Coordinating Initial and Final Action Goals in Planning Grasp-to-Rotate Movements: An ERP Study

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Abstract

Action goals have often been investigated in previous studies within a single action. However, most of the manual actions (such as prehension) are not restricted to a single action towards the object but can involve multiple follow-up actions to achieve a further purpose. The coordination of the initial (grip posture) and final (task purpose) action goals within such complex actions is still not fully understood. In the present experiment, the neural mechanisms underlying the goal coordination were investigated with the help of event-related potentials (ERP). With the "first cue – second cue – imperative signal" design, the action goals were presented separately in different sequences (either "final-initial" or "initial-final"), and participants were instructed to plan and execute a grasp-to-rotate movement with either free-choice or specified grasping. Results revealed that shorter reaction times were needed for the final-initial than for the initial-final trials only when the movement requires a free-choice grasping. At the moment when the goal information was incomplete (the first cue), final goals evoked a larger anterior P2 than initial goals, whereas initial goals elicited a larger anterior N2 and a more robust frontal negativity (400 to 550 ms) than final goals. When the goal information was complete (the second cue), we only found a larger P2 for final goals than for initial goals in free-choice grasping. Moreover, a larger N2 was also found for the specified than for the free-choice grasping in initial-final trials. These neurophysiological results indicate that final goals are more critical than initial grip postures in planning prehensile movements. The initial and final action goals seem to be preferably coordinated in a hierarchical manner, that is, the final task purpose is processed with precedence, whereas the initial grip posture is selected depending on the final task purpose.

Keywords:

motor planning /action goal /grasp /event-related potentials (ERP) /P2

INTRODUCTION

Most of the movements we perform every day are directed by desired goals instead of external stimuli (Hommel et al., 2001; Waszak et al., 2005). The term "action goal" entails the idea of "the final consequence of the movement" (almost) automatically. The final consequence, to some degree the desired final body posture, is anticipated by the actor, and the movement is stopped when the current posture fits the desired one, that is, when the final action goal is reached or satisfied (Dickinson and Balleine, 1995; Dolan and Dayan, 2013). However, the "final consequence" may be an adequate description for single actions, but not for complex movements that we perform every day. For example, the purpose of prehensile movements is not fulfilled with reaching and grasping, but manipulating the target object for later, overarching goals. The whole movement can be treated as a combination of single actions, and every single action has its own goal. That is, the action goal is always confounded with the intention of the last action. The intermediate states, such as the way to grip the object, are frequently neglected.

We usually do not pay much attention to how to grasp something, still, it is planned cognitively. Grasp planning requires the actor to select a particular combination of single actions from a possible movement set that contains nearly infinite possible options (Herbort and Butz, 2012; Wunsch et al., 2015). People tend to pick out the one which can optimally support achieving the final task goal. For example, when transporting a glass, individuals usually grip the glass with a thumb-up posture and then move it. However, when rotating an upside-down glass, most people tend to start with a less comfortable (thumb-down) posture and finish in a more comfortable (thumb-up) posture. This phenomenon has been termed as the "end-state comfort" effect, and it was first proposed by Rosenbaum (1990). Inspired by this seminal pioneering research, the end-state comfort effect was found in a considerable amount of manual tasks, and it was also suggested to be one of the most critical constraints for grasp planning (Rosenbaum et al., 2012 for review). The end-state comfort effect indicates the anticipating effect in movement preparation, that is, final task demands affect the selection of initial grip postures. On the other hand, end-state comfort studies also suggest both initial grip postures and final task demands should be studied in motor planning.

The selection of initial and final actions has been discussed in previous studies (Rosenbaum et al., 2012). Behavioral results (Rosenbaum et al., 1990; Cohen and Rosenbaum, 2004; Weigelt and Schack, 2010; Seegelke et al., 2011; Herbort and Butz, 2015; Belardinelli et al., 2016), as well as kinematic data (Ansuini et al., 2006; Zhang and Rosenbaum, 2008; Hughes et al., 2012), suggest initial grasp postures are selected for achieving the final task goal effortlessly. Moreover, in other studies (Van Schie and Bekkering, 2007; Westerholz et al., 2013), participants reacted faster when the final task goals were emphasized, even though the same movements were performed in both final- and initial-emphasized conditions. Altogether, these results indicate that grasp planning is primarily based on final goals, and the initial goals (grips) are determined by final goals. It can be further assumed that the initial and final goals are coordinated in a hierarchical manner: final goals are selected first, and then the corresponding initial goals are selected. Nevertheless, previous studies mainly focused on the outcome of movement selection, but not the selection itself. Hence, whether the initial and final action goals are processed in a hierarchical manner needs further clarification.

Going beyond behavioral studies, researchers have explored initial and final action goals from a neuroscientific perspective. A fronto-parietal network has been implicated in action organization for non-human primates (Jeannerod et al., 1995; Fogassi et al., 2005; Bonini et al., 2010) and humans (Hamilton and Grafton, 2006; Majdandžić et al., 2007; Marangon et al., 2011; Koester and Schack, 2016). To study the neural representation of action goals, Bonini et al. (2012) trained monkeys to grasp different objects (in shape) for different purposes (eat or place) and recorded the electrophysiological activities of the grasping neurons during the movement. Results suggest that the neurons reflect first "how" the object was grasped (initial goal) before grasping and then "why" the action was performed (final goal) during object transportation. Van Schie et al. (2007) investigated the neural mechanisms of initial and final goals in humans. In their study, participants were cued to grasp an object precisely and then transport it to one of the two target positions (precision grips). Either the initial (the way to grasp) or the final (target position) action goals were emphasized in the cues. Results suggest that initial and final goals are processed separately during grasping: the parietal-occipital sulcus was claimed to be involved in processing initial goals, while frontal regions were claimed to be involved in processing final goals. The temporal organization of neural activities is consistent with the primate study (Bonini et al., 2012): parietal slow waves peaked first when the object was grasped, and then peaked later over the left frontal areas when the object reached the target position. In another study (Westerholz et al., 2013), a similar temporal organization pattern was also found with goal-directed power grips. Those neurophysiological studies indicate that initial and final goals are processed sequentially. Increased posterior activities for initial goals are detected beforehand, and increased anterior activities for final goals are detected later. Nevertheless, the increased activities are only observed during movement execution, and the activation-sequence is also consistent with the involved actions. Therefore, the neurophysiological activations may reflect the online monitoring of motor plans instead of the action goal coordination. Hence, the existing results cannot clarify whether the action goals are coordinated sequentially or not.

In most previous studies, participants were cued with either integrated (both initial and final goals) or incomplete (only one of the goals) information. In such paradigms, it is difficult to distinguish between the cognitive processes related to initial and final action goals. Here, we sought to separate the processing for investigating the action goals coordination. The goals are cued with separated visual stimuli, and the stimuli are presented progressively. The sequence of the stimuli is manipulated in two ways, according to a hierarchical (final-initial) or a sequential (initial-final) processing of (sub) goals. Event-related potentials are used to distinguish the neural processes associated with the initial and final goals during motor planning. Besides, it has been reported that the planning and execution of free-choice grasping and specified grasping differs from each other (Westerholz et al., 2014b, 2014a), and the free-choice grasping seems to be much closer to the movements we use every day. Therefore, we investigated the action goal coordination in both free-choice and specified grasp tasks.

Based on previous results (Rosenbaum et al., 1992; Van Schie and Bekkering, 2007; Zhang and Rosenbaum, 2008; Weigelt and Schack, 2010; Hughes et al., 2012; Westerholz et al., 2013; Herbort and Butz, 2015), we assume that action goals are organized hierarchically during motor planning, that is, final goals (task purposes) are processed before initial goals (grip postures) when generating a motor plan. In agreement with this assumption, different neural activities between initial and final goals are expected when goal information is incomplete (first stimuli) because final goals are more critical than initial grips in motor planning (Rosenbaum et al., 1992; Westerholz et al., 2013).

More specifically, we expect a larger anterior P2 component for the final than the initial goal, since the anterior P2 has been associated with action planning and selection (Van Elk et al., 2010b, 2010a; Hakkarainen et al., 2012) and its amplitude is modulated by the evaluation of task-relevant feature of stimuli (Kenemans et al., 1993; Smid et al., 1999; Potts, 2004; Potts et al., 2004, 2006), as well as the organization of upcoming responses (Makeig et al., 1999; Gajewski et al., 2008; Nikolaev et al., 2008). We also expect a larger anterior N2 component for the initial than for the final goal, since the anterior N2 has been associated with conflict processing (Wang et al., 2000; Folstein and Van Petten, 2008), and planning the movement without knowing the task purposes is an unfamiliar situation for individuals, which may entail some conflicts with the (familiar) way to process the action goals (hierarchical).

