ACTION GOAL AND OBJECT MANIPULATION

THE ROLE OF INITIAL AND FINAL ACTION GOALS IN MANUAL ACTION

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Action Goal and Object Manipulation

The Role of Initial and Final Action Goals in Manual Action

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Candidate's Declaration

I hereby declare that the current dissertation with the title "*Action Goal and Object Manipulation: The Role of Initial and Final Goals in Manual Action*" is presented according to the doctoral regulations of the Faculty of Psychology and Sports Science. This dissertation is my original work unless otherwise referenced or acknowledged. This dissertation has not been submitted for a degree in this institution or any other professional qualifications elsewhere.

Lin Yu

Date: 03/24/2021 Lin Yu

Dedicated to the memory of my dear grandmother.

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Abstract

Instead of external stimuli, a majority of manual actions used in everyday life are triggered voluntarily by certain internal motivations, namely action goals. Individuals intentionally start a movement for a goal and terminate the movement when the desired goal (state) is achieved. Most of the previous studies only focused on a single action, such as the button-pressing, reaching, pointing, or grasping, and accordingly, the action goals (in these studies) were almost always manipulated as the last position or object involved in the tasks. However, manual actions can be more complicated than a single action. Multiple single actions can be integrated into a multi-step action in which single actions are arranged following specified (temporal or spatial) manners. In our everyday life, most manual actions involved in object manipulation are not merely limited to reaching toward an object but also contain grasping and some further actions for achieving the task goals, such as grasp a glass for drinking or pick-up a stone for throwing. In this regard, the "last position or object" seems to be insufficient for characterizing the action goal for manual actions, and the immediate grip demands (the way to grip the object) are mostly neglected (by previous studies). Hence, the functional roles of the initial action goal (grip posture) and the final action goal (task purpose) in manual actions are still not fully understood.

With the help of electroencephalogram (EEG) and event-related potentials (ERP), the current dissertation investigated the functional roles of the initial and the final action goals, as well as the neurophysiological mechanisms underlying the action goals, in multi-step goal-directed manual actions (object manipulations). A series of three experiments were carried out to explore the roles of the initial and the final action goal in the planning stage (Chapter 2), the re-planning stage (Chapter 3), and the online correction stage (Chapter 4) of the grasp-to-rotate movements.

By presenting the initial and the final action goals separately in different sequences during motor planning, the first experiment (Chapter 2) studied how individuals coordinate the action goals (top-down vs. bottom-up) during the preparation of grasp-to-rotate movements. Results mainly revealed that the final action goals elicited larger anterior P2s than the initial action goals, and the initial action goals evoked larger anterior N2s and frontal negativity than the final action goals. Importantly, these component differences were only significant when the goals were presented as the first cue of the stimulus sequence. The findings of the first experiment suggest that the final task goals are more critical than the initial grip postures in planning manual actions, and the action goals seem to be coordinated in a "top-down" (hierarchical) manner that task purposes are processed before the selection of grip postures during motor planning.

Through a modified "S1–S2" paradigm, the second experiment (Chapter 3) investigated the motor re-planning processes in adjusting to the unexpected changes in either initial or final action goals during the movement preparation. Results yielded that perturbations in anticipated initial goals significantly slowed down the motor re-planning, as compared to perturbations in anticipated final goals. Perturbed initial goals elicited a larger centro-parietal positivity (during 500–700 ms time-locked to the goal perturbation) than perturbed final goals, but the mean amplitudes of anterior P2, anterior N2, and P3 were not significantly different between the initial and the final goal perturbations. These results indicate that the re-planning costs (cognitive efforts) induced initial goal perturbations are higher than final goal perturbations, and the increased re-planning costs (initial vs. final) are more likely utilized in the implementation of a new action (plan) rather than the inhibition of the pre-planned actions.

Following the second experiment, the third experiment (Chapter 4) further explored the motor re-planning processes in response to the changes in the initial or final action goals during the movement execution (online correction). Results found that the re-planning time was significantly longer for initial goal perturbations than final goal perturbations. Moreover, initial goal perturbations elicited a larger anterior P3 and a larger central distributed late positivity (600–700 ms) time-locked to the goal-perturbations than final goal perturbation. Source analyses revealed that increased cortical activations in the left middle frontal gyrus (MFG, BA9) were found for the perturbed initial goals compared to the perturbed final goals in the P3 time window. These findings imply that perturbations in the initial goals have stronger interferences with the movement execution compared to perturbations in final goals, and the interferences seem to be derived from both inappropriate action inhibitions and new action implementations, that is, initial goal perturbations require more cognitive efforts than final goal perturbations in both pre-planned actions inhibition and new action implementation.

The current dissertation emphasizes that both initial and final action goals are important in the planning as well as execution of manual actions, and the frontoparietal cortical network is highly involved in manual action planning and control. More importantly, the current dissertation also demonstrates that final task goals are more important than initial grip goals during the movement preparation, and the action goals are organized in a “top-down” (hierarchical) manner in manual action planning, that is, the future task demands (final action goals) seem to be processed before the immediate task demands (initial grip goals). However, when re-planning or correcting a prepared manual action, perturbations in initial action goals seem to be more critical (urgent) than perturbations in final action goals. The unexpected changes in immediate task demands require more cognitive efforts in motor re-planning than the changes in final task demands. Different from the process manner in motor planning, the initial and final action goals seem to be represented in a chronological (“bottom-up”) way in the prepared motor plans.

The present dissertation provides a more comprehensive and nuanced understanding of human manual actions and how individuals plan as well as control their goal-directed actions. The findings of these studies may also contribute to other related research fields (such as cognitive robotics, and sports training) by providing several theoretical and practical implications.

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Abbreviations

ACC	anterior cingulate cortex
aIPS	anterior intraparietal sulcus
ANOVA	analysis of variance
BACs	basic action concepts
dPCC	dorsal posterior cingulate cortex
EEG	electroencephalography
EOG	electrooculogram
ERP	event-related potential
fMRI	functional magnetic resonance imaging
FP	final-perturbed (condition)
IFG	inferior frontal gyrus
IP	initial-perturbed (condition)
IPS	intraparietal sulcus
M1	primary motor cortex
MCP	metacarpophalangeal
MFG	middle frontal gyrus
NP	non-perturbed (condition)
PFC	prefrontal cortex
PMC	premotor cortex
PPC	posterior parietal cortex
ROI	region of interest
sLORETA	standardized low-resolution brain electromagnetic tomography analysis
SMA	supplementary motor area
SMG	supramarginal gyrus
SPL	superior parietal lobule
TEC	theory of event coding
TMS	transcranial magnetic stimulation

General Introduction

Chapter 1

"The hand is the tool of tools."

— *Aristotle (384–322 B.C.)*

Rather than the paws, hooves, fins, or wings, primates have a pair of hands that enabled them to hold something to eat and, more importantly, to use something as a tool. For example, gorillas have been overserved to use a wooden branch as a walking stick to test water deepness, which helps them to cross a pool (Breuer, Ndoundou-Hockemba, & Fishlock, 2005). The disappeared claws, flat fingernails, and larger fingertip pads bring primates more convenience for grasping than any other species on the planet. Compared to non-human primates, the hands of human beings have shorter palms, straighter, but shortened fingers, as well as longer, stronger, and fully opposable thumbs (Young, 2003). These anatomical features make human hands so dexterous that the thumb can touch the other fingers easily, which provides human beings with the ability to firmly grasp and manipulate objects in a variety of shapes from the tine (such as sewing needle) to the relatively large ones (such as basketball). This species-specific ability enables humans to develop complicated manual actions (Fragaszy & Crast, 2016; Napier, 1956; Napier, 1993) and thus facilitates humans to utilize various tools to interact with the external environment (Ambrose, 2001; Diogo, Richmond, & Wood, 2012; Napier, 1962). As the quotation from Aristotle, the highly dexterous human hand can be treated as the "tool of tools" (432a1–432a3, Aristotle & Barnes, 1984, p. 57).

As the primary effectors for tool use, human hands, together with the various manual actions made by hands, play a crucial role in the evolution of human beings and the development of human society (Parker & Gibson, 1977; Stout & Chaminade, 2009). For instance, Darwin (1871) argued that the necessity to use stone tools for food is an essential part of the reciprocal feedback loop with brain size, which may promote the appearance of habitual terrestrial bipedalism for getting rid of the hands from locomotor demands. Besides, with the help of dexterous hands, humans use tools and, more importantly, create new tools for hunting, firing, cooking, eating, building, and so on, which promotes the development of human intelligence as well (Ambrose, 2001; Diogo et al., 2012; Ko, 2016). Moreover, human hands and manual actions also influenced the social and cultural aspects of human society, especially in the language domain (Mittelberg, 2017; Shi, Liu, & Zhuo, 2020). For example, the word "hand" and other manual action verbs (such as "grab" and "grasp") are also mentioned when individuals discuss other movement-irrelevant topics, such as "on the one hand…on the other hand…", "a second-hand car", "an offhand remark", "you grabbed my attention", " the meanings are out of my grasp" and so on.

Given the fact that hands and manual actions play an essential role in human intelligence and human society, the production and controlling of manual actions have fascinated researchers in biology, neuroscience, rehabilitation science, sports science, human factor, robotics, as well as cognitive psychology. It has been indicated that the cognitive factors, such as perceptual effects (Hommel, 2013), attention (Hesse, Schenk, & Deubel, 2012; Hommel & Schneider, 2002), working memory (Spiegel, Koester, & Schack, 2013, 2014; Spiegel, Koester, Weigelt, & Schack, 2012), and movement intentions (Rosenbaum, Chapman, Weigelt, Weiss, & van der Wel, 2012; Waszak et al., 2005; Westerholz, Schack, & Koester, 2014), are highly associated to the planning and execution of manual actions. Additionally, several cognitive theories or models, such as the ideomotor principle (Shin, Proctor, & Capaldi, 2010), and the theory of event coding (Hommel, 2009; Hommel, Müsseler, Aschersleben, & Prinz, 2001), have been proposed to illustrate the planning and execution of actions, which also emphasizes the close connections between cognition and manual actions. However, due to the complexity of human manual actions, the functional role of some of the cognitive factors (such as intention) in manual action planning and execution has not been fully understood. Thus, the current dissertation seeks to extend our knowledge on the functional role of action intention in planning as well as controlling manual actions. With the help of the electroencephalogram (EEG) technique, neural mechanisms underlying the action intention are also investigated. In this introductive chapter, we will first have a brief overview of the categories, the cognitive frameworks, and the neural mechanisms of manual action, and then propose the research questions of the current dissertation.

Manual actions in object manipulation

Hands are one of the most important effectors of human beings. For most of us, hands seem to be the most indispensable "tool" in our daily life. By using the dexterous hands, we are capable of performing a variety of manual actions, from the fine-tuned ones (such as threading a needle) to the gross ones (such as gripping an apple), which is employed in plenty of real-life behaviors such as the feeding (eating, drinking), the body maintenance (cleaning, soothing and protection), the object manipulation, and the social communication. If you pay attention to these behaviors, you may realize that even though some of the manual actions may be executed without an external object, such as gestures and sign languages, most of the manual actions used in our daily lives seem to be object-related, that is, most of our everyday manual actions are object manipulations.

In the context of human evolution and civilization development, manipulating inedible objects can be considered as the most crucial application of human hands (Michel, 1991). Moreover, object manipulation also engages multiple cognitive processing, which contains the integration of sensory and motor information, attention, working memory, and decision making. Therefore, the manual actions involved in object manipulation provide researchers an excellent window to investigate motor control in humans (Flanagan, Bowman, & Johansson, 2006; Rosenbaum et al., 2012).

Considering the anatomical structure and the function of the human hand, the British primatologist John Napier (1956) divided manual actions into two primary groups, non-prehensile actions and prehensile actions. The non-prehensile actions are those in which "no grasping or seizing is involved but by which objects can be manipulated by pushing or lifting motions of the hand as a whole or of the digits individually" (p. 902), such as typing with a keyboard, or pushing a door. By contrast, the prehensile actions are those in which "an object is seized and held partly or wholly within the compass of the hand" (p. 902), such as holding a pen or gripping a glass of water. Moreover, the prehensile actions can be further categorized into two subordinate groups, power grips and precision grips. In Napier's words, the power grips are the actions in which the "object is held in a clamp formed by the partly flexed fingers and the palm, counter pressure being applied by the thumb lying more or less in the plane of the palm" (p. 903), such as a full hand grasp. In contrast, the precision grips are the actions in which the "object is pinched between the flexor aspects of the fingers and the opposing thumb" (p. 903), such as a pincer grasp. Napier (1956) also argued that these two sub-groups cover the whole range of prehensile actions, and all the other types of grip (such as hook grip) can be treated as the variations or combinations of these two patterns.

Figure 1.1 ***Power grip*** *(left)* ***vs. Precision grip*** *(right)*

Apart from Napier’s classification, Klatzky and her colleagues (Klatzky, Fikes, & Pellegrino, 1995) also proposed another taxonomy in which manual actions in object manipulation can be classified with two binary parameters: the size of the hand surface contacting the object (large or small) and whether the hand posture is open or closed. This leads to four prototypical and highly distinguishable types of object contact: clench (closed full hand), pinch (closed thumb and one or two fingers), palm (open full hand), and poke (open single finger). Similar to Napier’s classification, Klatzky’s classification also separates the prehensile and non-prehensile manual actions with the parameter “hand posture”. The clench in Klatzky’s classification refers to the power grip in Napier’s, and the pinch refers to the precision grip. However, Klatzky also categorized the non-prehensile actions into palm and poke, which makes this classification to be more comprehensive than the previous one.

