming biomechanical constraints associated with respective placement tasks – for inside placement positions participants almost always used pronated grasp postures whereas for outside placement positions participants almost always used neutral grasp postures.

4. Discussion

The current results provide evidence for the influence of recent motor history on the selection of hand, but not grasp, for a naturalistic object grasping and placement task. Participants were faster to initiate successive actions when hand was repeated, even though those actions involved distinct grasp postures and object placement movements to distinct locations. The findings are consistent with the idea that choices about which hand to use in the present are influenced by which hand was used in the recent past. When the same hand can be used for successive actions, planning is made more efficient, presumably because the motor parameters that specify which hand to use can be recalled from recent memory rather than formulated anew.

Very little previous work has addressed the possible influence of recent motor history on hand selection. Specifically, previous findings have shown that hand selection tendencies are sensitive to recent history for a ball catching task with 4 year-old children (Rostoft et al., 2002), and for a grasping and feeding task with cotton-top tamarins (Weiss & Wark, 2009). While consistent, the current findings significantly extend these previous results. First, we show that recent hand selection history influences times required for planning subsequent actions, whereas previous evidence is based entirely on changes in selection tendencies. Here we show that planning unfolds more efficiently when the same hand can be used for successive actions. Second, we show that this planning advantage holds even for successive actions that involve very different grasp responses and object placement movements to distinct locations. Finally, whereas previous evidence for history effects has been limited to tasks where successive actions were predictable, here we show hand selection priming for pairs of actions that in a predictive sense were unrelated.

Our findings provide novel support for computational efficiency accounts of motor history effects. Such accounts have been offered previously to explain a variety of history effects on the motor system (Rosenbaum et al., 2012). The basic tenet is that planning is made more efficient when aspects of recently executed motor plans can be reused as opposed to being specified from scratch. Notably, however, the majority of previous results explained by these accounts have been characterized by changes in selection tendencies rather than response times to initiate actions (although, see Rosenbaum, Weber, Hazelett, & Hindorff, 1986). If computational efficiency accounts of motor history effects are valid, reuse of previous motor plans should lead to faster response times to initiate actions. Here we provide such evidence. We show that RTs are faster for successive actions involving the

same hand, presumably because specification of the parameter ‘hand’ is made more efficient when recalled from recent memory versus newly programmed.

In contrast to hand selection, the current findings provide no evidence for the influence of recent motor history on grasp selection. With respect to RTs, our study was best suited to address the possibility of grasp selection priming *between* versus *within* hands. While it is possible that our results showing faster RTs for IR versus HR conditions partly reflect *within-hand* grasp priming, we cannot disentangle this possibility from the likelihood that these differences (also) reflect the fact that tools are repeated for the IR condition, and thus retrieval of tool-defined rules is made easier. In a study by Cant et al. (2005), participants used their right hands to grasp objects presented in one of two orientations, and each object orientation elicited a distinct grasp. Using a priming design similar to the current study, RTs were found to be the same for repeated versus non-repeated grasp conditions. In other words, their results showed no evidence for *within-hand* grasp selection priming. Here, we find no evidence for *between-hand* grasp selection priming; RTs for GR versus NR conditions failed to show reliable differences. Both sets of results are consistent with the view that grasp history is of little importance for future grasp planning and selection.

Inconsistent with this account, however, others have shown that grasp selection can reflect recent grasp history at the cost of ending actions relatively uncomfortably (e.g., Rosenbaum & Jorgensen, 1992), at odds with end-state comfort effects (for review, see Rosenbaum et al., 2012). Moreover, Dixon et al. (2012) recently showed that such history effects can transfer between hands. These findings directly conflict with ours. Our video results showed very few trials where grasps were inconsistent with end-state comfort effects, and further, these instances did not disproportionately occur for HR/NR conditions (see Supplementary Materials). How can these apparent discrepancies be reconciled? Here we consider the possibility that grasp history effects may depend on the relative costs of repeating grasps.