We do not expect different neural activities between initial and final goals when goal information is complete (second stimuli) because individuals receive the same amount of goal information at that moment. Moreover, based on previous findings (Westerholz et al., 2014a, 2014b), we also expect different neural activities (ERP slow waves) for different grip selections (specified, free-choice) in both first and second stimuli.

METHOD

Participants

Thirty students from Bielefeld University voluntarily participated in the experiment. However, four of them were removed due to EEG artifacts (less than 30 trails remained after artifact rejection). Finally, 26 participants (mean ± SD, age: 25.6 ± 3.9, 18 females) entered into data analyses. All participants were right-handed (Edinburgh Handedness Inventory: 84.2 ± 15.8, Oldfield, 1971) with normal or correct-to-normal vision, and none of them had known neurological disorders. Participants were compensated with either 15€ or two participation credits. The experiment was approved by the ethics committee of Bielefeld University. All participants gave their written informed consent following the Declaration of Helsinki.

Apparatus and design

Participants were asked to perform a grasp-to-rotate task with a rotation device shown in Figure 1 (cf. Westerholz et al. 2014b). A handle with two colored ends (yellow and blue) was attached to a rotatable disk. A pointing marker settled on the disk, which was used to illustrate the orientation of the handle. The marker was in-line with the handle and stayed close to the yellow end. Eight dial-displayed target positions were fixed outside of the disk. Participants were instructed to hold the handle with full-hand (power grip) and rotate the handle (pointing marker) to one of the target positions according to the given cues. A start button was placed in front of the device. By pressing the button, the handle moved and stopped at the start position automatically. In 80% of trials, participants were guided to perform 180-degree rotations (experimental trials). The remaining 20% of trials were used as filler trials in which the rotation degrees were random but not 180. The fillers were used to prevent participants from anticipating the target position. The handle could be rotated clockwise or counterclockwise, but changing direction during rotation was not allowed.

Please insert Figure 1 here.

Visual cues were presented by Presentation (Neurobehavioral Systems) on a 19-inch TFT monitor. Colored squares were used to cue the initial goals. The color indicated grip selection. Yellow represented the thumb-toward posture that the handle was held with thumb towards the yellow end, and blue represented the thumb-away posture that the handle was held with thumb towards the blue end. Participants had to grasp in consonance with colors on the handle (specified grasping). However, if the color was grey, participants could choose their postures (either thumb-toward or thumb-away, free-choice grasping). Final action goals were cued by white arrows. The arrows were shown in eight different orientations, which were associated with the target positions.

The colored squares and arrows were presented progressively, which followed the sequence either "initial-final" ("square-arrow") or "final-initial" ("arrow-square"). The cue sequence indicated different manners for action goal coordination: the "initial-final" represented a sequential manner (chronological order) in which the initial action goal was processed first; the "final-initial" represented a hierarchical manner in which the final action goal was processed first (see Figure 2).

Please insert Figure 2 here.

Procedure

After the EEG preparation, participants were seated in an electrically shielded room. The monitor was placed in front of participants, and the distance was about 75 cm. The rotation device was put next to the monitor, and the center faced the shoulder of participants' grasping arm. The rotation device was calibrated to each participants' size to prevent expansive movements. The start button was positioned in front of participants with a distance of about 20 cm. Participants were allowed to move the chair back and forth to ensure comfortable movements. Then a written instruction was given to participants. All of the questions regarding the experimental task were answered. Before the experimental trials, participants were asked to perform 24 practice trials to be familiar with the task. These practice trials were also used to detect noticeable individual artifacts in the EEG signals (such as gross movement artifacts).

Each experimental trial started with a self-paced button press. After the button press, the handle (pointing marker) moved to the start position. The start positions were randomized across trials, and each target position had the same number to start. Then, participants were instructed to hold the button until they heard a tone. Simultaneously, a fixation cross was shown with a variable duration from 500 to 1500 ms. Following the cross, the visual cues were presented one after another with a fixed duration of 2000 ms each. The cues were presented in the sequence, either “square-arrow” or “arrow-square”. Participants were asked to plan the upcoming movements only in mind and keep holding the button. Two seconds after the second cue, the imperative signal, a 400 Hz sinusoidal tone, was played for 100 ms. The tone was an imperative cue to initiate the grasp-to-rotate movement. The second cue disappeared after the handle (pointing marker) reached the target position. Henceforth, participants were guided to press the button again for the next trial. When the button was released before the tone, error feedback was presented for 1500 ms, and then the handle moved to a new start position (for the next trial) automatically.

Please insert Figure 3 here.

There were a total of 320 trials in the experiment, and the trials were equally divided into two blocks. Trials from 4 different conditions (cue sequence × grip selection) were randomly presented. To prevent the laterality effect caused by handedness (Westerholz et al., 2013), we instructed participants to use one hand for the first block and the other hand for the second. Half of them started with the right hand, and the rest started with the left hand. The starting hand was counterbalanced across participants. Participants received a 3-min break after performing every 40 trials. After the first block, the rotation device was moved and re-calibrated at the other side. The filler trials were randomly assigned to the experiment, and there were a total of 64 trials for each condition.

After the experiment, subjective difficulty ratings for different grips (from 1 to 6, from easy to difficult) were collected by a post-experiment questionnaire. The total experiment time was around 2 hours.

Behavioral and electrophysiological recordings

Participants’ performance was recorded by a video camera. By using micro-switches, time points of lifting hands from the start button, starting to rotate the handle, and reaching the target position were detected. Reaction time was defined as the duration between the imperative cue and hands lifting. Reach time was defined as the duration between the hands lifting and the beginning of the rotation. Rotation time was defined as the duration between the beginning of the rotation and reaching the target position.

The EEG signals were recorded by an ANT 64-channel amplifier (ANT Neuro) with WaveGuard EEG caps. Sixty-four Ag/AgCl electrodes were arranged on the cap according to the international 10-10 system. Two bipolar electrodes were used to record the vertical and horizontal EOG. The impedance of all electrodes was kept below 5kΩ. The signals were average-referenced during recording, and AFz was chosen as the recording ground. All signals were sampled at 512 Hz and filtered from DC to 138 Hz online before digitization and storage by ASA 2.0 (ANT Neuro).

Data analysis

The performance videos were analyzed offline. Trials that contained wrong grasp posture, changing grasp posture during execution, or letting the handle go before reaching the target positions were marked as errors and excluded from the behavioral and neurophysiologic analysis. It has been argued that manual asymmetries (laterality) are hardly evident in planning grasping movement (Seegelke et al., 2014 for review). Besides, we double-checked the results, and no main effects as well as interactions involving "hand use" were found. Therefore, we pooled the left- and right-hand trials together in both behavioral and neurophysiologic analysis.

The reaction time, reach time, and rotation time were pre-processed by excluding extreme values (outside ± three standard deviations of the mean). Trials containing extreme value were also excluded from behavioral and ERP analyses. Table 1 shows the average number of remaining trials. To determine within-subject effects for *cue sequence* (final-initial, initial-final) and *grip selection* (specified, free-choice), we performed repeated-measures ANOVAs on participants' averaged reaction times, reach times, and rotation times separately.

EEG signals were analyzed offline in Matlab (MathWorks, USA) with EEGlab (Delorme and Makeig, 2004) and ERPlab (Lopez-Calderon and Luck, 2014). All signals were filtered with a high-pass at 0.01 Hz and a low-pass at 30 Hz. Then the filtered signals were re-referenced with the averaged bilateral mastoid electrodes. Independent Component Analysis (ICA) was applied to the continuous signals, and ocular artifact components were removed following the suggestions from previous studies (McMenamin et al., 2010; Mennes et al., 2010). A 4400 ms interval time-locked to the onset of the first cue was selected for ERP analyses (-400 – 4000 ms). Baseline correction was performed with the 400 ms pre-stimulus activity. The peak-to-peak moving window method was used for artifact detection (200 ms window; 50 ms steps). Epochs containing peak-to-peak amplitudes above the threshold of 80µV within the moving window were rejected. The epochs were also visually double-checked for artifacts that would have been missed by the detection algorithm. The numbers of remaining trials in different conditions and different cues were listed in Table 1.

Please insert Table 1 here.