Even though Napier’s classification seems not to be detailed enough in grouping non-prehensile actions, the classification, as well as the terminologies, are still highly acceptable by later studies. An important reason is that prehensile actions are more typical, as well as seem to be more critical for humans than non-prehensile actions, especially when manipulating external objects. Compared to non-prehensile actions, prehensile actions are more frequently used in daily life. Most of the tools (i.e., cutlery, glass, pen, key, et al.) are used with prehensile actions instead of non-prehensile. Furthermore, the planning and control of a prehensile action seem also to be more sophisticated than non-prehensile actions, in both physical and cognitive considerations

(Bozzacchi, Giusti, Pitzalis, Spinelli, & Di Russo, 2012). Physically, compared to non-prehensile actions (i.e., button press), shaping the hand in prehensile actions (i.e., grasping) involves more bones, joints, and muscles, in which individuals have to coordinate more body parts, as well as more degrees of freedom[1]. Cognitively, prehensile actions involve more perceptual processing than non-prehensile actions since the appropriate grasp points, grasp strategies, and grasp forces need to be selected based on the input sensory information (object size, shape, weight, etc.). The prehensile actions are also more complicated so that individuals need more cognitive efforts to plan the actions before initiation, for example, the end-state comfort effect in grasping (Rosenbaum et al., 2012). In this regard, the present dissertation will take the prehensile actions (especially the power grips) as examples to explore the planning and control of manual actions.

Cognitive frameworks for manual action control

Due to the morphological and anatomical constraints, most of the manual actions are not limited to fingers and palms but involve wrists, arms, and even other body parts (such as shoulders). For instance, by twisting the radius and ulna, the hand can be moved to supination or pronation positions effortlessly. Therefore, the control of manual actions can hardly be independent, and a more comprehensive perspective (more generalized) seems to be needed when referring to manual action control.

Apart from the physiological structures such as muscles, bones, and nerves, the psychological (cognitive) factors have also been proved to be essential for motor control. The memory systems and forms of mental representations are used in motor control (Rosenbaum, 2010). Previous studies have also suggested that motor planning and motor control can be influenced by perceptual information (Bozzacchi et al., 2012; Wenke, Waszak, & Haggard, 2009), attention (Baldauf, Wolf, & Deubel, 2006; Hossner & Ehrlenspiel, 2010; Thomas, 2013), working memory (Spiegel et al., 2013, 2014), intention (Bonini, Ferrari, & Fogassi, 2013; Hughes, Seegelke, Spiegel, et al., 2012; Rosenbaum et al., 2012; Waszak et al., 2005), as well as emotion (Beatty, Fawver, Hancock, & Janelle, 2014; Coombes, Higgins, Gamble, Cauraugh, & Janelle, 2009). Meanwhile, several cognitive frameworks have been proposed to understand motor

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[1] Degrees of freedom are the set of independent dimensions of motion of the rigid body that completely specify the movement and orientation of the body in space.

control. Therefore, in this session, a brief overview will be conducted on the cognitive frameworks in motor planning and control.

Using an aim-to-reach task, Woodworth (1899) proposed a two-stage model for goal-directed manual actions such as reaching or grasping. The model holds the idea that the execution of manual actions contains two different phases, that is, an initial impulse phase and a current control phase. Typically, the impulse phase encloses a pre-programmed ballistic reaching, which brings the limb to the vicinity of the target object. Once the area of the target object is reached, the limb comes under feedback-based control (current control phase). During this phase, individuals can use visual and proprioceptive feedback to minimize the errors between the limb and the target object. Moreover, compare to the first phase, the actions in the second phase are much slower because the second phase requires more accuracy in controlling the limb. Woodworth's model highlighted for the first time that both feedforward (pre-programmed) and feedback mechanisms are involved in human motor control, and, more importantly, the seminal study opened a new window for psychologists, that is, understanding motor control from a cognitive perspective.

Inspired by the "two-stage model", more and more psychologists began to focus on motor control research, and numerous studies were conducted to explore the relationship between action and cognition. Based on the studies, several frameworks have been proposed, and the ideomotor principle and its successors seem to be the most influential.

The ideomotor approach is trying to explain how individuals are able to perform goal-directed movements without having direct conscious access to or any conscious knowledge about their own motor system (Koch, Keller, & Prinz, 2004; Shin et al., 2010; Stock & Stock, 2004). The early idea of ideomotor approaches can be traced back to the 19th century (Stock & Stock, 2004). The term "ideomotor" was initially coined by William Benjamin Carpenter (1852), and it was used to refer to the idea that every thought, no matter conscious or unconscious, spawns a commensurate action. Subsequently, in the famous book *Principles of Psychology* (1890, 2007), William James summarized the early ideomotor ideas and brought them to the attention of many psychologists. However, with the prevalence of behaviorism in mainstream psychology, the ideomotor ideas were not recognized by many psychologists since the behaviorists believed actions are guided by external stimuli instead of internal (voluntary) thoughts. In the 1970s, the ideomotor ideas were taken seriously again by cognitive psychologists when a modern version of ideomotor ideas was proposed by Greenwald (1970). In his ideomotor mechanism, the sensory feedback resulting from self-action is considered a crucial mediator in action control. The “sensory feedback – action” association is a fundamental mechanism of voluntary action control. Greenwald also suggested using a two-phase (practice & test) experimental paradigm to study the ideomotor ideas, which has become the leading paradigm for investigating perceptual effects in action control (Greenwald, 1970; Shin et al., 2010).

Following Greenwald’s idea, the current ideomotor ideas emphasize the role of anticipatory representations of intended action effects in action control, and individuals tend to generate actions for which the sensorial or perceptual feedback is similar to already experienced action effects (Hommel et al., 2001; Shin et al., 2010). The ideomotor principle also requires that actions and their anticipatory effects are tightly associated, and the associations are bidirectionally predictable, that is, an anticipatory effect can be predicted by a given action, and conversely an action can also be predicted by a given effect. There are no intermediate processing steps between the action and effect, which means ideas (anticipatory effects) can be transferred to motor plans directly without any intermediate processes.

Ideomotor ideas have been broadly supported by a series of empirical research (Hommel et al., 2001; Kunde, 2001; Pfister, Melcher, Kiesel, Dechent, & Gruber, 2014; Waszak et al., 2005; Westerholz, Schack, & Koester, 2014). For example, by using a modified choice reaction time task, Kunde (2001) studied the action-effect compatibility in action control. The results yielded that motor actions were emitted faster as well as with fewer errors when individuals perceived a compatible action effect (pressing a left key with a left light on or pressing a key softly with a quiet tone) rather than an incompatible effect (pressing a left key with a right light on or pressing a key softly with a loud tone). Similar results were obtained in their later studies with other action-effect combinations (Herwig & Waszak, 2012; Hubbard, Gazzaley, & Morsella, 2011; Kunde, 2003; Kunde, Koch, & Hoffmann, 2004; Pfister & Kunde, 2013; Rieger, 2007). In these studies, action effects (light, tone, etc.) were presented after the motor response had been carried out. Therefore, the results suggest that effect representations are activated before motor action onset (during the response selection and initiation), which is in line with the ideomotor ideas that actions and their anticipatory effects are tightly connected.

One of the latest and frequently cited accounts of ideomotor ideas is the theory of event coding (TEC; Hommel et al., 2001). It can be considered as an elaboration of the common coding hypothesis (Prinz, 1997) and a successor of the ideomotor ideas (Hommel, 2009). The TEC is a general framework that illustrates how the to-be-perceived event (perception) and the to-be-generated event (action) are cognitively represented and how their mental representations interact to generate perception and action (Hommel, 2009). As an elaboration of the common coding hypothesis, the TEC holds a basic idea that the to-be-perceived events and the to-be-produced actions are cognitively represented on the same codes that consist of integrated networks of the sensorimotor features (common coding). In this regard, the TEC suggests that the perceptual consequence of the action and the action intention are the same (carrying movements to create particular effects in the external environment). The TEC has been supported by the behavioral results (Fagioli, Hommel, & Schubotz, 2007; Hommel, Proctor, & Vu, 2004) and the neuroscientific results (Elsner et al., 2002; Kühn, Keizer, Colzato, Rombouts, & Hommel, 2011; Petruo, Stock, Münchau, & Beste, 2016; Takacs et al., 2020; Waszak et al., 2005). It is also supported by several computational models (Haazebroek, Raffone, & Hommel, 2017; Haazebroek, van Dantzig, & Hommel, 2013; Kachergis, Wyatte, O'Reilly, de Kleijn, & Hommel, 2014). Moreover, the original framework has been further extended therefore more complex action tasks, such as actions in social settings, can also be explained by the extended version of the TEC (Hommel, 2019).

The ideomotor principle as well as the TEC, take both the action intention and the goal-directed nature of action into consideration, which provides an alternative (better) perspective to understand the relationship between perception and action. Both theories emphasize the importance of action intentions and the anticipated perceptual effects of action in motor planning and control, and they share the basic idea that "voluntary movements may be planned, performed, and stored in memory by representations of anticipated effects" (Schack, 2004; Schack & Ritter, 2009). However, these theories mainly focused on the role of the anticipatory effect in goal-directed actions. The question of how individuals represent the anticipated effects seems to be neglected. Moreover, most of the above-mentioned theories are only based on simple actions (such as button press), and complex movements (such as multi-step actions or sport movements) were not mentioned. Therefore, a hierarchical framework was proposed by Schack (2004) for explaining the cognitive structures of complex movements.

Inspired by Bernstein's hierarchical model of motor coordination (Bernstein, 1947, 1967), Schack (2004) proposed a more comprehensive hierarchical framework for complex movements, which integrates cognitive components into Bernstein's model. Schack's model views the functional construction of actions on the basis of a reciprocal assignment of performance-oriented regulation levels and representational levels, and these levels can be distinguished according to the main tasks on the regulation and representation levels. There are four levels (mental control, mental representation, sensorimotor representation, and sensorimotor control; from top to bottom) in the model, and all levels are assumed to be functionally autonomous (see Table 1.1).

Table 1.1 ***Levels of action organization for Schack's hierarchical model.*** *Adapted from Schack (2004)*

Code	**Level**	**Main function**	**Sub-function**	**Means**
IV	Mental control	Regulation	Volitional initiation; control strategies	Symbols; strategies
III	Mental representation	Representation	Effect-oriented adjustment	Basic action concepts (BACs)
II	Sensorimotor representation	Representation	Spatial-temporal adjustment	Perceptual effect representations
I	Sensorimotor control	Regulation	Automatization	Motor primitives; basic reflexes

The level of mental control (level IV) is induced intentionally, and it is assumed to code the anticipated outcomes of movement into action intentions. A sub-function of the mental control level is the control strategies, which can be the inner speech or other symbolic instructions. The level of mental representation (level III) is considered as a dominating cognitive benchmark for mental control (level IV). The mental representation is organized conceptually, and it is responsible for transferring the anticipated action effects (intentions) into motor plans that are sufficient to bring the desired movement outcomes. The mental representation lays a foundation for movement programming processes, and it consists of the Basic Action Concepts (BACs), which are identified as the central representational units for movements in long-term memory (Schack, 2004; Schack & Ritter, 2009). The BACs are the mental counterparts of functional elementary components of complex movements, and they are based on chunked body postures related to common functions for achieving action goals. The BACs are generated from previous movement experiences and tie together functional and sensory features of movements (Schack, 2004). Since the functional features are derived from the anticipated action effects (intentions), so the mental representation level (level III) links the mental control level (level IV). Moreover, the mental representation level (level III) is also connected to the sensorimotor representation level (level II) by the sensory features of movements. The connection between mental representations (BACs) and sensory-effect representations allows individuals to manipulate the cognitive conditions of sensorimotor coordination intentionally. In this regard, the mental representations (BACs) act as the core structure in Schack's hierarchical model for complex movements. The sensorimotor representation level (level II) is assumed to store the kinesthetic modality information (sensory, perpetual, and so on) of particular movements. The relevant modalities can be changed as a result of motor learning or expertise development, and the modalities are relied on the concrete movement tasks (modalities may be different across tasks). The kinesthetic modality information is obtained from the sensorimotor control level (level I), which is directly connected to the environment. The sensorimotor control level is induced perceptually, and it is built on functional units composed of perceptual effect representations, afferent feedback, and effectors. The level is broadly autonomous, and the automatisms emerge when this level possesses sufficient correction mechanisms to ensure the stable attainment of the intended effect (Schack, 2004).

Schack's model establishes a cognitive architecture for complex movement, and the model is also consistent with the basic ideas of the ideomotor approach and the TEC. The lower two levels (I and II) are responsible for the functional manipulation of the environment-related information, and the higher two levels (III and IV) are responsible for the functional manipulation of the event(effect)-related information. Moreover, through the concept of BACs, Schack and his colleagues provide a new perspective on how complex movements are structured in long-term memory, which is in line with the idea that information is cognitively represented in different common-feature categories (Rosch, 1975; Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976). In order to test the cognitive structures, a method termed the structural dimensional analysis - motoric

(SDA-M) was proposed (Schack, 2012), and it has been applied in many different complex movements, such as sport skills (Bläsing, Güldenpenning, Koester, & Schack, 2014; Land, Frank, & Schack, 2014; Lex, Essig, Knoblauch, & Schack, 2015; Lex, Weigelt, Knoblauch, & Schack, 2012; Schack, Essig, Frank, & Koester, 2014), dance skills (Bläsing & Schack, 2012; Bläsing, Tenenbaum, & Schack, 2009), and manual actions (Bläsing et al., 2014; Schack & Ritter, 2009; Stöckel, Hughes, & Schack, 2012).

To sum up, most of the cognitive frameworks and theories mentioned above share the idea that motor action and cognition are connected, and the anticipated action effects (action intentions) play an essential role in the planning and control of goal-directed motor actions. Therefore, in the coming section, the functional role of the action intention in manual actions will be briefly reviewed.

Action intention: a driving factor of manual action control

In daily life, most manual actions are driven by a particular internal intention instead of an external stimulus (De Kleijn, Kachergis, & Hommel, 2014; Hommel, 2009; Hommel et al., 2001). Individuals perform manual actions to achieve their intentions. In this regard, action intentions seem to be necessary for manual action control. Taking the prehensile movement as an example, in the pioneering work, Napier (1956) mentioned that even though the physical properties of the to-be-grasped object (shape, size, texture, temperature, etc.) may somewhat influence the way to grasp the object, the intention of the movement seems to be the decisive factor for individuals to select the pattern of the grip. For example, a knife might be grasped in different ways depending on the different purposes. If it is used for cutting, one will most probably cover the handle with the palm and fingers (a power grip on the handle). However, if the knife is supposed to be passed to others, most people will probably hold the blade flat with their thumb and opposed fingers (a power or precision grip on the blade flat, relying on the side and weight of the knife) so that the handle can be easily accessed by others (social consideration). In another similar case, when opening a bottle of water, one may hold the jar tightly at the beginning, with their fingers and their palm pressed against the lid, to lose the jar. When the jar becomes loose, one will switch to a precision grip that only fingertips are in contact with the jar so that the lid can be removed easily and quickly. In this respect, manual actions seem to be selected and determined by the action intentions.