In the current study, selecting grasps that were inconsistent with end-state comfort meant that participants ended up in body positions at extreme joint angles, to an extent that it was more difficult to complete the task (see Supplementary Materials for examples from video data). In contrast, previous studies showing effects of grasp history have tended to involve tasks where repeating features of recent grasps did not greatly impede task performance. For example, in the work by Dixon et al. (2012), the biomechanical consequences of repeating recent grasps when at odds with end-state comfort were minimal – in doing so, participants were still able to complete the task relatively comfortably. We conjecture that when the costs of repeating grasps are high, history effects may be nullified. Consistent with this hypothesis, others have shown that grasp history effects are diminished when biomechanical consequences of repeating actions are high (e.g., Cohen & Rosenbaum, 2011). The current results may provide a new, more pronounced example of this, whereby the absence of history effects for grasp is attributable to the relatively high costs of repeating grasps without predicting the biomechanical outcomes. Notably, in the study by Cant et al. (2005), the costs of repeating grasps when at odds with target object orientations were also high. A corollary of this interpretation is that the system underlying action selection is flexible, able to adjust the relevance of different factors according to task constraints (Hughes & Franz, 2008; van der Wel & Rosenbaum, 2010). Generating a better understanding of how the different factors that can influence action selection are balanced according to task is an important objective for future work.

Finally, it is worth mentioning that the nature of motor history effects remains uncertain. Here we interpret our repetition effects as arising from computational gains in the processes that underlie hand selection, and speculate that this involves the recycling of recently executed motor parameters that transiently persist within the sensorimotor system. While

other findings support similar accounts (e.g., Jax & Rosenbaum, 2007), Dixon et al. (2012) provide compelling evidence for grasp history effects based on episodic memory representations. Their grasp history results were sensitive to contextual similarity, seemingly tied to object identity, and were shown to persist across several intervening trials involving distinct grasps. Still, we find it difficult to attribute the current results showing hand selection priming to mechanisms underlying episodic memory retrieval. Clearly more research is needed to better elucidate the nature of motor history effects.

In the current study we show that planning times associated with hand selection for an object grasping task are influenced by recent hand selection history. We believe that a better understanding of the principles that govern hand selection will have important implications for improving therapeutic and rehabilitation programs for patients suffering from movement disabilities associated with one or both of their upper limbs. We are presently pursuing a functional MRI variant of the current task that we predict will provide new insights as to which brain areas are important for selecting and switching between hands for actions.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Figure 1. Methods

(A) The experimental setup is shown from an overhead view. Tools are presented centrally, flanked on either side by left and right placement platforms, with outside and inside placement positions specified by horizontally-oriented sets of hash marks. Outside object placement tasks for both left and right handed actions were predicted to involve neutral grasp postures while inside placement tasks were predicted to involve pronated grasp postures. (B) Four conditions were defined by the relationship between prime and probe events. The top part of the figure indicates the timing of events and the state of the LCD goggles within a trial.

Figure 2. RT results

Group mean RTs are shown as a function of Hand (A), Grasp (B), and Condition (C). Error bars reflect mean standard errors. There were no reliable differences between RTs for actions made with the right (RH) versus left (LH) hands, or for actions made with pronated (Pro) versus neutral (Neu) grasp postures. There was a significant main effect of Condition. Post-hoc pairwise comparisons revealed hand selection priming, evident as the mean difference between RTs for NR – HR conditions (*upper right panel*). Error bars reflect 95% confidence intervals based on the standard errors of the mean difference scores (NR – HR) across individuals. Conversely, there was no reliable evidence for grasp selection priming, shown as the mean difference between RTs for NR – GR conditions (*lower right panel*), not statistically different from zero. Error bars reflect 95% confidence intervals based on the standard errors of the mean difference scores (NR – GR) across individuals. (* indicates $p < .05$, ** indicates $p < .001$).

Table 1

Video observations

Number of trials observed to involve hand, grasp, placement, or experimenter errors per condition across all individuals. Hand errors occurred when movements were initiated with the wrong hand, grasp errors occurred when grasp choices were inconsistent with end-state comfort effects, placement errors occurred when tools were placed in wrong positions/orientations, and experimenter errors occurred when the experimenter placed down the wrong tools. Overall, very few trials were observed to involve any given type of error, evident as the percent values per error type per total number of trials. Data reflect observations recorded from a single rater, and Cohen's Kappa coefficients indicate measures of inter-rater reliability. See Supplementary Materials for results of Chi-Squared tests of observed versus expected frequencies for hand and grasp errors per condition.

Error Type	IR	HR	GR	NR	Total	Cohen's Kappa
Hand	2	8	11	14	35 (1.7%)	0.77
Grasp	1	6	15	13	35 (1.7%)	0.84
Placement	0	1	3	4	8 (0.4%)	0.80
Experimenter	2	4	5	4	16 (0.8%)	0.87