To compare different cognitive processes in motor planning, we investigated the ERP components P2, N2, and P3 for both of the cues. Based on the previous literature (Luck et al., 1990; Hillyard and Anllo-Vento, 1998), mean amplitudes were obtained in the following time windows time-locked to the cues' onset: 175 – 225 ms (P2), 250 – 325 ms (N2), and 350 – 600 (P3) for the first cue, and 2175 – 2225 ms (P2), 2250 – 2325 ms (N2), and 2350 – 2600 (P3) for the second cue. The analyses were conducted over three different electrode clusters: frontal (F1, Fz, and F2), central (C1, Cz, and C2), and parietal (P1, Pz, and P2). The amplitudes were tested for significance using repeated-measures ANOVAs with the factors *cue sequence* (final-initial, initial-final), *grip selection* (specified, free-choice), and *area* (frontal, central, and parietal).

In addition, previous studies reported that different slow-wave potentials were found during grasping when emphasizing the initial or the final action goals (Van Schie and Bekkering, 2007; Westerholz et al., 2013). So, we also focused on slow-wave potentials from 600 ms to 2000 ms (the first cue) and from 2600 ms to 4000 ms (the second cue). The slow-wave potentials were tested in 4 regions of interest (ROI) to determine the scalp distribution. The 4 ROIs were anterior-left (AL): AF7, AF3, F5, F3, F1; anterior-right (AR): AF8, AF4, F6, F4, F2; posterior-left (PL): PO5, PO3, P5, P3, P1; posterior-right (PR): PO6, PO4, P6, P4, P2. We first performed a repeated-measures ANOVA with the factors *cue sequence* (final-initial, initial-final), *grip selection* (specified, free-choice), *front-back* (anterior, posterior), and left-right (left, right) for the mean amplitude of the slow waves in 100 ms step windows. Then we combined the windows that showing consecutive significant effects and compared the mean amplitude of the combined window as the final results. To correct for falsepositive effects, we only combined the windows if three or more consecutive windows revealed significant main or interaction effects (Van Schie and Bekkering, 2007; Westerholz et al., 2013, 2014b).

For all the ANOVAs we made, Greenhouse-Geisser correction was applied when evaluating effects with more than one degree of freedom. Post hoc multiple comparisons among means were calculated with Bonferroni-corrected *t*-tests. Generalized eta squared (η_G^2) was calculated for evaluating effect size.

RESULTS

Behavior & Timing

For specified grasping, participants executed correctly in 92% of the trials in the final-initial condition and 91% of the trials in the initial-final condition. For free-choice grasping, participants executed correctly in 95% of the trials for both final-initial and initial-final conditions. Participants used thumb-toward posture in 75% of the free-choice trials. The probability of thumb-toward grasping was shown in Figure 4. Participants rated the difficulty of free-choice grasping for 1.27 on average (range 1-easy to 6-difficult). The average difficulty was 1.65 for thumb-toward trials and 2.31 for thumb-away trials in specified grasping. Paired *t*-tests revealed the rating was significantly lower for the free-choice than specified grasping, $t_{25} = -4.05$; $p < 0.001$.

Please insert Figure 4 here.

Participants' average reaction times, reaching times, and rotation times are shown in Figure 5. The ANOVA for reaction times revealed no main effect for the factor *cue sequence* (initial-final, final-initial) or *grip selection* (free-choice, specified) but a significant interaction between *cue sequence* and *grip selection*, $F_{1, 25} = 5.24$; $p < 0.05$; $\eta_G^2 = 0.029$. Further analyses showed that reaction time in final-initial trials (526 ms) was significantly shorter than initial-final trials (541 ms) for free-choice grasping, $t_{25} = -3.04$; $p < 0.01$, whereas the reaction time between different cue sequences was similar for specified grasping, $t_{25} = 1.11$; $p > 0.05$.

For the analysis of reach times, the ANOVA only revealed a main effect on *grip selection*, $F_{1, 25} = 24.56$; $p < 0.001$; $\eta_G^2 = 0.018$. Participants moved faster towards the handle in free-choice conditions (668 ms), as compared to specified conditions (623 ms).

A main effect for *grip selection* was also found in the analysis of rotation time, $F_{1, 25} = 15.99$; $p < 0.001$; $\eta_G^2 = 0.016$. Surprisingly, a significant interaction was also found between *cue sequence* and *grip selection*, $F_{1, 25} = 6.16$; $p < 0.05$; $\eta_G^2 = 0.001$. Further analysis revealed a significant *cue sequence* effect for free-choice grasping, $t_{25} = -2.53$; $p < 0.05$. Participants moved faster in the final-initial condition (768 ms) than the initial-final condition (783 ms). By contrast, no *cue sequence* effect was found for specified grasping, $t_{25} = 1.05$; $p > 0.05$. Meanwhile, significant *grip selection* effects were found in both final-initial condition, $t_{25} = 4.79$; $p < 0.001$, and initial-final condition, $t_{25} = 2.80$; $p < 0.05$. The handle was moved faster for the free-choice grasping (776 ms) than the specified grasping (829 ms).

Please insert Figure 5 here.

Electrophysiology

ERPs at the first cue (incomplete information)

In this section, reported ERPs are time-locked to the first cue (0 to 2000 ms). At this point, participants only receive incomplete goal information. The "initial goal" here refers to the cue's instruction of grip posture, and the "final goal" refers to the cue's instruction of the target (handle) position of the movement.

P2 (175 to 225 ms) With the factors *cue sequence* (final-initial, initial-final), *grip selection* (specified, free-choice), and *area* (frontal, central, and parietal), the ANOVA of P2 amplitude revealed a significant interaction effect for *cue sequence* * *area*, $F_{2,\,50} = 13.85$; $p < 0.001$; $\varepsilon = 0.637$; $\eta_G^2 = 0.006$, a significant main effect for *cue sequence*, $F_{1,\,25} = 24.75$; $p < 0.001$; $\eta_G^2 = 0.116$, and a significant main effect for *area*, $F_{2,\,50} = 3.74$; $p < 0.01$; $\varepsilon = 0.713$; $\eta_G^2 = 0.013$. Further analyses yielded significant *cue sequence* effects at all areas (all *t*s > 3.65, all *p*s < 0.01). The P2 amplitude was larger in the trials with final goal (final[1]-initial, 2.80 µV), as compared to the trials with initial goal (initial-final, 0.59 µV). The *area* effect was significant only in the final-initial condition, $F_{2,\,50} = 8.00$; $p < 0.01$; $\varepsilon = 0.706$; $\eta_G^2 = 0.034$. Post hoc analyses revealed P2 amplitudes at the frontal (3.22 µV) and central area (3.19 µV) were significantly larger than the parietal area (1.98 µV), all *t*s > 3.41; all *ps* < 0.01. However the amplitude difference was not significant between the frontal and central area, $t_{25} = 0.10$; $p > 0.05$. No significant *area* effect was found for the P2 amplitude in the initial-final condition, $F_{2,\,50} = 0.58$; $p > 0.05$; $\varepsilon = 0.723$.

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[1] The underline implies the type of action goal which was presented in this condition for the current analysis epoch. For example, the "final-initial" here indicates the final goal (arrow) was presented in the "final-initial" condition as the first cue. Same as below.

N2 (250 to 325 ms) In the analysis of N2, we found a significant main effect for *cue sequence*, $F_{1,\,25} = 5.86$; $p < 0.05$; $\eta^2_G = 0.011$. The mean amplitude was more negative in the initial-final condition (-0.14 μV), as compared to the final-initial condition (0.79 μV). In addition, a significant main effect for *area* was also found, $F_{2,\,50} = 10.63$; $p < 0.001$; $\varepsilon = 0.604$; $\eta^2_G = 0.031$. Post hoc analyses revealed that the mean amplitude of N2 was more negative at the frontal (-0.27 μV) and the central areas (-0.13 μV) than the parietal area (1.37 μV), all *t*s > 1.51; all *ps* < 0.01. No interaction effect was found in the analysis of N2.