The idea has been supported by recent kinematic results (Belardinelli, Stepper, & Butz, 2016; Hughes, Seegelke, Spiegel, et al., 2012). For example, by using the motion tracking technique, Belardinelli et al. (2016) recorded the participant's index finger position in an object manipulation task. In this experiment, participants were instructed to interact with different objects (bottle, cup, and can) for different purposes (either to drink or to hand). The objects were also placed either upright or upside-down. The results revealed that the grasping heights of the index finger were different in different objects and different tasks: the bottle was grasped significantly higher in the drink task than in the hand task when the bottle was upright. Moreover, the upright can was also grasped higher in the drink as compared to the hand task. No grasping height difference was found for the cup, and the authors attributed that to the size of the cup, which seems to be too small to indicate the task difference.

However, manual actions can also be distinct even though the action intentions are the same. It is worth noting that the motor system is capable of achieving the same intention by different means, and it has been termed as motor equivalence (Lashley, 1930). Even though the action intention is the same, individuals may still perform different movements to achieve it. The motor equivalence phenomenon is somewhat closely related to the degrees of freedom problem (Bernstein, 1967), which also holds the idea that the same action intention can be achieved by an infinite number of different movements. The motor system has redundant anatomical, kinematic, neurophysiological degrees of freedom, and planning the intentional movements can be considered to be the process that individuals determine all the movement parameters to reduce the uncertainties (caused by the degrees of freedom) for a particular purpose.

Moreover, manual actions, especially object manipulations, are also complicated (in terms of movement steps). Most of the object manipulations are composed of multi-step manual actions (Rosenbaum et al., 2012; Seegelke, Hughes, Knoblauch, & Schack, 2013; Van Schie & Bekkering, 2007). That is, the hand-object interactions are not merely limited to a single reaching or grasping toward the object but involve further steps to manipulate the object for achieving the ultimate action intention, such as grasp a glass for drinking or hold a stone for throwing. In this regard, the concept of intention is somewhat ambiguous for object manipulations because there is more than one single action involved in the complex movement, and there could also be one or even more sub-intentions for object manipulations. So, how do individuals deal with the sub-intentions in the complex movement (such as object manipulation)? The phenomenon of end-state comfort (Rosenbaum et al., 2012, 2019) may have an answer to the question.

When asked to turn over an upside-down cup, most people would twist their arm before grasping so that they can hold the cup with an awkward (thumb-down) posture. During the rotation, the arm, as well as the grasping hand, would then supinate into a more comfortable (thumb-up) posture, which allows them to put the cup gently on the table. By contrast, people probably do not execute the actions conversely, that is, grasping the cup with a thumb-up posture at the beginning and then ending up with a thumb-down posture. However, when asked to move the cup elsewhere without rotating it, people would select almost certainly a thumb-up posture to grasp the cup and then move it elsewhere. The phenomenon that individuals tend to select an initial grasp posture to facilitate a comfortable end posture, has been termed as the "end-state comfort" effect (Rosenbaum & Jorgensen, 1992; Rosenbaum et al., 1990). The "end-state comfort" has been considered to be one of the most critical constraints in grasping posture selection (Fischman, 1998; Herbort & Butz, 2015; Rosenbaum, Chapman, Coelho, Gong, & Studenka, 2013; Rosenbaum et al., 2012).

Following the seminal pioneering study (Rosenbaum et al., 1990), the end-state comfort effect has been replicated in many object manipulation tasks (for a review, see Rosenbaum et al., 2012). These tasks not only involve the classical manipulation task such as unimanual object transport task (Belardinelli et al., 2016; Chapman, Weiss, & Rosenbaum, 2010; R. G. Cohen & Rosenbaum, 2004, 2011; Hughes, Seegelke, & Schack, 2012; Hughes, Seegelke, Spiegel, et al., 2012; Lam, McFee, Chua, & Weeks, 2006; Schütz, Weigelt, Odekerken, Klein-Soetebier, & Schack, 2011; Seegelke, Hughes, & Schack, 2014) and object rotation task (Herbort & Butz, 2015; Herbort, Mathew, & Kunde, 2017; Rosenbaum, Vaughan, Barnes, & Jorgensen, 1992; Westerholz, Schack, Schütz, & Koester, 2014), but also contain other more complex tasks such as bimanual object manipulations (Fischman, Stodden, & Lehman, 2003; Hughes, Reißig, & Seegelke, 2011; Janssen, Beuting, Meulenbroek, & Steenbergen, 2009; Seegelke & Weigelt, 2018; Weigelt, Kunde, & Prinz, 2006) and joint manual actions (Dötsch & Schubö, 2015; Gonzalez, Studenka, Glazebrook, & Lyons, 2011; Herbort, Koning, van Uem, & G.J. Meulenbroek, 2012). Besides, several researchers also studied the end-state comfort effect from a developmental perspective (Jovanovic

& Schwarzer, 2017; Knudsen, Henning, Wunsch, Weigelt, & Aschersleben, 2012; Robinson & Fischman, 2013; Stöckel et al., 2012; Weigelt & Schack, 2010; Weigelt, Wolfgram, & Schack, 2007; Wunsch, Weigelt, & Stöckel, 2017; Wunsch, Weiss, Schack, & Weigelt, 2015). For instance, Weigelt and Schack, (2010) investigated the development of the end-state comfort effect in preschool children (3-, 4-, and 5-year-old) with a bar-transport task. Results yielded a significant increase in end-state comfort performance from 13% in the 3-year-olds to 67% in the 5-year-olds. Similar results were also found in a later study with 3- to 8-year old children (Knudsen et al., 2012).

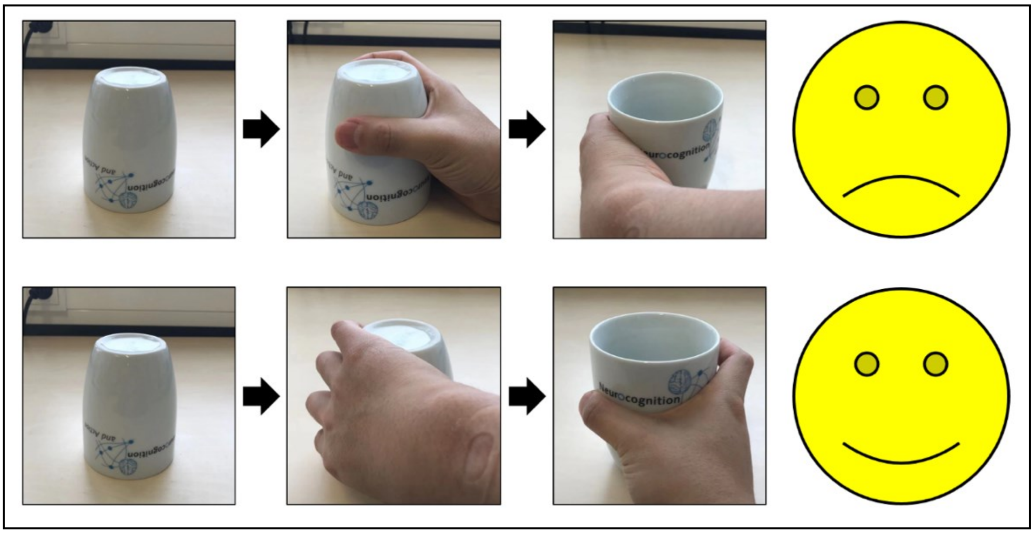

Figure 1.2 The illustration of the End-state comfort effect.

When grasping an upside-down mag, one may feel uncomfortable if he (she) starts with a thumb-up posture and ends up with an awkward thumb-down posture (as shown in the top row). However, one may feel more comfortable if he (she) holds the mag with a thumb-down posture and ends up with a comfortable thumb-up posture (bottom row).

Several explanations have been proposed to interpret the end-state comfort performance, such as the working backward hypothesis (Rosenbaum et al., 1990), the fatigue hypothesis (Rosenbaum et al., 1990), minimizing time in awkward postures (Rosenbaum et al., 1990; Seegelke, Hughes, & Schack, 2011), or the precision hypothesis (Rosenbaum, Van Heugten, & Caldwell, 1996; Short & Cauraugh, 1999). Among them, the precision hypothesis seems to be the most influential one. The precision hypothesis states that motor precision increases when individuals are in a comfortable posture. Compared to the uncomfortable postures, the comfortable end postures allow individuals to control their movements more precisely, which is also in line with the precision demand at the movement end (movement ends typically demand more precisions than movement starts). In this regard, individuals tend to end with a more comfortable position even though the start position is awkward. The precision hypothesis has been supported by several empirical studies (Herbort & Kunde, 2019; Hughes, Seegelke, & Schack, 2012; Short & Cauraugh, 1999). For example, by using a series of five studies, Herbort and Kunde (2019) tested the precision hypothesis directly in a virtual reality environment. The kinematics data illustrates that the grasp selections maximize the speed and accuracy of object manipulations. These findings indicated that the end-state comfort emerges because it maximizes the control over the manipulated object at the end of object manipulations, which supports the precision hypothesis directly.

The end-state comfort effect emphasizes the anticipatory (cognitive) aspects of manual action control that people tend to plan the movement for a future, anticipated intention (action effect). It seems to be consistent with the basic ideomotor ideas (Greenwald, 1970; Rosenbaum & Jorgensen, 1992; Stock & Stock, 2004; Westerholz, Schack, & Koester, 2014) and the anticipative behavioral control framework (Hoffmann et al., 2007; Hoffmann, Stoecker, & Kunde, 2004). On the other hand, the end-state comfort effect also highlights the role of sub-intentions in object manipulations. When planning an action for manipulating an object, individuals should not only pay attention to the final task demand (i.e., how to use the object), but also the immediate task demand (i.e., how to grip the object). The end-state comfort effect supports the idea that manual actions are controlled with hierarchically organized motor plans (Rosenbaum, Cohen, Jax, Weiss, & van der Wel, 2007). In such plans, the starting and the ending postures are located at the top level of the plan. The postures represent the corresponding task demands (immediate for the starting, final for the ending), and they act as the crucial phases of the manual actions. However, the intermediate states comprising the transition from the starting posture to the ending posture are located at the lower levels of the motor plan. These intermediate states are used to connect the crucial phases and sustain the continuity of the movement.

Moreover, the end-state comfort effect seems to indicate a different hierarchy between the anticipated starting and the ending postures in the motor plans, that is, the anticipated ending postures (which represent the final task demand) are more important than the anticipated starting postures (which represent the immediate task demand) during motor planning (Rosenbaum & Jorgensen, 1992; Westerholz, Schack, & Koester, 2013). The end-state comfort phenomenon has revealed that the initial grasp postures are typically selected for achieving the final task demand in a more comfortable way. In other words, individuals tend to grasp the object for the future, anticipated needs instead of the upcoming grip requirements in object manipulations; for example, choosing a thumb-down posture instead of a more comfortable thumb-up posture at the beginning to ensure a comfortable ending posture. Rosenbaum et al. (2012) termed that as "second-order planning" for object manipulations. Second-order planning entails that one's object manipulation movement is not just selected on the basis of immediate task demands but also on the basis of the next task to be performed. Back to the overturn cup example, the initial thumb-down grip posture is not only selected by the physical properties of the cup (i.e., size, shape, etc.), but selected by the action intention that is turning over the cup. In this regard, the selection of initial grasp postures seems to fulfill requirements for the final task demands in object manipulation. The sub-intentions, initial grasp goals (i.e., how to grip the object), and the final task goals (i.e., how to use the object), seem to be organized in a "top-down" manner wherein final task goals bias the selection of more immediate initial grasp goals.

Apart from the end-state comfort effect, the idea that action goals are organized in a "top-down" manner has also been confirmed by kinematics (Ansuini, Santello, Massaccesi, & Castiello, 2005; Hughes et al., 2012; Zhang & Rosenbaum, 2008) and reaction time results (van Schie & Bekkering, 2007; Westerholz, Schack, & Koester, 2013). For instance, by using the motion tracking technique, Hughes et al. (2012) recorded and analyzed participant's kinematics data with a bar-transfer task in which the cue action goals (final task goals) would be perturbed unexpectedly. The results showed that in the non-perturbed trials, participants tended to select the grips to ensure comfortable end postures, which is in line with the end-state comfort effect. However, in the perturbed trials, participants were found to modify their grasp postures, which were characterized by longer reaching times and shorter times to peak velocity during reaching, to ensure comfortable postures at the end. The results suggest that the grasp postures (initial grasp goals) are highly influenced by the final task goals, which is also consistent with the "top-down" manner. In other cases, researchers found that the time for movement preparation (reaction time) was faster when the final task goals were emphasized, as compared to when the initial grasp goals were emphasized, even though the actions involved in the movement tasks were the same in both final-emphasized and initial-emphasized trials (van Schie & Bekkering, 2007; Westerholz, Schack, & Koester, 2013). These results are also consistent with the suggestion that sub-intentions are preferably organized in a “top-down” manner.

Nevertheless, the sub-intentions can also be organized in a reversed way, that is, the selection of final goals may be in accord with the dominance of initial grasp goals, even though it is less often in practice. The utilization behavior (Archibald, Mateer, & Kerns, 2001; Lhermitte, 1983) could be one of the cases. The utilization behavior refers to the automatic elicitation of instrumentally correct yet highly exaggerated or inappropriate motor responses to environmental cues and objects (Archibald et al., 2001; Eslinger, Warner, Grattan, & Easton, 1991; Hashimoto, Yoshida, & Tanaka, 1995). Patients with utilization behaviors are always reaching out and automatically using objects that are within reach or in their visual field in an “object-appropriate” way that is inappropriate for the particular context. For example, a patient is likely to put on a pair of glasses when they are shown to him (her) without being told or asked to do so. The utilization behavior illustrates that the initial grasp goals and the final task goals might be organized in a “bottom-up” (chronological) way that initial grip goals seem to be selected before the final task goals.

Because a limited number of studies have focused on the organization of initial grasp goals and final task goals in object manipulation, the existing behavioral results cannot provide an accurate answer for the question that how the sub-intentions of complex movements are organized. Meanwhile, such a topic has also been investigated by several neuroscientific studies (Bonini et al., 2012; Majdandžić et al., 2007; Van Schie & Bekkering, 2007; Westerholz et al., 2013), and maybe the answer could be found in these studies. Therefore, in the upcoming section, the neural mechanisms underlying goal-directed manual actions, as well as the cognitive neuroscientific basis of the initial and final action goals anticipations, will be overviewed briefly.

Neural mechanisms underlying goal-directed manual action

It has been reported by previous studies that the frontoparietal cortical network is involved in the planning and execution of goal-directed manual actions (Buch, Mars, Boorman, & Rushworth, 2010; Cisek & Kalaska, 2010; Glover, Wall, & Smith, 2012; Iturrate et al., 2018; Sebastian et al., 2013; Tunik, Rice, Hamilton, & Grafton, 2007; Turella & Lingnau, 2014). Within the network, the cortical structures such as the pre-supplementary motor area (pre-SMA, Hoshi & Tanji, 2004; Lee et al., 2016; Macuga

& Frey, 2012; Neubert, Mars, Buch, Olivier, & Rushworth, 2010), the supplementary motor area (SMA, Hoshi & Tanji, 2004; Ikudome, Nakamoto, Yotani, Unenaka, & Mori, 2015; Pellegrino, Tomasevic, Herz, Larsen, & Siebner, 2018), the anterior cingulate cortex (ACC, Glover et al., 2012; Hanakawa, Dimyan, & Hallett, 2008), the inferior frontal gyrus (IFG, Buxbaum, Kyle, Tang, & Detre, 2006; Randerath, Goldenberg, Spijkers, Li, & Hermsdörfer, 2010; Sulpizio et al., 2017), the premotor cortex (PMC, Bortoletto & Cunnington, 2010; Culham et al., 2003; Masson, Bub, & Breuer, 2011; Tunik, Lo, & Adamovich, 2008), the anterior intraparietal sulcus (aIPS, Buxbaum et al., 2006; Schaffelhofer & Scherberger, 2016; Tunik et al., 2008; Zaepffel & Brochier, 2012), the superior parietal lobule (SPL, Kurz, Becker, Heinrichs-Graham, & Wilson, 2014; Pellegrino et al., 2018), and the supramarginal gyrus (SMG, Bortoletto & Cunnington, 2010; Tunik et al., 2008; Ward et al., 2010), have been proved to be the essential cortical nodes for controlling the intentional manual actions, especially for goal-directed reaching or grasping. The frontal and parietal areas are functionally connected, and patient studies indicate that lesions in either frontal or parietal areas are associated with difficulties (disorders) in goal-directed reaching or grasping (Archibald et al., 2001).

The frontal areas of the brain, through rich connections to other brain systems, subserve several complex functions that are critical for goal-directed actions. Generally speaking, one of the main functions of the frontal lobes is to plan, control, and execute voluntary movements. The sub-cortices in the frontal lobe, such as the primary motor cortex (M1), the PMC, and the SMA, are widely known as the crucial parts of the "motor cortex". The M1 is one of the principal brain areas involved in motor function, and the role of the M1 is to generate neural impulses that control the execution of movement directed to skeletal muscles on the contralateral side of the body (Marmarou, 2011). Other areas, such as the PMC and the SMA, are known as the "secondary motor cortices". The PMC is involved in selecting a specific (complex) movement or sequence of movements from the repertoire of possible movements (Purves et al., 2001). Neurophysiological studies found that the PMC receives perceptual information from other cortical cortices (such as the posterior parietal cortex/PPC) to select the appropriate movements (Bonini et al., 2010, 2012) or to correct the ongoing movement (Archambault, Ferrari-Toniolo, Caminiti, & Battaglia-Mayer, 2015; Hartwigsen et al., 2012; Hartwigsen & Siebner, 2015; Pellegrino et al., 2018). The SMA is also proved to be engaged in higher-order motor processing. Studies have revealed that the SMA, as well as the pre-SMA, are involved in the preparation and programming of complex movements (such as the sequential or multi-step movements) and the coordination of bimanual actions (Kaas & Stepniewska, 2002; Leuthold, 2003; Leuthold, Sommer, & Ulrich, 2004; Sulpizio et al., 2017).

Moreover, the frontal lobe, especially the prefrontal cortex (PFC), has also been associated with the cognitive execution functions; for example, the inhibition function, which seems to be necessary for motor planning and control as well. The inhibition functions are highly involved in motor re-planning and online movement corrections, which requires individuals to terminate their prepared motor plans or actions when the actions (plans) are not suitable for the current situation. Neuroscientific studies have revealed that the SMA, as well as the prefrontal structures such as the IFG and the ACC, are associated with the inhibition of pre-planned actions (Angelini et al., 2015; Boecker, Gauggel, & Drueke, 2013; Leuthold, 2003; Pellegrino et al., 2018; Sammler, Novembre, Koelsch, & Keller, 2013; Smith, Jamadar, Provost, & Michie, 2013). Patient studies have also yielded that frontal lobe damages, or the loss of normal inhibitory functions of the frontal lobes may release parietal lobe activity elicited by visual, auditory, and tactile sensory information, which could be the neurological reason for several unrestrained movements such as utilization behavior or imitation behavior (Archibald et al., 2001; Lhermitte, 1983).

The parietal lobe, especially the posterior part (the posterior parietal cortex, PPC), has been recognized as one of the most important sensory associative cortical regions in which neural information derived from the various sub-modalities of the somatosensory system are integrated. The integrated multimodal sensory association provides the basis for some perceptual processes, such as spatial perception and navigation (proprioception). According to the “two visual systems” hypothesis (Goodale & Milner, 1992; Milner & Goodale, 2008), the PPC is a crucial node for visuomotor transformations (“vision for action”), that is, converting visual information into movement-related parameters. Patient studies (Darling, Pizzimenti, & Rizzo, 2003; Goldenberg, 2009; Hyvärinen, 1982; Purves et al., 2001) have yielded that lesions of the parietal cortices (particularly in the PPC) may not only cause the disorders in visuospatial perception, reading, and number understanding, but also produce several movement-related symptoms, such as misreaching, writing disorders, and apraxia[2]. In this regard, apart from the sensory association functions, the PPC also seems to play a vital role in motor planning and motor control.

Primate studies have suggested that the PPC is a mosaic of sub-areas that each of which receives specific sensory input and transfers the neural input into information that is appropriate for movement (Bonini et al., 2010; Colby, 1998; Fogassi et al., 2005; Fogassi & Luppino, 2005; Rizzolatti, Fogassi, & Gallese, 1997; H. Sakata, Taira, Kusunoki, Murata, & Tanaka, 1997). Furthermore, the PPC has been involved in higher-level motor functions, such as organizing goal-related movements and understanding the action intentions of others. For example, Fogassi and Luppino (2005) examined the motor organization functions of the PPC by using single neuron recordings. Monkeys were trained to grasp a piece of food and then place it into either month (to eat) or a container (to place). The results showed that most neurons in the inferior parietal lobule (IPL) were influenced by the different follow-up actions (eat or place), that is, presenting a selective discharge during grasping according to the action sequence in which grasping was embedded. Desmurget et al. (2009) used electrical stimulation in patients with brain tumors (located around the central sulcus). Results indicate that stimulating the right inferior parietal areas triggered a strong intention that patients desire to move the contralateral hand, arm, or foot. Conscious intention and motor awareness arise from increased parietal activity before movement onset.

The above-mentioned frontal and parietal cortical structures are functionally connected when planning, performing, observing, and even imaging goal-directed movements. Within the frontoparietal network, the frontal and parietal cortical structures work together to convert sensory information about the object or environment into movement-related parameters that can be used to execute the upcoming movements. It is typically believed that these parietal and frontal cortices are reciprocally interconnected (Luppino, Murata, Govoni, & Matelli, 1999; Murata, Gallese, Luppino, Kaseda, & Sakata, 2000; Rushworth, Behrens, & Johansen-Berg, 2006; Rushworth, Johansen-Berg, Göbel, & Devlin, 2003; Hideo Sakata, Taira, Murata, & Mine, 1995). The parietal areas (such as the IPL) send the related sensory information

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[2] Apraxia refers to a wide spectrum of disorders that have in common the inability to perform a skilled or learned act that cannot be explained by an elementary motor or sensory deficit or language comprehension disorders (Zadikoff & Lang, 2005).

to the frontal motor cortices (such as the PMC and the SMA), so that the motor cortices can select an appropriate plan for the upcoming movement. On the other hand, the frontal motor areas may also send the efference copy[3] of the selected motor command back to the parietal areas, which acts as the internal feedback from the motor system to the sensory system.

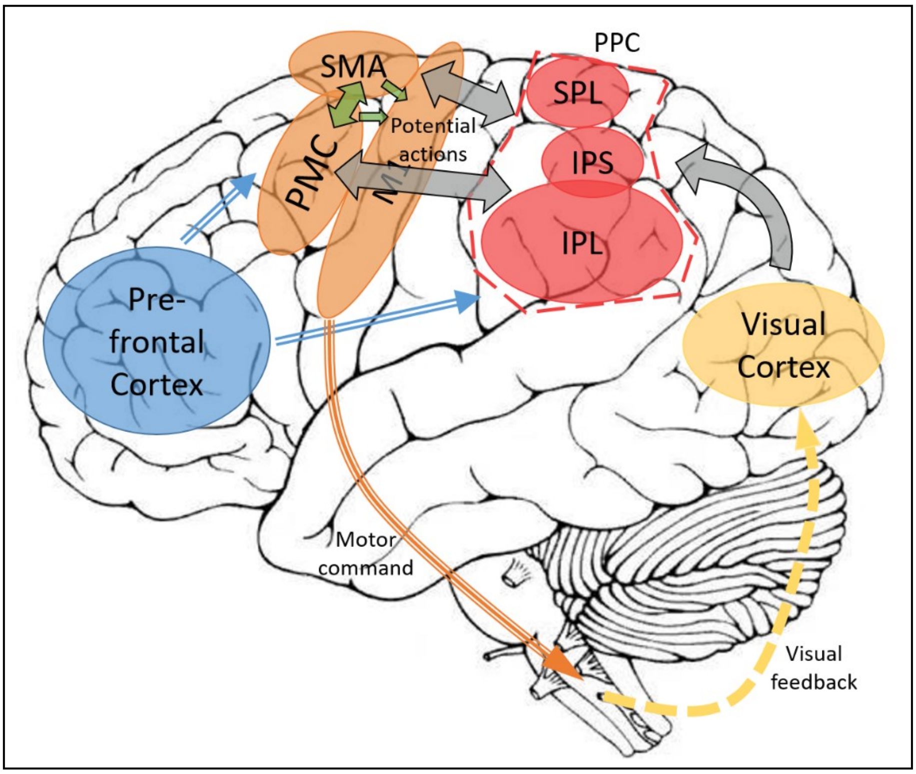

Figure 1.3 Schematic of the frontoparietal cortical network for manual action.

The posterior areas (SPL, IPS, IPL …) receive visual information from the visual cortex, and then send the "potential actions" to the motor cortex (PMC, SMA …). The Prefrontal cortex is also involved in the cortical network for manual action with the executive functions.

It is recognized that different parts of the frontoparietal network are involved in the different functions of the goal-directed manual actions (Koester, Schack, & Westerholz, 2016). Among these cortices, the intraparietal cortex has been considered as an essential node within the frontoparietal involved in the planning and control of grasping movements for both primates (Intveld, Dann, Michaels, & Scherberger, 2018; Menz, Schaffelhofer, & Scherberger, 2015; Murata et al., 2000; Hideo Sakata et al., 1995) and human beings (Martin, Jacobs, & Frey, 2011; Rice, Tunik, & Grafton, 2006; Tunik, Frey, & Grafton, 2005; Tunik et al., 2007; Tunik, Ortigue, Adamovich, & Grafton, 2008;

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[3] The efference copy refers to an internal copy of the motor command (neural signal) that was sent from the brain to the corresponding muscles (Wolpert & Flanagan, 2001).

Verhagen, Chris Dijkerman, Pieter Medendorp, & Toni, 2012). Murata et al. (2000) have reported that neurons in monkeys' anterior intraparietal area (area AIP) are related to hand manipulation, and most of these neurons are visually responsive. Moreover, visual responses of some neurons (more than half) are associated with representing the shape, size, and orientation of the objects, whereas the remaining neurons are associated with representing the shape of the handgrip, grip size, or hand-orientation. In this regard, the grasping neurons in the anterior intraparietal area have both visual and motor properties. In a meta-analysis, Tunik et al. (2007) summarized 22 published functional neuroimaging studies that involving reach-to-grasp movements or object manipulations (action observation tasks were also included), and the meta-analysis of the reported activations yielded a remarkable and consistent overlap within the anterior intraparietal sulcus (aIPS, the human homolog of aIPS in monkey). More recent functional magnetic resonance imaging (fMRI) studies have also suggested that the activations of aIPS are associated with grasping or object manipulations (Marangon, Jacobs, & Frey, 2011; Martin et al., 2011; Przybylski & Króliczak, 2017). Transcranial magnetic stimulation (TMS) studies suggest that virtual lesions of the aIPS interfered with the performance of goal-directed grasping (N. R. Cohen, Cross, Tunik, Grafton, & Culham, 2009; Le, Vesia, Yan, Niemeier, & Crawford, 2014; Verhagen, Dijkerman, Medendorp, & Toni, 2013). Moreover, the aIPS has also been involved in online movement control (Tunik et al., 2005, 2007). Dozens of TMS studies showed that virtual lesions of the aIPS lead to impaired dynamic control of reach-to-grasp movements, and the aIPS is associated with the dynamic error detection during the visual-guided online movement correction (N. R. Cohen et al., 2009; Gutteling, Park, Kenemans, & Neggers, 2013; Reichenbach, Bresciani, Peer, Bülthoff, & Thielscher, 2011; Rice et al., 2006; Verhagen et al., 2012).