P3 (350 to 600 ms) A significant interaction effect for *cue sequence* * *area*, $F_{2,\,50} = 14.62$; $p < 0.001$; $\varepsilon = 0.716$; $\eta^2_G = 0.006$, was found in the analysis of P3 mean amplitude. The main effect for *cue sequence*, $F_{1,\,25} = 11.43$; $p < 0.01$; $\eta^2_G = 0.022$, and the main effect for *area*, $F_{2,\,50} = 19.58$; $p < 0.001$; $\varepsilon = 0.619$; $\eta^2_G = 0.072$, were also significant. Further analyses yielded that P3 for final-initial trials (0.38 μV) was more positive than initial-final-trials (-0.83 μV) at the frontal area, $t_{25} = 3.91$; $p < 0.001$. Besides, at the central area, the P3 mean amplitude was also larger in the final-initial (0.91 μV) than initial-final trials (-0.003 μV), $t_{25} = 3.64$; $p < 0.01$. The mean amplitude of P3 was not different between the different cue sequences at the parietal area, $t_{25} = 1.13$; $p > 0.05$. Moreover, the *area* effects were also significant in both cue sequences, all *F*s > 8.41; all *p*s < 0.01. In the initial-final condition, the mean amplitude of P3 was larger at the parietal area than the frontal and central areas, all *ts* > 1.44; all *p*s <0.001. The P3 mean amplitude was also larger at the central area than the frontal area, $t_{25} = 2.87$; $p < 0.05$. However, in the final-initial condition, the mean amplitude of P3 at the parietal area was only larger than the frontal area, $t_{25} = 4.08$; $p < 0.001$. No other significant effects were found for the P3s in the final-initial trials.

Slow-wave potentials (600 to 2000 ms) With the factors *cue sequence* (final-initial, initial-final), *grip selection* (specified, free-choice), *front-back* (anterior, posterior), and *left-right* (left, right), the ANOVAs for average slow waves in successive 100 ms time windows yielded continuous significant interaction effects for *cue sequence* * *grip selection* from 600 to 1300 ms, and continuous significant interaction effects for *cue sequence* * *front-back* from 600 to 2000 ms. The results of these ANOVAs can be found in the supporting information (Table S1).

Following the continuous significant effects, we combined the time windows and compared the mean amplitude of slow waves in a larger, combined time window (600 to 2000 ms). In the combined window, ANOVA showed a significant interaction effect for *cue sequence * front-back*, $F_{1, 25} = 28.26$; $p < 0.001$; $\eta_G^2 = 0.015$, and a significant interaction effect for *cue sequence * grip selection*, $F_{1, 25} = 6.39$; $p < 0.05$; $\eta_G^2 = 0.008$. The main effect for front-back was also significant, $F_{1, 25} = 20.47$; $p < 0.001$; $\eta_G^2 = 0.029$. Further analyses yielded that in the final-initial condition, the mean amplitude of the anterior slow waves (0.71 µV) was more positive than the posterior slow waves (-0.56 µV), $t_{25} = 5.76$; $p < 0.001$. Moreover, the mean amplitude of slow waves was also larger for free-choice grasping in the initial-final condition (0.36 µV) than free-choice grasping in the final-initial condition (-0.12 µV), $t_{25} = 2.09$; $p < 0.05$. No other significant effects were found in further analyses.

Please insert Figure 6 here.

ERPs at the second cue (complete information)

In this section, ERPs at the second cue (2000 – 4000 ms) are reported. At this point, participants have received the remaining goal information. Together with the first cues, participants have complete goal information. Same as the first cue, "initial goal" here refers to the second cue's instruction of the grip, and "final goal" means the second cue's instruction of the target (handle) position of the given grasping action.

P2 (2175 to 2225 ms) With the factors *cue sequence* (final-initial, initial-final), *grip selection* (specified, free-choice), and *area* (frontal, central, and parietal), the ANOVA of P2 amplitude revealed a significant interaction effect for *cue sequence * grip selection*, $F_{1, 25} = 12.98$; $p < 0.01$; $\eta_G^2 = 0.014$. The main effects for *cue sequence*, $F_{1, 25} = 6.44$; $p < 0.05$; $\eta_G^2 = 0.037$, and for *area*, $F_{2, 50} = 22.86$; $p < 0.001$; $\varepsilon = 0.870$; $\eta_G^2 = 0.086$, were also significant. Further analyses yielded that the mean amplitude of P2 was larger in the initial-final condition (4.37 µV) than the final-initial condition (1.98 µV) for free-choice grasping, $t_{25} = 3.47$; $p < 0.01$. However, for specified grasping, the amplitude difference was no significant between the initial-final (2.52 µV) and final-initial (3.10 µV) conditions, $t_{25} = 1.00$; $p > 0.05$. Moreover, for the *grip selection* effect, results yielded that the P2 amplitude was significantly larger for free-choice grasping than specified grasping in the initial-final condition, $t_{25} = 4.88$; $p < 0.001$. No significant *grip selection* effect was found in the final-initial condition, $t_{25} = 1.03$; $p > 0.05$.

N2 (2250 to 2325 ms) The ANOVA of N2 amplitude revealed a significant interaction effect for *cue sequence* * *grip selection*, $F_{1,25} = 5.38$; $p < 0.05$; $\eta_G^2 = 0.004$. Further analyses revealed that the *grip selection* effect was significant in the initial-final condition, $t_{25} = 3.07$; $p < 0.01$. The mean amplitude of N2 was more positive for the free-choice grasping (3.07 μV) than the specified grasping (1.91 μV). No other significant effects were found.

P3 (2350 to 2600 ms) The ANOVA of P3 amplitude yielded a significant main effect for *area*, $F_{2,50} = 6.93$; $p < 0.01$; $\varepsilon = 0.843$; $\eta_G^2 = 0.024$. Post hoc analyses yielded that the mean amplitude of P3 was larger at the central (1.82 μV) and the parietal (2.00 μV) areas than the frontal area (0.66 μV), all *t*s > 2.98; all *p*s < 0.05. The P3 amplitude was not significantly different between the central and parietal areas, $t_{25} = -0.45$; $p > 0.05$.

Slow-wave potentials (2600 to 4000 ms) With the factors *cue sequence* (final-initial, initial-final), *grip selection* (specified, free-choice), *front-back* (anterior, posterior), and *left-right* (left, right), the ANOVAs for 100 ms time windows only revealed continuous significant interaction effects for *cue sequence* * *grip selection* from 2800 to 3600 ms. The results of these ANOVAs can be found in the supporting information section (Table S2). Following the continuous significant effects, we combined the time windows and compared the mean amplitude of slow waves in the combined window (2800 to 3600 ms). The ANOVA revealed a significant main effect for *front-back*, $F_{1,25} = 6.03$; $p < 0.05$; $\eta_G^2 = 0.017$, and a significant interaction effect for *cue sequence* * *front-back*, $F_{1,25} = 11.59$; $p < 0.01$; $\eta_G^2 = 0.004$. Further analyses yielded that in the final-initial condition, the mean amplitude of slow waves was larger over the anterior (0.89 μV) than the posterior areas (-0.30 μV), $t_{25} = 3.40$; $p < 0.01$, whereas in the initial-final condition, the *front-back* effect was not significant, $t_{25} = 1.27$; $p > 0.05$. A brief summary of the main ERP results can be seen in Table 2.

Please insert Figure 7 here.

Please insert Table 2 here.

DISCUSSION

With the help of ERP, we explored the coordination of initial (grip posture) and final (task purpose) action goals in planning specified or free-choice manual actions. The goals were pre-cued by two successive visual stimuli in the sequence, either “final-initial” or “initial-final”. Reaction times were only shorter for the final-initial trials compared to the initial-final trials when participants were asked to perform free-choice grasping. At the moment when only incomplete information was available (the first cue), a larger anterior P2 and a larger P3 were found for the final than the initial goals. Conversely, the anterior N2 was larger for the initial than for the final goals. Moreover, the slow-wave potentials (600 – 2000ms) were more positive-going for the initial than the final goals in free-choice grasping. At the second cue, when the goal information was complete, we only found a larger P2 for the final goals than for the initial goals in free-choice grasping. Moreover, an increased N2 was also found for the specified compared to the free-choice grasping in the initial-final trials. Overall, the results suggest that cognitive processes differ between initial and final action goals during motor planning. The “final-initial” sequence seems to be a more effective way of processing the goals than the “initial-final,” thus broadly supporting the hierarchical hypothesis.

The probability of thumb-toward grips indicates that participants tended to hold the handle with thumb-toward posture in free-choice conditions. The tendency is consistent with the previous literature and termed as thumb-toward bias (Rosenbaum et al., 1983). Compared to the results in previous research (Westerholz et al., 2014b), the thumb-toward bias in our experiment seems to be somewhat weaker, even though we used a similar rotation apparatus and movement tasks (180-degree rotations). Compared to the previous study, the weaker thumb-toward bias in the current study can be attributed to lower time pressures. Participants were asked to move as soon as they received the cues in the previous study, whereas in the current study, the “pre-cue and imperative” design gave participants enough time to plan the movement, which may result in more (cognitive) thumb-away instead of (intuitive) thumb-toward postures to ensure an end-state comfort.