Compared to the area AIP in monkeys, the functional roles of the aIPS in humans are not limited to the low-level representations (physical features such as size, type, etc.) of the grasping, but also related to higher-level motor cognitions, such as action goal representation (Hamilton & Grafton, 2006; Tunik et al., 2007). By using fMRI, Hamilton and Grafton (2006) instructed participants to watch video clips that a grasping hand is reaching to one of the two objects (located at two different places) and holding the object. The clip was either the same as or different from the previous one in the action goal (object), the movement trajectory, or both the goal and the trajectory. Significant reduced cortical activations were observed in the aIPS when the action goals were repeated (compared to when the goals were novel). Similar results were found in later studies (Ramsey & Hamilton, 2010; Southgate, Begus, Lloyd-Fox, di Gangi, & Hamilton, 2014). These results suggest that the aIPS represents the goal of an observed grasping. In a more recent study (Sacheli, Candidi, Era, & Aglioti, 2015), the aIPS in the left hemisphere was found to represent the shared action goals when participants were performing complementary grasping together with others. Such results provide evidence that the aIPS is not only coding the observed grasping goals but also representing the action goals when individuals plan and execute grasping movements.

It is worth noting that the above-mentioned results that the aIPS represents action goals seem to be somewhat limited because the movements involved in these studies are limited to simple reaching and grasping. Prehensile manual actions, as well as the goals for manual actions, are more complex in daily life than in these above-mentioned studies. Most prehensile manual actions are multi-step actions that are hardly limited to reaching and grasping the object but manipulating the object for further tasks. In this regard, the action goals in prehensile manual actions contain not only the initial grasp goals (grip postures), but also the final task goals (task purposes). Therefore, the aIPS may represent the grip postures merely. Given the fact that not so many neuroscientific studies have focused on the initial and the final goals, it is not yet known whether the aIPS codes only the initial grasp goals or both the initial and the final action goals. In other words, the neural mechanisms underlying the initial and final action goals for grasping movements are still unclear.

Among the few studies, Majdandžić et al. (2007) investigated neural correlates of the initial and final action goals in planning grasp-to-place movements by fMRI. In this experiment, participants were instructed to grasp a unique object consisting of a large red cube and a small green cube and then place the object into the same-size small or large target slots. The target slots were colored in either yellow or blue, and participants were cued with different colored signals to perform either the initial goal emphasized (grasping the large vs. the small part) or the final goal emphasized (placing into the small vs. the large slot) grasping movements. Although the imaging results showed common activations over the frontal (the precentral gyrus) and the parietal (the calcarine fissure) areas in both initial-emphasized and final-emphasized grasping, different cerebral activations were still found between the initial-emphasized and final-emphasized grasp planning. When initial goals were emphasized, increased preparatory activities were found over the dorsal portion of the occipito-parietal fissure in the right hemisphere and the occipito-temporal fissure in the left hemisphere. However, when final goals were emphasized, increased preparatory activities were found over the bilateral superior frontal gyrus and the left supramarginal gyrus (SMG). The different activations may suggest that the initial and final action goals are represented differently in the cerebral cortex: the frontal areas are more likely to be involved in representing final action goals, whereas the parietal areas seem to be involved in representing both initial and final action goals. Due to the technical limitation (low temporal resolution), the imaging results can hardly provide temporal information about the initial and final goal representations.

To explore the temporal organization of the initial and the final goal representations in grasping, Van Schie and Bekkering (2007) conducted an EEG experiment. Participants were asked to grasp an object precisely and then transfer it to a target position. Visual cues were presented to emphasize the initial action goal (to hold one of the two graspable parts) or the final action goal (to transfer the object to one of the two target positions) when participants were planning their movements, but executed movements were the same in initial-emphasized and final-emphasized trials. Slow-wave event-related potentials (ERP) were used to distinguish between the processes supporting the initial and the final action goals during motor planning and execution. The ERP results revealed different neural activities between the processes related to initial and final action goals: processing the initial goal was accompanied by the development of a parieto-occipital slow wave that peaked at the moment when the object was gripped, whereas processing the final goal was accompanied by another slow-wave component developing over left frontal regions with a peak toward the movement end. Further source analyses found that the parieto-occipital slow-wave for the initial goals was centered on the parieto-occipital sulcus, whereas the frontal slow-wave for the final goals was located in the anterior prefrontal cortex.

In later studies, similar temporal organization of the initial and final action goals has been found in monkeys (Bonini et al., 2012) and humans with power grips (Westerholz et al., 2013). For example, Bonini et al. (2012) studied the initial and final action goals in monkeys' grasping. The monkeys were trained to grasp the object in different sizes (large vs. small) for different purposes (to eat vs. to place). With the help of single neuron recordings, selectivity was recorded and analyzed among the grasping neurons in the inferior parietal lobule (area PFG) and the ventral premotor cortex (area F5). Results of the population analyses showed that the grasping neurons in both the inferior parietal and the ventral premotor areas were selective for both initial and final action goals, but 36% of the inferior parietal neurons and 48% of the ventral premotor neurons were only selective for initial goals. Moreover, the time course of the selectivity illustrated a similar temporal pattern as the previous human study (Van Schie & Bekkering, 2007), that is, the grasping neurons reflect firstly "how" the object has to be grasped (initial goal) during reaching toward the object, and then "why" the action was performed (final goal) after the object was grasped.

In a bar-transfer experiment, Westerholz et al. (2013) investigated the initial and final action goals with power grips. Similar to Van Schie and Bekkering's (2007) experiment, participants in this experiment were also emphasized on the initial goal (how to grip, thumb up vs. thumb down) or the final goal (where to place, left position vs. right position) with visual cues during movement preparation, and instructed grasp-to-place movements were also identical between the two goal-emphasized conditions. The ERP slow-wave results yielded a similar neural mechanism, as well as a (broadly) similar temporal organization of the neural activities, for the initial and the final goal as the precision grip results (Van Schie & Bekkering, 2007): a larger parieto-occipital negativity was found for the initial-emphasized than the final-emphasized condition preceding grasping execution (time-locked to grasping), whereas a larger positivity was observed over the right frontal areas for the final-emphasized than the initial-emphasized condition before the bar was placed to target positions (time-locked to movement end). The results of these studies confirm that the frontoparietal cortical network is crucial for the planning and execution of goal-directed grasping. The initial goals seem to be represented mainly in posterior (parietal and occipital) regions, while the final goals seem to be represented in anterior (frontal) regions. More importantly, the temporal course of these neural activities seems to be consistent with the chronological sequence of the involved actions: parietal activities for initial goals are found first before grasping, and then frontal activates for final goals are found later when the object is close to the target. However, these neural activities are temporally overlapped with motor execution, therefore it still seems to be hard to decide whether the initial and final action goals (sub-intentions) are organized in a "top-down" or "bottom-up" way.

In another bar-transfer experiment (Westerholz, Schack, & Koester, 2014), participants were cued with either free or specified choices about the initial or the final action goals. Slow-wave ERPs were recorded to distinguish the neurophysiological mechanisms underlying the what-decision of grasp planning and execution. The slow waves revealed that the cortical activities were different between the free-choice and the specified final goals over the mid-line regions (mid-frontal, mid-central, and mid-parietal) before grasping and over the right frontal regions before movement end. However, no significant difference was found for the slow-wave activities between the free-choice and the specified initial goals. These results seem to be in line with the idea that the initial and final action goals are organized in a “top-down” manner. It is worth pointing out that the different neural activities in this study seem to reflect the different selection of the initial and final action goals (free-choice vs. specified-choice), not the different initial and final action goals. Moreover, the movements involved in different experimental conditions are not the same. Because of the free-choice goals, the movements may be different between the free-choice and the specified conditions (in terms of grip/target selections). Therefore the different neural activates between the free-choice and the specified final goals might be caused by the motoric difference in these different conditions. Therefore, the neural mechanisms underlying the initial and the final action goals for manual actions are still not fully understood.

The above-mentioned neuroscientific findings suggest that the frontoparietal network is crucial for the planning and execution of goal-directed manual actions. Considering the fact that a limited number of studies focused on both the initial grip goals and the final task goals simultaneously, the current neuroscientific findings can hardly provide a comprehensive picture of the neural mechanisms underlying the organization of the sub-intentions in goal-directed manual actions.

Purpose of the dissertation and research questions

As mentioned previously, little research attention has been focused on the initial and final action goals during the preparation and execution of manual actions. With the limited research findings, it is difficult to provide a comprehensive answer to the question proposed ahead (how the sub-intentions of manual actions are organized). The functional roles of the initial and final action goals in manual actions, as well as the neural mechanisms underlying, are still not fully understood.

Additionally, from a methodological perspective, action goals in previous research were frequently manipulated as the final position or the final object of a single (simple) action, such as button-pressing, reaching, pointing, or grasping (Baldauf et al., 2006; Bozzacchi et al., 2012; Gaveau et al., 2014; Hamilton & Grafton, 2006; Sacheli et al., 2015; Tunik, Ortigue, et al., 2008). In the research involving multi-step (complex) manual actions (i.e., end-state comfort studies), the action goals were mostly manipulated with either a single cue (specifying only one of the action goals and leaving the other as free-choice) or an integrated cue (presenting both initial and final action goals simultaneously). The cognitive processing of the initial and the final action goals, as well as the neural mechanisms underlying the cognitive processing, can hardly be distinguished with these experimental paradigms. New paradigms, which can differentiate the processes, are needed to investigate the initial and final action goals in manual actions.

Accordingly, the current dissertation focused on the functional roles of the initial and final action goals in multi-step object manipulations. The functional roles of the initial and final action goals were studied in different stages of the grasp-to-rotate movement (motor planning, motor re-planning, and online correction). New experimental paradigms were proposed to separate the processes of the initial and the final action goals during the preparation and execution of the movement.

Moreover, EEG/ERP was applied to investigate the neurophysiological correlations of the initial and final action goals during movement preparation and/or movement performance. Compared to other neuroimaging techniques (such as fMRI), EEG/ERP allows a fine-grained perspective on the temporal dynamics (the level of milliseconds) of neural processes in the course of movement preparation and/or performance, which is one of the most significant advantages to using EEG/ERP. Additionally, compared to fMRI, movements involved in EEG/ERP experiments are not constrained by the limited space in the scanner. Furthermore, in EEG/ERP experiments, participants can perform the manual action tasks in a standing or sitting position instead of a lying position in the fMRI scanner, which is closer to the situation in everyday life.

Hence, the current dissertation is trying to answer the following research questions:

1) How are the initial and final action goals organized (coordinated) during the preparation of multi-step manual actions? Moreover, what are the neural mechanisms underlying the initial and final goals coordination?
2) How do individuals re-plan their movement in response to the unexpected changes in the initial or final action goals during the movement preparation? Moreover, what are the neural mechanisms (of the goals) underlying the motor re-planning?
3) How do individuals re-plan (correct) their movement in response to the unexpected changes in the initial or final action goals during the movement execution? Moreover, what are the neural mechanisms (of the goals) underlying the online movement corrections?

To answer these questions, a series of three EEG/ERP studies were conducted. The first study (Chapter 2) aimed to answer the first research question. In the first study, participants were instructed to perform a grasp-to-rotate movement with the action goals that were presented in separate cues successively. More specifically, during the movement preparation, the initial action goals (grip postures) and the final action goals (target locations) were cued in succession, and the sequence of the cues was either "initial–final" or "final–initial" (which corresponds to the two possible ways to coordinate the goals, "bottom-up" or "top-down"). The behavioral performance (timings), as well as the ERPs elicited by the action goals, were recorded and compared to determine the way that individuals coordinate the initial and the final action goals in motor planning.

The second study (Chapter 3) sought to answer the second question. The functional roles of initial and final action goals during motor re-planning were investigated in this study. In order to trigger the motor re-planning, a modified "S1–S2" paradigm was applied to the study. Firstly, participants were instructed to plan a grasp-to-rotate movement with an initial and a final action goal (S1). After a certain period, an imperative signal, together with another stimulus (S2), were presented. The S2 stayed the same as the S1 in 75% of the trials but was perturbed unexpectedly in one of the pre-cued action goals in 25% of the trials. Participants were asked to re-plan their movement to adapt to the changes in either the initial or the final action goal. The behavioral performance (timings), as well as the ERPs elicited by the perturbed action goals, were recorded and compared to determine the roles of the initial and the final action goals and the neurophysiological mechanisms in motor re-planning.

The third study (Chapter 4) addressed the third question. This study focused on the functional roles of the initial and the final action goals in online movement correction. A similar design that was used in the second study was adopted to this study. In the third study, instead of the imperative signal, the goal perturbations (S2) were triggered by participants' self-paced movement initiation (button release), that is, as soon as participants start their movements, one of the pre-cued action goals were changed in 25% of the trials, and participants were asked to correct their movements to adapt to the changes in either the initial or the final action goal. The behavioral performance (timings), as well as the ERPs elicited by the perturbed action goals (also the movement onset), were recorded and compared to determine the roles of the initial and the final action goals during the execution of manual actions.

Initial and Final Action Goals in Motor Planning

Chapter 2

This chapter is based on the paper Yu, L. Schack, T., and Koester, D. (2021). Coordinating Initial and Final Action Goals in Planning Grasp-to-Rotate Movement: An ERP Study. *Neuroscience, 459*, 70-84. https://doi.org/10.1016/j.neuroscience.2021.01.033.

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 toward 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 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 (400–550 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 the 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.