Participants rated the free-choice grasping as easier than the specified grasping. Also, the thumb-towards grips were also rated easier than the thumb-away grips. The findings are in line with the previous study (Westerholz et al., 2014b). Self-regulated actions seem to be more flexible and modifiable than actions with instructed plans, as suggested by Fleming et al. (2009), so less cognitive effort may be needed for the free-choice grasping in accordance with the current difficulty ratings.

Due to the "pre-cue and imperative" design and the long preparation duration (four seconds in total before the imperative signal), we did not expect reaction times were different among the different conditions. Surprisingly, we found participants reacted faster for free-choice grasping in the final-initial than the initial-final condition, whereas no difference was found for specified grasping between the cue sequences. Compared to the final-initial condition, planning a free-choice grasping in the initial-final condition seems to be an unfamiliar (less preferred) preparation mode because initial grip postures are selected based on the final task demands (Hughes et al., 2012; Rosenbaum et al., 2012; Westerholz et al., 2013; Wunsch et al., 2015). Even though participants had enough time for a well-established motor plan before the imperative signal, they might "double-check" the motor plan after the imperative signal to avoid potential errors. Compared to the familiar preparation mode (final-initial), the unfamiliar mode demands more "double-check" processing because participants had less experience in it, and they tried to prevent errors. Accordingly, longer reaction times seem to be a consequence of the unfamiliar preparation mode.

Another explanation could be that participants had less effective preparation time for free-choice grasping in the initial-final condition. A free-choice initial goal seems to be insufficient for movement preparation until a final goal (target position) is given. Thus, for free-choice grasping in the initial-final condition, effective motor planning apparently started after the final goal (second cue) is given. However, for specified grasping in the final-initial condition, participants may have started to plan their movements right after the first cue, which means the effective preparation time is twice as much as what they have in the initial-final condition. The motor plans established within less effective preparation durations may have prolonged the reaction time for free-choice grasping in the initial-final condition.

The reach and rotation time differed significantly between free-choice grasping and specified grasping. Participants moved faster in free-choice conditions than specified conditions. These results are consistent with previous findings (Westerholz et al., 2014a, 2014b). It is argued that movements are executed faster for free-choice conditions because free choice actions are more flexible and modifiable than the actions with specified movement plans (Fleming et al., 2009).

Interestingly, for rotation times, we found a significant interaction effect between *cue sequence* and *grip selection*. Further analysis revealed that the handle was rotated more slowly in the initial-final compared to the final-initial condition for free-choice grasping. The explanation can be that participants selected less optimal initial grips in the initial-final condition. Participants started motor planning after the second cue was presented in the initial-final condition when the grip selection was free-choice. Compared to the final-initial condition, participants had less effective time for selecting an optimal initial grip to finish the rotation (for example, using thumb-away grasping if the target was located at the lower part of the disk to ensure a comfortable rotation). In the initial-final condition, participants selected the thumb-toward grasping for 77% of the free-choice trials, whereas the number was only 73% in the final-initial condition. The less optimal initial grips presumably require more online-corrections of the body (arm) to reach the target position, and the increased correction demanding may have slowed down the movement execution (i.e., rotation).

As we expected, final goals evoked a larger P2 component than initial goals when only partial goal information was available to participants (the first cue). From the topographical map in Figure 6, we can see the amplitude difference of P2 mainly distributes over the frontal and central areas. It has been suggested that anterior P2 is associated with the feature processing of the stimulus, and the stimulus with more task-relevant features is accompanied by a larger anterior P2 (Potts, 2004; Potts et al., 2004, 2006). Therefore, in the present experiment, the larger P2 for final goals indicate that final action goals are more task-relevant than the initial action goals for planning the grasp-to-rotate movements. The P2 result is in substantial agreement with the idea that final action goals seem to be more critical in motor planning than initial grip postures (Rosenbaum and Jorgensen, 1992; Westerholz et al., 2013).

It is worth noting that the P2 effect might also be explained by the physical salience of visual cues. As we employed different symbols (square or arrow) for cueing the initial and final goals, the present P2 effect might also reflect the difference in visual attention (Karayanidis et al., 2000; Taylor and Khan, 2000) or physical feature processing (Luck and Yard, 1995; Anllo-Vento and Hillyard, 1996). Together with the P2 results for the second cue (see below), we argue that the P2 effect in the present study is related to motor planning instead of stimulus salience.

In line with our hypothesis, a larger N2 was found in the initial-final condition for the first cue, as compared to the final-initial condition. The difference is mainly seen over the frontal and central areas (see topographic map in Figure 6). It has been argued that the anterior N2 component is an electrophysiological marker for conflict monitoring (Van Veen and Carter, 2002; Yeung and Cohen, 2006; Enriquez-Geppert et al., 2010) and conflict processing (Wang et al., 2000; Folstein and Van Petten, 2008; Gajewski et al., 2008). So, the fronto-central N2 component elicited by the initial goals suggests that planning a grip posture (initial goal) without a yet known target position (final goal) seems to be a less familiar (compatible) preparation mode for goal-directed prehensile movements. Instead, the initial and final action goals seem to be coordinated in a hierarchical manner that final goals might be selected and processed before initial goals (in the sense of preferred processing sequence).

Another explanation for the N2 effect here can be that participants were conflicting with the multiple potential motor plans when only the initial goals were available. Motor planning can be viewed as a selection processing that the most suitable plan is picked out of the set of potential plans, which is parallelly organized in the mental representations (Cisek and Kalaska, 2010; Wunsch et al., 2015). In the initial-final trials, there may have been a conflict among potential plans since the final goals were not given, and there were eight different target positions. However, in the final-initial trials, because the target position was given, there were only two potential plans for grip selection, and conflicts were reduced compared to the initial-final trials.

As for the P3 component at the first cue, the mean amplitude was larger for final goals than initial goals over the frontal and central areas, but not at the parietal area. Based on the previous studies concerning P3 (Comerchero and Polich, 1999; Polich, 2007), the present P3 component seems to be the P3b. The different fronto-central activities found in the time window (350 – 600 ms) can hardly be explained by the "novelty" of the stimulus. However, the different activities over the frontal and central areas seem to be caused by the fronto-central negativity for the initial goals in the P3 time window. From the ERP waveforms in Figure 6, a noticeable negativity around

400-550ms can be seen at frontal electrodes (cf. Fz) for the initial-final conditions, whereas the ERP waves for the final-initial conditions are more positive. The topographic map of the P3 difference and the statistics results also illustrate a frontal maximum of the amplitude difference. It has been reported that the medial-frontal negativity is associated with conflict-monitoring and error-processing (Bartholow et al., 2005; Cohen et al., 2008). Therefore, the frontal negativity for the initial goals is suggested to reflect a similar conflict processing mechanism as the N2 result. The frontal negativity suggests that initial goals may be processed after final goals for planning the prehensile movements.

As for the slow-wave potentials, we found the mean amplitude was more positive for the initial than the final goals in free-choice grasping trials in the duration of 600 – 2000 ms. From the topographic map in Figure 8, one can see that the difference was mainly distributed over the posterior areas. It has been reported that the parietal cortices, such as the anterior intraparietal sulcus (aIPS), are critical for humans to plan and control goal-directed grasping (Begliomini et al., 2007; Tunik et al., 2008; Marangon et al., 2011; Martin et al., 2011). The posterior distributed ERP late negativity is associated with effortful motor planning and execution in grasping tasks (Van Schie and Bekkering, 2007; Westerholz et al., 2013, 2014b; Koester et al., 2016). So, the posterior positive slow waves may indicate that (at this moment) processing free-choice initial goal (without knowing target position) requires less effort, as compared to the processing of final goals (target positions). The participants seem not to start effective motor planning when they only received a free-choice initial cue. The present result confirms the idea that the selection of initial grip posture is based on the final action goal (Rosenbaum et al., 2012) and broadly supports our hypothesis that action goals are organized in a hierarchical manner during motor planning as well.

Please Insert Figure 8 here.

Surprisingly, when complete information was available to participants, we also found a larger P2 for the final than for the initial goals. However, the P2 effect was only significant for the free-choice grasping. Moreover, the P2 amplitude was also larger for free-choice grasping than for specified grasping in the initial-final condition. That means the P2 component for free-choice grasping in the initial-final condition is more robust than any other experimental conditions. According to previous findings (Potts, 2004; Potts et al., 2006), the anterior P2 reflects feature processing, and the amplitude of P2 is associated with evaluating the task-relevance of the stimulus. Furthermore, the anterior P2 has also been associated with motor planning, and the larger P2 amplitude is found in planning a more sophisticated movement (Van Elk et al., 2010a, 2010b). The enlarged P2 amplitude suggests that planning the free-choice grasping with the cue sequence "initial-final" requires more effort than any other conditions. In the initial-final condition, a free-choice initial goal seems to be not helpful for planning the action unless a final goal is given, and motor planning may begin after the final goal (second cue) is presented. However, in other experimental conditions, motor planning begins when the first cue (specified grip or target position) is presented, and at least part of the motor plan is established with the first cue. Therefore, at this moment (second cue), the whole motor plan (including both grip selection and target position) needs to be established with the (second) cue for the free-choice grasping in the initial-final condition, which requires more effort and enlarges the P2 amplitude. The P2 result here is in accordance with the idea that initial action goals are selected for achieving the final action goals (Rosenbaum et al., 2012; Wunsch et al., 2015), and it also supports our hypothesis that action goals are organized hierarchically in motor planning.

As for the N2 component at the second cue, we found the mean amplitude was smaller (more positive-going) for the free-choice grasping than the specified grasping. However, the effect was only significant in the initial-final condition. From the ERP waveforms and the topographic maps shown in Figure 7, the amplitude difference can be seen over the centro-parietal areas. The possible explanation for the amplitude difference between the specified and free-choice grasping can be the N2 amplitude in the free-choice trials was influenced by the slow-wave potentials before the second cue, which was found more positive-going over the posterior areas. The slow waves may enlarge the mean amplitude of N2 for the free-choice trials and make it more positive-going so that the difference becomes significant in statistics.

The amplitude of P3 elicited by the second cue was not significantly different among the four experimental conditions. We only found that the mean amplitude of P3 was larger over the central and parietal areas than the frontal area. The increased centro-parietal P3 activities may be interpreted by the increased cognitive demand for converting the cued information into motor plans.

In the combined time window 2800 to 3600 ms, we found the mean amplitude of the slow waves was larger at the anterior areas than the posterior areas. However, the difference was only significant in final-initial conditions, not in the initial-final condition. The possible explanation can be the initial action goals evoked more posterior negativity in final-initial conditions. Bozzacchi et al. (2012) have reported that compared to reaching or impossible grasping movements, the planning grasping movements evoked larger posterior negative slow waves during the motor planning phase. At the moment, the initial goals (squares) are presented on the screen, and they may emphasize the grip information, which could evoke the posterior negativity. However, the difference in slow waves might also be attributed to eye movements. Even though we removed the ocular artifacts by the Independent Component Analysis (ICA), the possible residual effects might still remain in the EEG signal, which could influence be reflected (partially) in the slow waves. The slow-wave effect in final-initial conditions is still an open question, and it deserves further research.

Taking the ERP results together, we can draw a more comprehensive picture for the coordination of initial and final action goals in prehension preparation. Even though the P2 effect at the first cue might be attributed to the stimulus salience, considering the N2 effect at the first cue, the frontal negativity in the P3 window at the first cue, and the P2 result at the second cue, we infer that the P2 effect at the first cue probably reflects the task relevance evaluations, rather than the physical properties processing. Overall, the results suggest that compared to the "initial-final" sequence, processing the goals in the "final-initial" sequence seems to be a preferable (familiar) way that individuals coordinate the grip posture and task purpose in motor planning. The findings are in congruence with the idea that final task goals are more important than initial grip postures in motor planning (Rosenbaum et al., 1992; Westerholz et al., 2013) and support our hypothesis that the initial and final action goals are hierarchically coordinated during movement preparation.

Limitations of the present study should be taken into consideration. Even though we set 20% of the random fillers, the target positions in the 80% experimental trials are predictable. That means, in initial-final conditions, it is not necessary to wait for the second cue to know the instructed target positions. However, none of the participants reported using the strategy in the post-questionnaire, even when they were asked directly. For future research, it might be of interest to engage the unpredictable target positions for the topic. Besides, as we mentioned above, we did not control the gaze behaviors during the experiment (except for the fixation cross), which might influence the ERP results (especially the ERP slow waves). Although we employed the ICA to correct the ocular artifacts, there is a possibility in principle for the residual effects, which may differ between the ERPs for the experimental conditions. Moreover, the present study employed a "pre-cue and imperative" design to investigate the goal coordination during motor planning. Therefore, our behavioral results can hardly be linked to the ERP effects directly because the ERP epochs do not overlap with any behavioral time epochs. It might be interesting for future research to study this topic with other designs.

To conclude, the present study investigated the neurophysiological mechanisms underlying the coordination of initial (grip posture) and final (task purpose) action goals during the preparation of free-choice and specified manual actions. With the "first cue – second cue – imperative signal" design, the action goals were given separately in different sequences (either "final-initial" or "initial-final"). Results yielded shorter reaction time for the final-initial than the initial-final trials but only when the movement requires a free-choice grasping. At the moment when the goal-related information was incomplete (the first cue), final goals evoked a larger anterior P2 than initial goals. Conversely, also time-locked to the first cue, initial goals elicited a larger anterior N2 and more robust frontal negativity in the P3 window than final goals. When the goal-related information was complete (the second cue), a larger P2 was found for the final than initial goals, whereas it was only found in free-choice grasping. Moreover, a larger N2 was also found for the specified compared to the free-choice grasping in the initial-final trials. The results suggest that final task goals are more important than initial grip postures in the preparation of manual actions. The initial and final action goals seem to be preferably coordinated in a hierarchical manner. That is, the final task purpose is processed with precedence, whereas the initial grip posture is selected depending on the final task purpose.

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DECLARATION OF INTEREST

The authors declare that they have no competing interests. The funders had no role in study design, data collection, data analysis, decision to publish, or preparation of the manuscript.

AUTHOR CONTRIBUTIONS

Conceptualization, Methodology: *LY, DK, TS*. Data Collection: *LY*. Data Analysis and Visualization: *LY, DK*. Writing, Reviewing, and Editing: *LY, DK, TS*.

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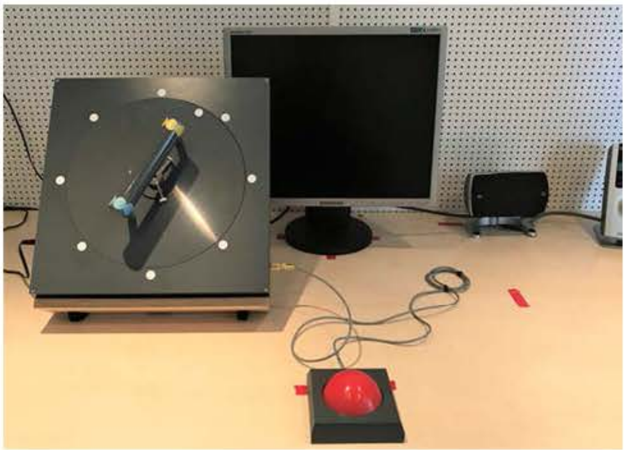

Figure 1 Experimental setup

The experimental setup includes a rotation apparatus and a 19-inch TFT monitor. The rotation apparatus contains a handle (decorated with yellow and blue stripes), a rotatable disk, a pointing marker (the white dot on the disk), eight target markers (the dial-displayed white dots out of the disk), and a start button (red button).

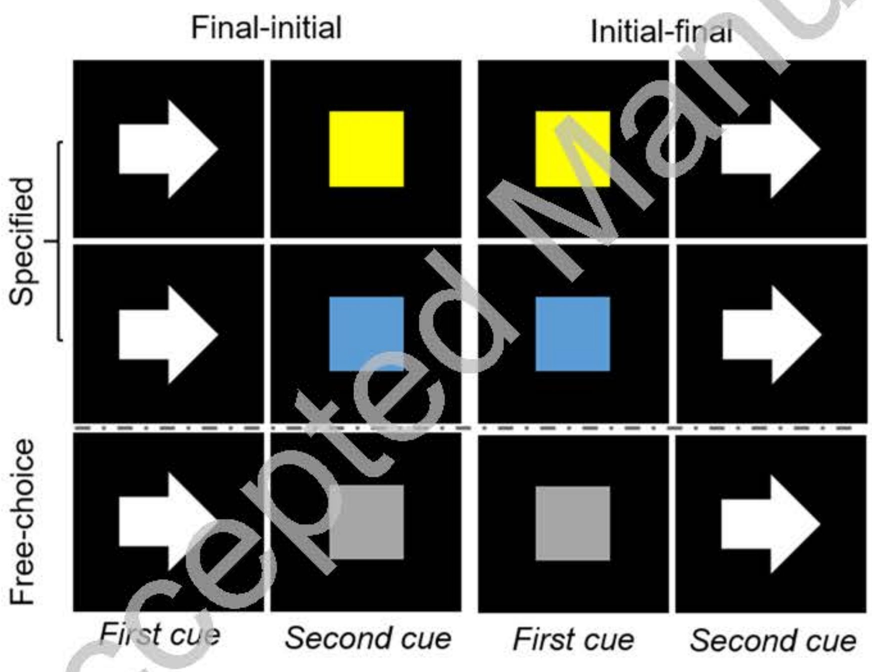

Figure 2 Illustrations of possible stimuli

Arrows represent final goals, and the direction of the arrow indicates the target position (only target position three is shown). Colored squares represent initial goals. Yellow and blue squares indicate the specified grasping thumb toward the corresponding to the color ends. Grey squares indicate free-choice grasping. The arrows and squares are presented in different sequences (either "arrow-square" or "square-arrow").