Introduction

Most of the movements we perform every day are directed by desired goals instead of external stimuli (Hommel, Müsseler, Aschersleben, & Prinz, 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 & Balleine, 1995; Dolan & 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 & Butz, 2012; Wunsch, Weiss, Schack, & Weigelt, 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 that 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 (Belardinelli, Stepper, & Butz, 2016; R. G. Cohen & Rosenbaum, 2004; Herbort & Butz, 2015; Rosenbaum et al., 1990; Seegelke, Hughes, & Schack, 2011; Weigelt & Schack, 2010), as well as kinematic data (Ansuini, Santello, Massaccesi, & Castiello, 2006; Hughes et al., 2012; Zhang & Rosenbaum, 2008), suggest that initial grasp postures are selected for achieving the final task goal effortlessly. Moreover, in other studies (Van Schie & Bekkering, 2007; Westerholz, Schack, & Koester, 2013), participants reacted faster when the final task goals were emphasized, even though the same movements were performed in both final-emphasized 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 frontoparietal network has been implicated in action organization for non-human primates (Bonini et al., 2010; Fogassi et al., 2005; Marc Jeannerod, Arbib, Rizzolatti, & Sakata, 1995) and humans (Hamilton & Grafton, 2006; Koester & Schack, 2016; Majdandžić et al., 2007; Marangon, Jacobs, & Frey, 2011). 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, Schack, & Koester, 2014; Westerholz, Schack, Schütz, & Koester, 2014), 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 (Herbort & Butz, 2015; Hughes et al., 2012; Rosenbaum, Vaughan, Barnes, & Jorgensen, 1992; Van Schie & Bekkering, 2007; Weigelt & Schack, 2010; Westerholz et al., 2013; Zhang & Rosenbaum, 2008), 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 (Hakkarainen, Pirilä, Kaartinen, & Meere, 2012; Van Elk, Crajé, et al., 2010; Van Elk, Van Schie, Neggers, & Bekkering, 2010) and its amplitude is modulated by the evaluation of task-relevant feature of stimuli (Kenemans, Kok, & Smulders, 1993; Potts, 2004; Potts, Martin, Burton, & Montague, 2006; Potts, Patel, & Azzam, 2004; Smid, Jakob, & Heinzh, 1999), as well as the organization of upcoming responses (Gajewski, Stoerig, & Falkenstein, 2008; Makeig et al., 1999; Nikolaev, Ziessler, Dimova, & Van Leeuwen, 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, Schack, & Koester, 2014; Westerholz, Schack, Schütz, et al., 2014), 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 trials 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 2.1. 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.

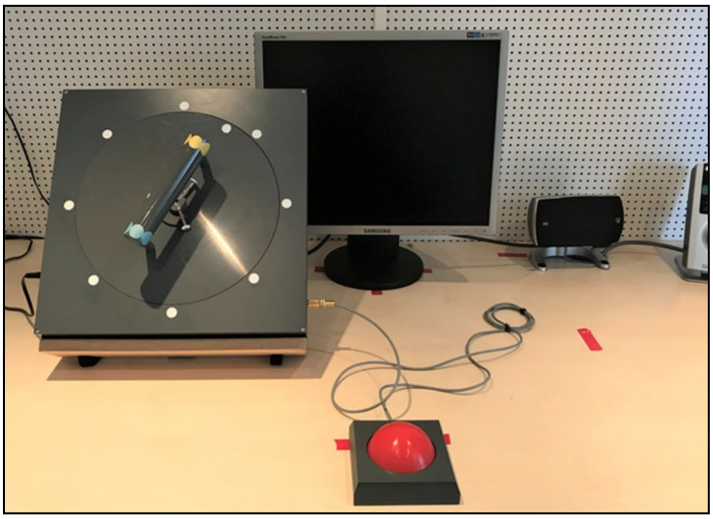

Figure 2.1 Experimental setup.

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).

Visual cues were presented by Presentation (Neurobehavioral Systems, USA) 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 the thumb toward the yellow end, and blue represented the thumb-away posture that the handle was held with the thumb toward 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 2.2).

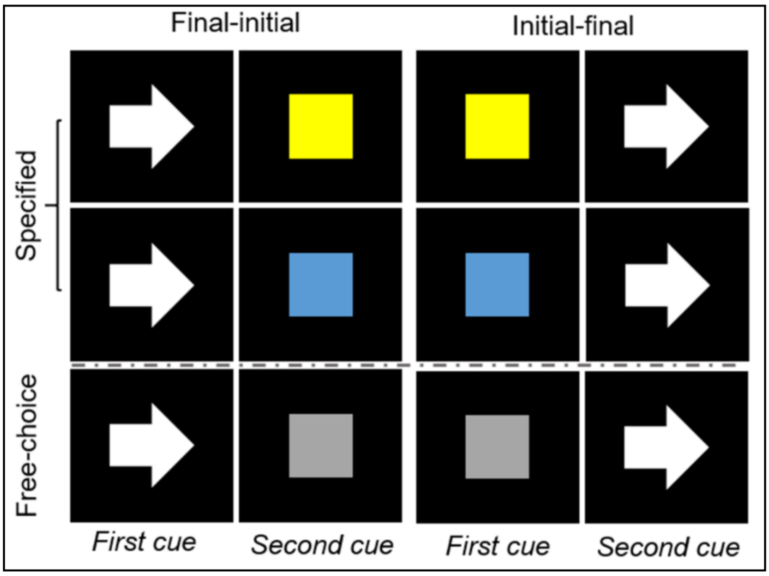

Figure 2.2 Illustrations of possible stimuli.

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").

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).

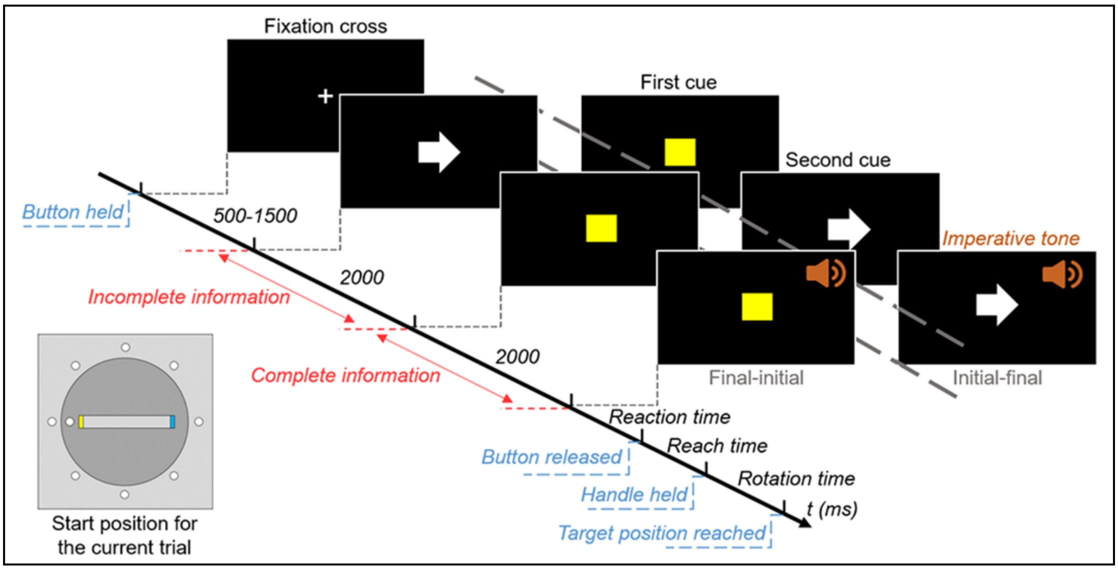

Figure 2.3   Time course of an experimental trial.

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.

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.

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, Netherlands) 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, Netherlands).

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-hand 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 values were also excluded from behavioral and ERP analyses. Table 2.1 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 & Makeig, 2004) and ERPlab (Lopez-Calderon & Luck, 2014). All signals were filtered with a high-pass at 0.1 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, Wouters, Vanrumste, Lagae, & Stiers, 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 2.1.

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 (Hillyard & Anllo-Vento, 1998; Luck, Heinze, Mangun, & Hillyard, 1990), 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).

Table 2.1 ***The number of averaged trials (percentage) for analysis separately for the experimental conditions.***

	Behavioral		ERP	
	Specified	Free-choice	Specified	Free-choice
Final–initial	59(92%)	61(95%)	53(83%)	55(86%)
Initial–final	58(91%)	61(95%)	52(81%)	55(86%)

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 & 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 four regions of interest (ROI) to determine the scalp distribution. The four 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 false-positive effects, we only combined the windows if three or more consecutive windows revealed significant main or interaction effects (Van Schie & Bekkering, 2007; Westerholz et al., 2013; Westerholz, Schack, Schütz, et al., 2014).

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 2.4. 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, $t(25) = -4.05$; $p < 0.001$.

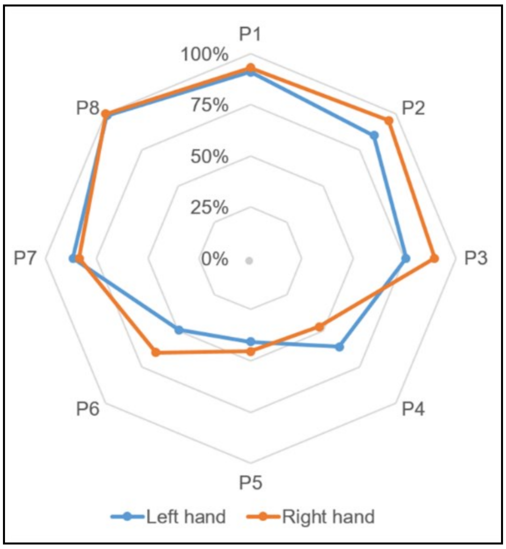

Figure 2.4 Grip selections in free-choice grasping.

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.

Participants' average reaction times, reaching times, and rotation times are shown in Figure 2.5. 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, $t(25) = 1.11$; $p > 0.05$.

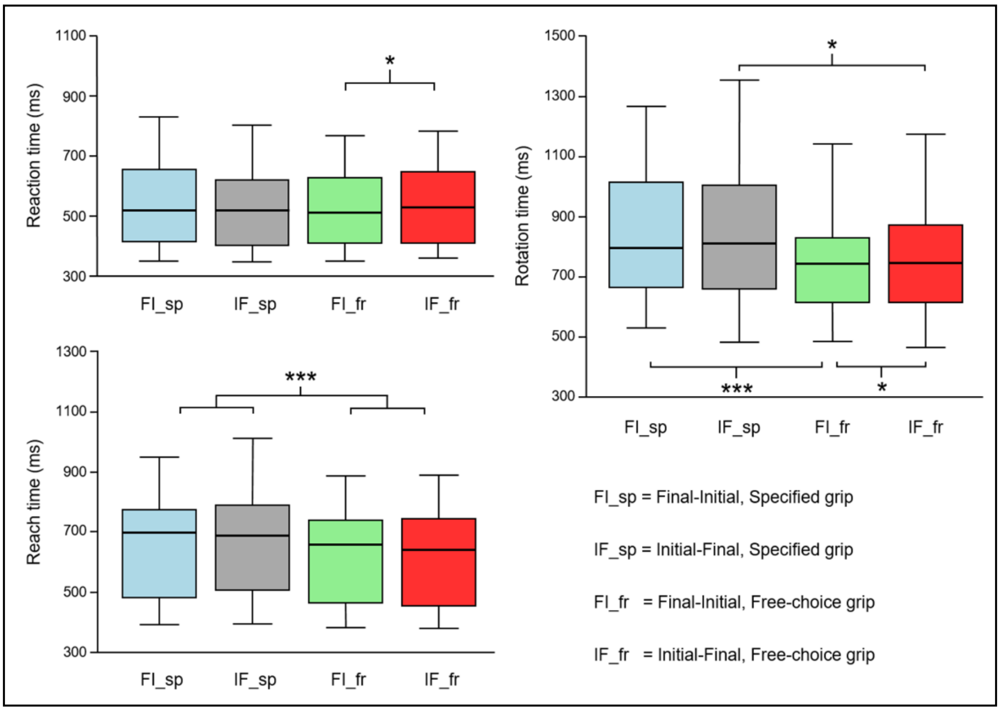

Figure 2.5 Timing of behavior.

Box plots representing reaction times (top left), reach time (bottom left), and rotation time (top right) 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 $p < 0.001$.*

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 toward 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).

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 ($\underline{\text{final}}$[4] –initial, 2.80 μV), as compared to the trials with initial goal ($\underline{\text{initial}}$–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 *p*s < 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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[4] 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.

N2 (250 to 325 ms) In the analysis of N2, we found a significant main effect for *cue sequence*, $F(1,25) = 5.86$; $p < 0.05$; $\eta_G^2 = 0.011$. The mean amplitude was more negative in the <u>initial</u>–final condition (−0.14 μV), as compared to the <u>final</u>–initial condition (0.79 μV). In addition, a significant main effect for *area* was also found, $F(2,50) = 10.63$; $p < 0.001$; $\varepsilon = 0.604$; $\eta_G^2 = 0.031$. 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 ts > 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*, $F(2,50) = 14.62$; $p < 0.001$; $\varepsilon = 0.716$; $\eta_G^2 = 0.006$, was found in the analysis of P3 mean amplitude. The main effect for *cue sequence*, $F(1,25) = 11.43$; $p < 0.01$; $\eta_G^2 = 0.022$, and the main effect for *area*, $F(2,50) = 19.58$; $p < 0.001$; $\varepsilon = 0.619$; $\eta_G^2 = 0.072$, 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 <u>final</u>–initial (0.91 μV) than <u>initial</u>–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 Fs > 8.41; all ps < 0.01. In the <u>initial</u>–final condition, the mean amplitude of P3 was larger at the parietal area than the frontal and central areas, all ts > 1.44; all ps <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 <u>final</u>–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 A1 in the Appendix).

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 <u>final</u>–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 <u>initial</u>–final condition (0.36 µV) than free-choice grasping in the <u>final</u>–initial condition (−0.12 µV), $t(25) = 2.09$; $p < 0.05$. No other significant effects were found in further analyses.