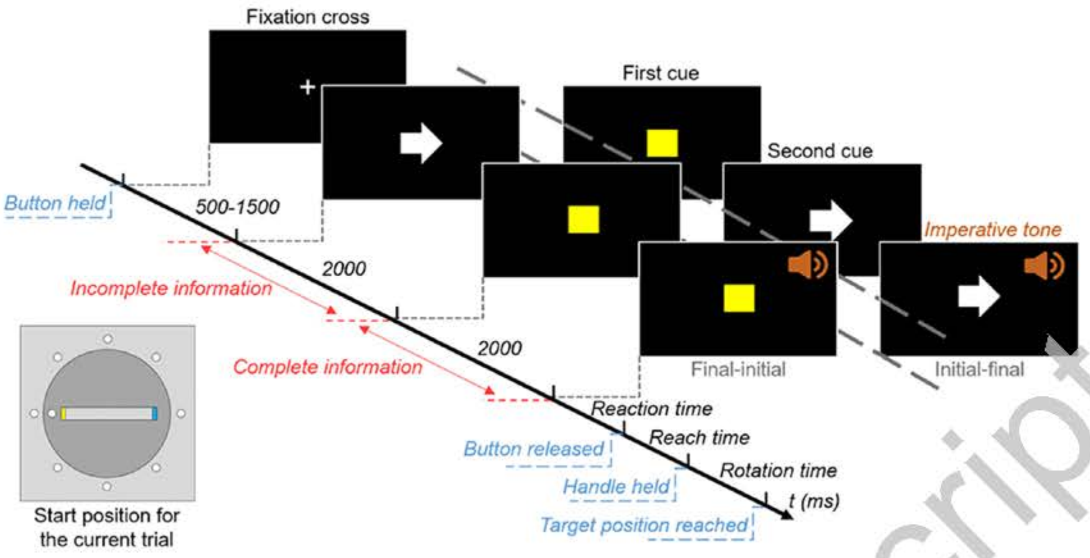

Figure 3 **Time course of an experimental trial**

Time is shown in milliseconds. The start position of the trial is shown as the illustration at the bottom left. Participants held the start button to start the trial. This was followed by a fixation cross and the cues. The cues were shown in different sequences. In the final-initial condition (left side of the dotted lines), the final goal (arrow) was the first cue, and the initial goal (square) was the second. In the initial-final condition (right side of the dotted lines), the initial goal was the first cue, and the final goal was the second. The imperative signal was played 2000 ms after the second cue onset. The second cue disappeared after the target position was reached.

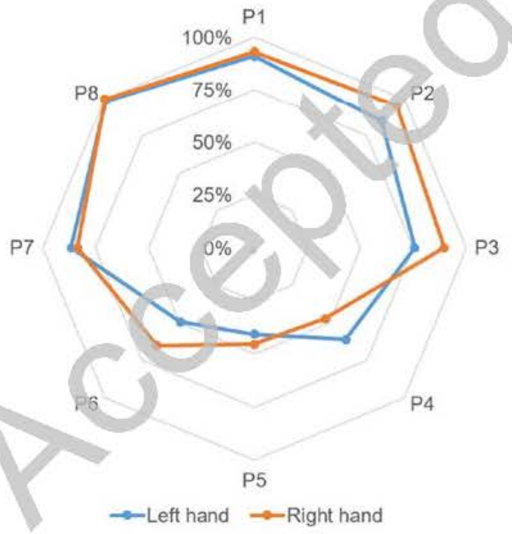

Figure 4 **Grip selections in free-choice grasping**

The probability of thumb-toward grasping in free-choice grasping is shown in percentage. The positions (from 1 to 8) correspond to the target makers on the rotation apparatus clockwise. Blue dots show the data from left-hand trials, and orange dots show the data from right-hand trials.

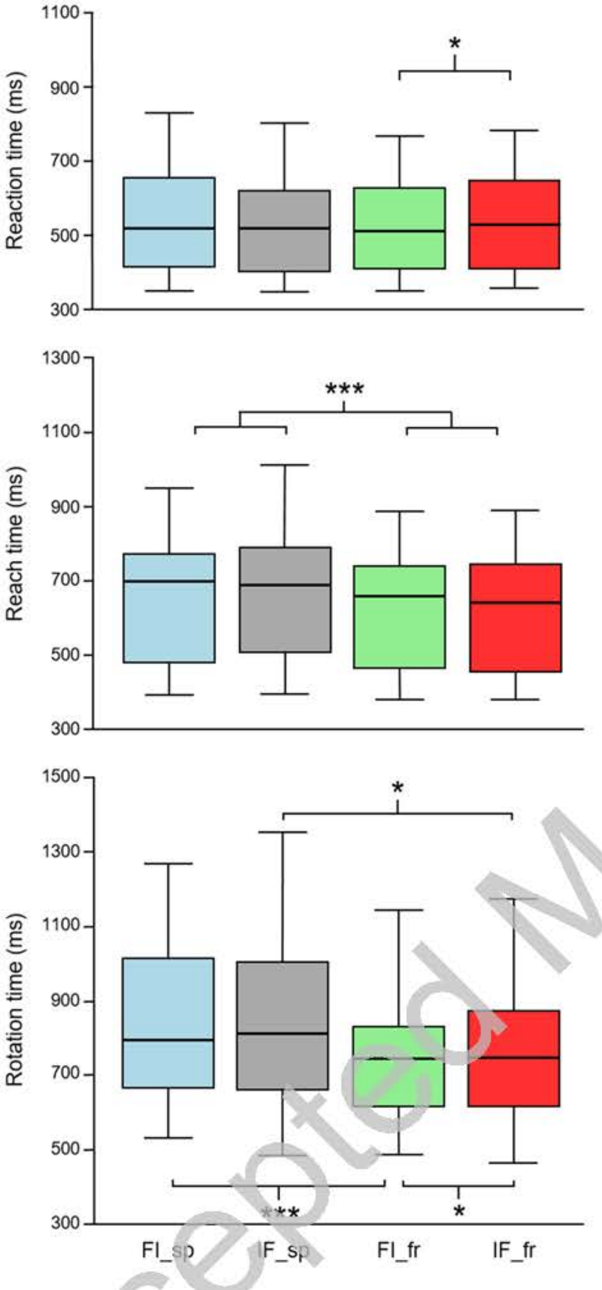

Figure 5 Timing of behavior

Box plots representing reaction times (top), reach time (middle), and rotation time (bottom) of the 26 participants (time is shown in milliseconds). Light blue boxes show the data for the specified grasping in the final-initial condition (FI_sp). Grey boxes show the data for the specified grasping in the initial-final condition (IF_sp). Light green boxes show the data for the free-choice grasping in the final-initial condition (FI_fr). Red boxes show the data for the free-choice grasping in the initial-final condition (IF_fr). The "*" stands for $p < 0.05$, and the "***" stands for $p < 0.001$.