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–<u>final</u> condition (4.37 µV) than the final–<u>initial</u> 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–<u>final</u> (2.52 µV) and final–<u>initial</u> (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–<u>final</u> condition, $t(25) = 4.88$; $p < 0.001$. No significant *grip selection* effect was found in the final–<u>initial</u> condition, $t(25) = 1.03$; $p > 0.05$.

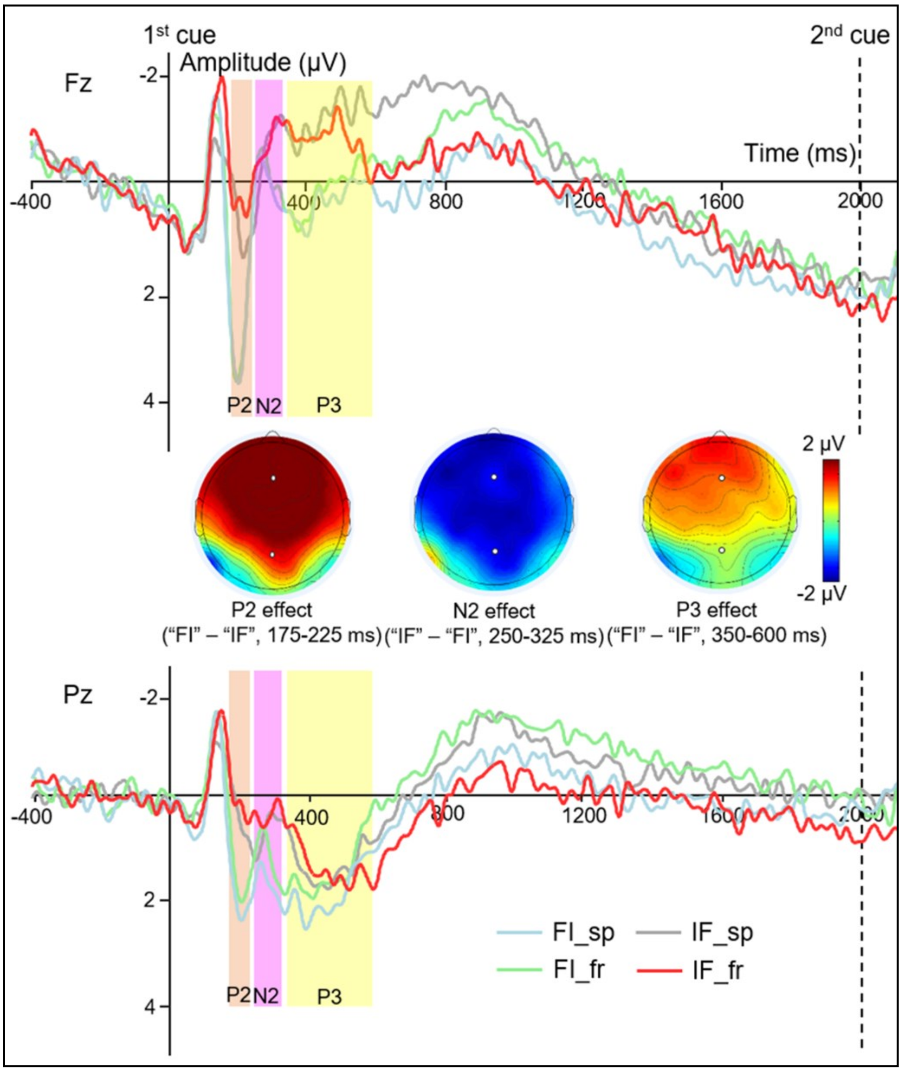

Figure 2.6 ERP waveforms at the first cue.

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.

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, $t(25) = -0.45$; $p > 0.05$.

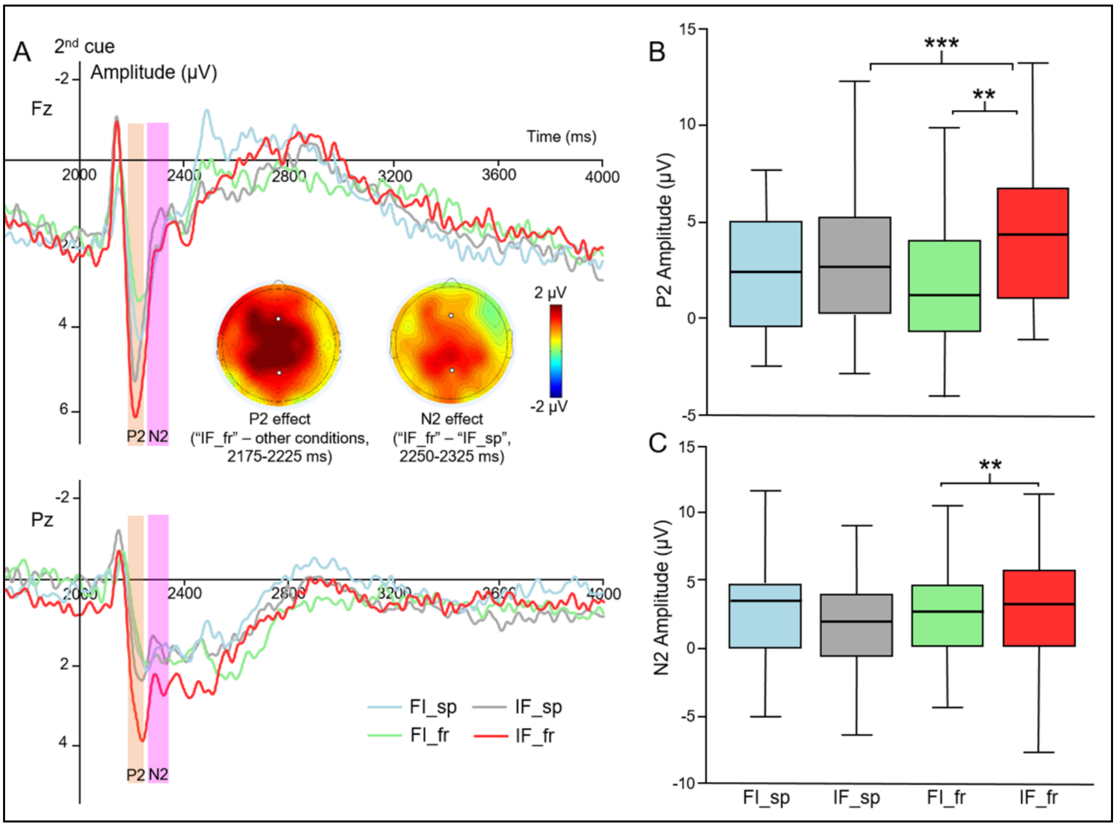

Figure 2.7 *ERP waveforms at the second cue.*

(A) *Grand-averaged ERPs recorded at the midline electrodes (Fz and Pz) from 2000 to 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 $p < 0.001$.*

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 A2 in the Appendix). 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–<u>initial</u> 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–<u>final</u> condition, the *front–back* effect was not significant, $t(25) = 1.27$; $p > 0.05$. A summary of the main ERP results can be seen in Table 2.2.

Table 2.2 A summary of the main ERP results

	Cue1	Cue2
P2	Final is more positive than Initial	Final is more positive than Initial (free-choice only)
N2	Initial is more negative than Final	Specified is more negative than Free-choice (final only)
P3	Final is more positive than Initial (anterior only)	--
Slow-wave potentials	Initial is more positive than Final (free-choice only, 600–2000 ms)	Anterior is more positive than Posterior (initial only, 2800–3600 ms)

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, Schack, Schütz, & Koester, 2014), 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 free-choice grasping as easier than the specified grasping. Also, the thumb-toward grips were rated easier than the thumb-away grips. The findings are in line with the previous study (Westerholz, Schack, Schütz, & Koester, 2014). 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 that 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, Schack, & Koester, 2014; Westerholz, Schack, Schütz, & Koester, 2014). 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 2.6, 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 indicates 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 2.6). It has been argued that the anterior N2 component is an electrophysiological marker for conflict monitoring (Enriquez-Geppert et al., 2010; Van Veen and Carter, 2002; Yeung and Cohen, 2006) 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 2.6, 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 that 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 2.8, 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; Westerholz, Schack, Schütz, & Koester, 2014; Koester et al., 2016). So, the posterior positive slow waves may indicate that (at this moment) processing free-choice initial goals (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.

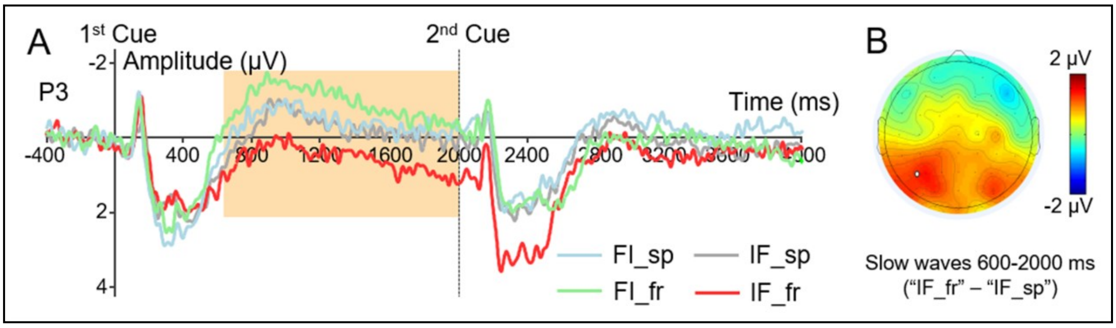

Figure 2.8 ERP waveform at the left posterior electrode (P3).

*(**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.*

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 that 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 2.7, 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 of 2800–3600 ms, we found that the mean amplitude of the slow waves was larger over the anterior areas than over 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 and Jorgensen, 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 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 a 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.

Initial and Final Action Goals in Motor Re-planning

Chapter 3

This chapter is based on the manuscript Yu, L. Schack, T., and Koester, D. (under review). Neurophysiology of Motor Re-planning: ERP correlates of Initial and Final Goal Perturbations. Submitted to *Biological Psychology*.

Abstract

For prehensile movements, action goals are not restricted to grasping the object but also essential for a subsequent goal. In this study, event-related potentials were used to investigate the motor re-planning in response to an unexpected change in the initial or final action goals. Subjects performed a grasp-to-rotation task in which initial (how to grip) or final (target position) goals were perturbed unexpectedly. Results reveal longer reaction and execution times were needed for initial-perturbed than for final-perturbed trials. ERPs showed no amplitude difference in P2, N2, and P3 between the perturbed conditions. However, initial-perturbed trials elicited a more positive centro-parietal slow-wave potential (500–700 ms) than final-perturbed trials. The results suggest that motor re-planning with a perturbed initial goal is more cognitively demanding than with a perturbed final goal, and the increased efforts seem to be engaged in implementing a new motor plan instead of inhibiting the pre-planned movements

Introduction

Human movements are either intention-based or stimulus-based. Usually, everyday movements are driven by internal intentions rather than external stimuli (Hommel et al., 2001). Movement intentions involve representations of the motor plan, which mentally reflect the structure of movement (Miller et al., 1960). Generally, motor plans are well organized before movement execution (Henry & Rogers, 1960; Rhodes et al., 2004; Rosenbaum, 1980). Prehensile movements can be planned and covertly represented up to the third act before movement onset (Haggard, 1998). Additionally, both the first action and the last action of the prehensile movements are mentally anticipated ahead (Rosenbaum et al., 2012). In addition, we are surrounded by a dynamic environment. The previously planned movements may not be suitable if the surrounding circumstances change. To avoid inadequate movements and fulfill the movement intentions, motor re-planning is needed to modify the pre-planned movement as soon as individuals realize the inconsistency. In this regard, motor re-planning seems to be one of the essential abilities for human beings to interact and cope with the dynamic environment.

Even though motor re-planning is crucial for humans to adapt to changing environments, it has received little attention in the field of psychology. Compared with motor planning, motor re-planning engages more cognitive recourses such as attention (Fischer, 1997; Verbruggen et al., 2010) and working memory (Spiegel et al., 2012, 2013). For example, by using a dual-task paradigm, Spiegel et al. (2012) found that re-planning a pre-planned movement impaired participant's performance on a verbal working memory task. A later study (Spiegel et al., 2013) found that motor re-planning not only interfered with participant's verbal working memory performance but also reduced the performance of spatial working memory tasks. Additionally, studies with aging individuals (Korotkevich et al., 2014; Teixeira, Franzoni, et al., 2006; Trewartha et al., 2013) and patients with autism (Nazarali et al., 2009; Rinehart et al., 2001) also suggested that the motor re-planning performance of these participants got impaired due to the deterioration of their cognitive capacity.

It has been suggested that two distinguished processes are involved in motor re-planning, inhibiting the pre-planned actions and implementing a new motor plan (Quinn & Sherwood, 1983; Venkataramani et al., 2018). As soon as the inconsistencies between ongoing movements (or motor plans) and current environment situations are detected, individuals first inhibit their ongoing movements (or motor plans) and then generate a new motor plan to adapt to the changes. The two processes are carried serially, and they can be completed within a short time (Quinn & Sherwood, 1983; Teixeira et al., 2005; Teixeira, Chua, et al., 2006).

To re-plan the movement, in the first place, individuals have to inhibit their current movements or abort the ongoing motor plan. Inhibition is one of the core executive functions for humans (Diamond, 2013). Neurophysiological processes underlying the cognitive process of inhibition can be recorded through EEG recordings. Previous event-related potential (ERP) studies have suggested that the fronto-central N2 (Iannaccone et al., 2015; Kopp et al., 1996; Ramautar et al., 2006; Recio et al., 2014; Tzagarakis et al., 2010; Vidal et al., 1995) and the fronto-central P3 (Leuthold & Jentzsch, 2002; Ramautar et al., 2004, 2006; Smith et al., 2008) can be considered as neuro-electrophysiological markers for movement inhibition. Further source analyses of these components suggested that the increased frontal activities can be localized in the pre-supplementary motor area (pre-SMA) and the anterior cingulate cortex (ACC; Leuthold & Jentzsch, 2002; Vidal et al., 1995). Neuroimaging and brain stimulation studies have also confirmed that the pre-SMA and ACC contribute to inhibiting a pre-planned movement (Braver et al., 2001; Iannaccone et al., 2015; Lee et al., 2016;

Neubert et al., 2010). Furthermore, other frontal areas, such as the ventral premotor cortex (PMv) (Buch et al., 2010) and the right inferior frontal gyrus (rIFG) (Nakamoto & Mori, 2012; Neubert et al., 2010; Verbruggen et al., 2010) can also be involved in suppressing prepared movements.