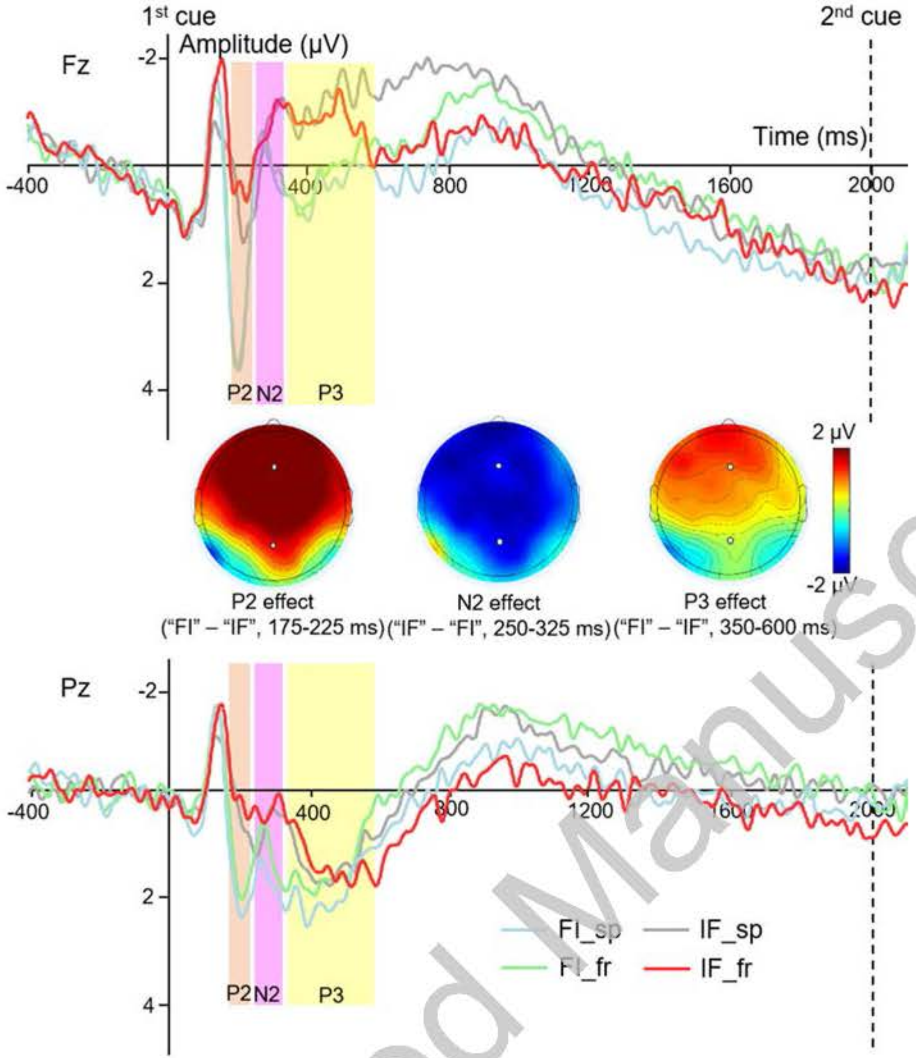

Figure 6 ERP waveforms at the first cue

Grand averaged ERPs recorded at the midline electrodes (Fz and Pz) time-locked to the onset of the first cue, for the specified grasping in initial-final condition (IF_sp, grey), the free-choice grasping in initial-final condition (IF_fr, red), the specified grasping in final-initial condition (FI_sp, light blue), and the free-choice grasping in final-initial condition (FI_fr, light green). The topographic maps illustrate the scalp distributions of difference waves for P2, N2, and P3 components between conditions. The subtraction of conditions and the time window are listed in corresponding brackets under the topographic maps.

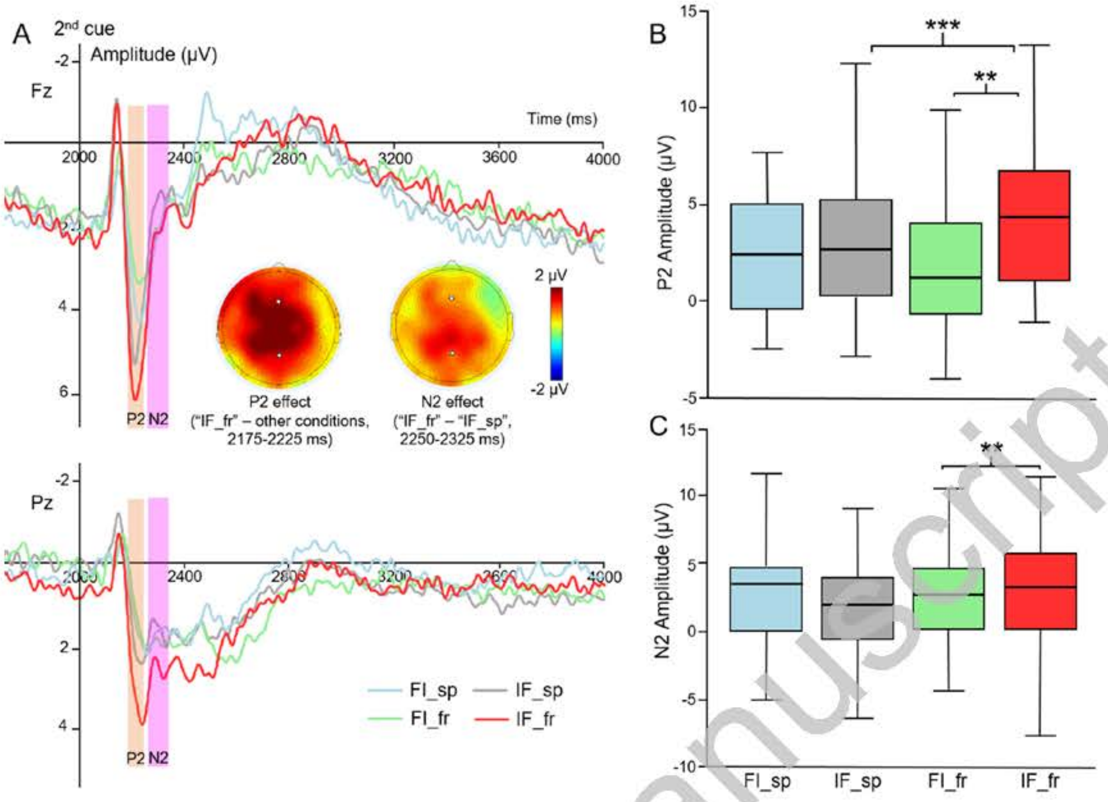

Figure 7 **ERP waveforms at the second cue**

(A) Grand averaged ERPs recorded at the midline electrodes (Fz and Pz) from 2000 – 4000 ms (see also text for more details), for the specified grasping in initial-final condition (IF_sp, grey), the free-choice grasping in initial-final condition (IF_fr, red), the specified grasping in final-initial condition (FI_sp, light blue), and the free-choice grasping in final-initial condition (FI_fr, light green). The topographic maps illustrate the scalp distributions of (mean) difference waves between conditions. The subtraction of conditions and the time window are listed in corresponding brackets under the topographic maps. (B) Mean amplitude of P2 component over different areas. (C) Mean amplitude of N2 component over different areas. The "**" stands for $p < 0.01$, and the "***" stands for $p < 0.001$.

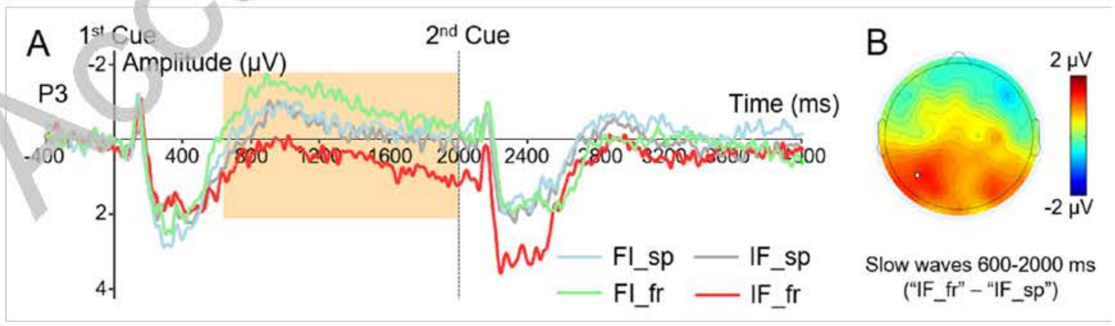

Figure 8 **ERP waveform at the left posterior electrode (P3)**

(A) Grand averaged ERPs recorded at the left posterior electrode (P3), for the specified grasping in initial-final condition (IF_sp, grey), the free-choice grasping in initial-final condition (IF_fr, red), the specified grasping in final-initial condition (FI_sp, light blue), and the free-choice grasping in final-initial condition (FI_fr, light green). (B) The topographic map illustrates the scalp distribution of difference waves between specified and free-choice grasping in the initial-final condition from 600 to 2000 ms.