After the inconsistent movements or motor plans have been aborted, cognitive resources are devoted to the implementation of a new motor plan. Based on the changed environment, a new motor plan is generated by a set of new movement parameters and action goals. Due to the engagement of cognitive resources, previous studies reported that the centro-parietally distributed P3 (P3b) seems to be a neuro-electrophysiological marker for the implementation of new motor plans (Recio et al., 2014; Trewartha et al., 2013). Larger centro-parietal P3 was found in trials with motor re-planning compared to the trials without re-planning. In another study, Tunik et al. (2008) also found the increased parietal-distributed positivity during the re-planning of grasping movements. By using the distributed linear source estimation, the parietal activities were localized in the anterior intraparietal sulcus (aIPS), which is associated with the representation of action goals (Hamilton & Grafton, 2006) and the integration of related action goals to generate a new motor plan (Tunik et al., 2008).

Most motor re-planning studies employed a single action as the movement task, such as button press (Golob et al., 2002; Rinehart et al., 2001; Trewartha et al., 2013; Vidal et al., 1995), saccade (Hocking et al., 2014; Winograd-Gurvich et al., 2006), or reaching (Buch et al., 2010; Nashed et al., 2014; Neubert et al., 2010). In these studies, action goals have typically been operationalized as the final position (action effect), and participants have been cued with the final position as well. Even in other research with more complex movements, such as grasp-to-place (Spiegel et al., 2012, 2013), participants were still cued with the final position to prepare or re-plan their movements. In addition to the final action effect, the initial action effect (such as how to grip the object) is also critical for the preparation and execution of prehensile movements.

It has been claimed by Rosenbaum et al. (2007) that movements are controlled with hierarchically organized plans. In a hierarchical motor plan, both initial action goals (starting postures) and final action goals (goal postures) are represented at the top level, and the intermediate states comprising the transition from the initial action goals to the final action goals are represented at the lower levels. Therefore, it seems to be essential to select and coordinate both the initial and the final action goals in motor planning for having an efficient as well as smooth movement execution. Given that previous motor re-planning studies have neglected the initial action goals, the functional roles of the initial and final action goals in motor re-planning are still not fully understood.

The present study aims to investigate the functional roles of the initial and final action goals in re-planning the prehensile movement and neurophysiological correlates. To address this issue, we modified the “S1-S2” paradigm and introduced an unexpected perturbation in either the initial goal (grip posture) or the final goal (target position) for a quarter of trials. Participants were cued to prepare the grasp-to-rotate movement with the first stimuli, which contain both initial and final goals. The imperative signal also indicated whether the action goals had changed or not. In the goal-changed trials, participants had to re-plan their prepared movements to adapt to the unexpected changes in either initial or final goals. ERPs were used to investigate the neural processes associated with motor re-planning (inhibition and implementation). The fine-grained temporal resolution of ERPs provides further, namely neurophysiological, information about the motor re-plan processing in addition to reaction time.

The question of primary interest is whether the unexpected perturbations in the initial or final action goals interfere with the preparation of reach-to-grasp movements. Furthermore, we asked how the initial-perturbed and the final-perturbed action goal affect movement preparation. On the basis of previous studies (Golob et al., 2002; Leuthold & Jentzsch, 2002; Vidal et al., 1995), we expect that the perturbations in action goals require more cognitive efforts to re-plan the movement than the motor planning without perturbation. Prolonged reaction times, enlarged anterior P2s, anterior N2s, and larger P3s were expected for the goal-perturbed trials. We also assume that the motor re-planning in response to the perturbation in the initial goals is more cognitively demanding, as compared to the perturbation in final goals. When the final goals have been perturbed, individuals may reuse at least part of their previously prepared motor plan because the reaching and grasping requirements are the same as the pre-planned movement. However, when the initial goals have been perturbed, individuals may have to re-plan the whole movement because a new initial goal (start posture) leads to a distinguished movement from the pre-planned movement even though the final goal stays the same.

Method

Participants

Thirty right-handed students from Bielefeld University were recruited for this study. Four of them had to be excluded due to either artifacts or manipulation checking. Finally, 26 participants (Mean age = 25.08, SD = 3.60, 16 females) were analyzed, and all of them had a normal or correct-to-normal vision. Participants were compensated with either 20-euro or two participation credits. This experiment was approved by the ethics committee at Bielefeld University (EUB). All participants gave their written informed consent under the Declaration of Helsinki.

Setup and design

The experiment was conducted in an electrical-shielded room. A 19-inch TFT monitor and a rotation device (Westerholz et al., 2014) were placed on an experimental desk (see Figure 3.1). Participants were asked to grasp the handle of the rotation device and rotate it to a given position. The handle was decorated with two colored stripes (yellow and blue), and it was attached to a rotatable disk. On the disk, a white pointing marker was fixed in a straight line with the handle, and it was used to indicate the handle direction. Outside of the disk, eight dial-displayed target markers were evenly fixed on the frame. A button was connected to the rotation device, which serves as the start button (button release).

Colored arrows were employed as visual stimuli, and they were presented by Presentation (Neurobehavioral Systems, USA). The color (yellow or blue) indicated the initial action goal: participants should grasp the handle thumb-toward the corresponding stripe. The direction of the arrow represented the final action goal: participants should move the handle (pointing marker) to the indicated target marker. The given direction was always perpendicular to the handle's initial orientation, and participants were instructed to make only 90-degree rotations.

A modified "S1–S2" paradigm was used in the experiment. With the first stimuli (S1), the initial and final goals were given. Participants were instructed to plan the movement based on the given information and wait for the imperative signal. Then, the secondary stimuli (S2) were presented together with the imperative signal. The secondary stimuli were either as same as the first (non-perturbed) or different from the first (perturbed). Different secondary stimuli divided the experiment into three conditions (see Figure 3.2). (1) Final-perturbed: The arrow changed to the opposite direction, but the color stayed. (2) Initial-perturbed: The color changed to the opposite (yellow to blue or blue to yellow), but the direction stayed. (3) Non-perturbed: Neither color nor direction changed.

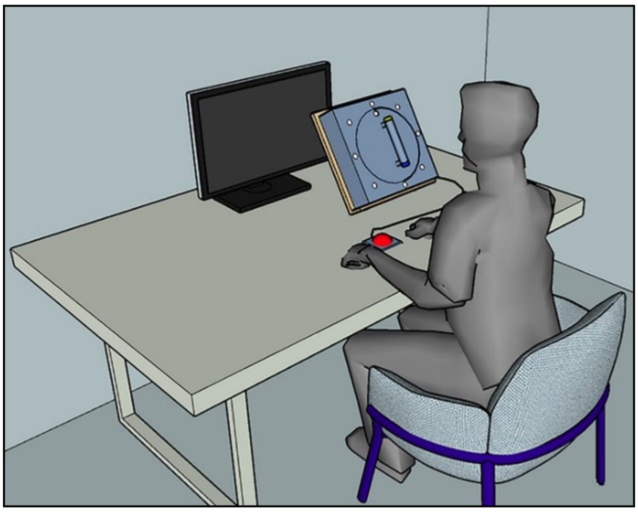

Figure 3.1 Front view of the experimental setup.

The rotation device is placed in front of the participant's shoulder that the arm and hand will be used for the grasp-to-rotate movement (right side in the current setting), and the start button is positioned in front of the participant. Only the right-hand movement setting is illustrated here.

Procedure

After filling out the consent form and Edinburgh Handedness Inventory (Oldfield, 1971), participants were prepared for EEG recording. Then participants were seated comfortably at the experimental desk. The monitor was placed about 75 cm in front of participants. The rotation device was settled where its center was faced to the shoulder of the participant's grasping arm. The distance was calibrated to each participant's arm length for preventing expansive movements. The start button was placed in front of the participants. The distance was also calibrated to each participant's arm, but the distance between the rotation device and the button was constant for each participant (35 cm). A written instruction was given to explain the experimental task. Potential changes in stimuli (perturbations) were not mentioned in the instruction to reduce expectancy effects. Participants were instructed to grip the handle and rotate it according to the visual stimulus that was showing on the screen. All of the questions regarding the experimental task were answered.

The experiment began with a practice block. Thirty-two practice trials were all non-perturbed trials, and they were used to familiarize the participants with the task. These trials were also used to detect any apparent EEG artifacts (such as motoric artifacts).

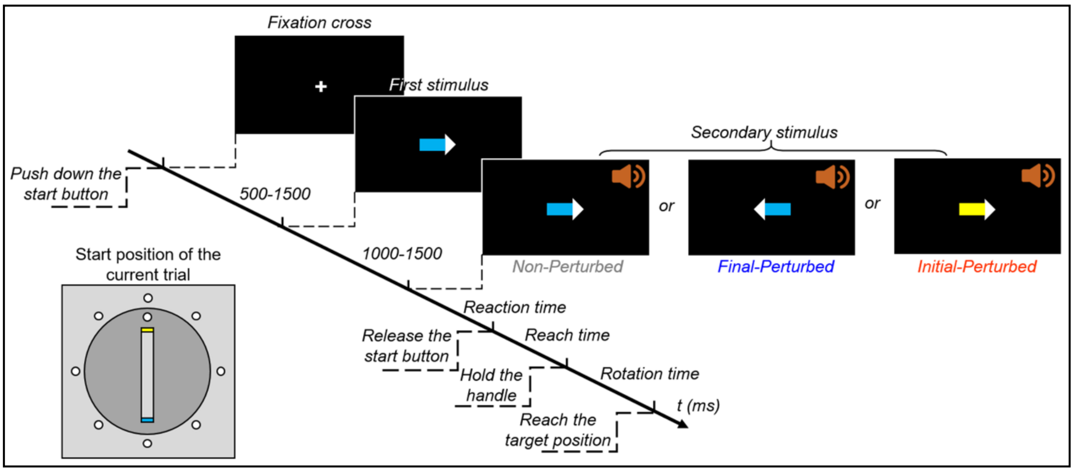

Figure 3.2 The temporal organization of an experimental trial.

A fixation cross was presented for a randomized duration of 500–1500ms. After that, the first stimulus (S1) appeared and indicated the initial goal (color) and final goal (direction) of the movement. It was presented for a randomized duration of 1000–1500ms. Then, the secondary stimulus (S2) appeared with the imperative signal. In the non-perturbed condition (left), the secondary stimulus stayed the same as the first stimulus. In the final-perturbed condition (middle), the arrow changed in the opposite direction, but the color stayed the same. In the initial-perturbed condition (right), the color changed to the other, but the direction stayed the same.

The experimental trials were self-paced, i.e., started by participant's button presses. Then the handle moved to the start position automatically. The start positions were randomly assigned to each target marker, and every marker was used for the same number of trials. Participants were asked to continuously hold the button with their palms until they heard a tone. Meantime, a fixation cross was presented at the center of the screen with a variable duration from 500 to 1500 ms. After the fixation cross, the first stimulus was presented at the center as well for a random duration between 1000 and 1500 ms. Participants were instructed to prepare the movement mentally and keep holding the button. Thenceforth, a 400 Hz sine-tone was played for 100ms, and it was employed as the imperative signal. Simultaneously with the tone, the second stimulus was presented. Participants were allowed to release the button, grasp the handle (with the same hand), and rotate the handle to the target position. The stimulus would always appear on the screen until the handle reached the target position. Then, participants were guided to press the button shortly again to get into the next trial. If the button were released before the imperative signal, error feedback would be delivered for 1500 ms. Then the handle moved to the next start position, and participants could start the next trial by pressing the button. To minimize the ocular artifacts, participants were instructed to keep their gaze at the center of the screen during movement preparation and execution. The stimulus sequence in one trial can be seen in Figure 3.2.

The experiment consisted of 384 trials. The trials were divided into eight blocks (48 trials each). Two-minute breaks were given between the blocks. Participants were asked to start with one hand for the first four blocks and then use the other hand for the remaining four blocks. The starting hand (left/right) was counterbalanced across participants. The rotation device was moved to the other side after the first four blocks, and it was re-calibrated.

Half of the trials requested for the grips with thumb toward the yellow stripe, and the other half requested for thumb toward the blue stripe. Besides, participants had to rotate the handle clockwise for half of the trials and counter-clockwise for the rest. The grips and rotation directions were randomly assigned to the trials. To reduce expectancy effects, we set the ratio of "perturbed/non-perturbed" to 1/3. In the perturbed conditions, the ratio of "final-perturbed/initial-perturbed" was 1/1. Thus, participants performed 48 final-perturbed trials, 48 initial-perturbed trials, and 288 non-perturbed trials in total. All trials were fully randomized except that the first trial of each block was always non-perturbed (to reduce expectancy effects).

Subjective difficulty ratings for different perturbed conditions were queried by a post-experimental questionnaire (1/easy to 6/difficult). Besides, manipulation checking questions, such as "did you always start to plan your movement after the tone" and "did you have specified strategies", were also asked in the questionnaire. On average, two hours were needed to finish the whole experiment.

Data recording

Participants' behavioral performance was recorded by a video camera. The time points of button-released, handle-griped, and target-position-arrived were detected by the micro-switches in the rotation device. Based on these time points, reaction time (duration between imperative signal and button-released), reach time (duration between button-released and handle-griped), and rotation time (duration between handle-griped and target-position-arrived) were recorded by Presentation.

EEG was recorded by a 64-channel amplifier (ANT Neuro, Netherlands). Sixty-four Ag/AgCl electrodes were arranged according to the international 10–10 system. EOG was recorded by two bipolar electrodes placed above and below the right eye and lateral to both eyes. Scalp impedance was less than five kΩ. All signals were band-pass filtered (DC–138 Hz) and digitized at 512 Hz. All signals were average-referenced, and AFz was selected as the recording ground.

Data analysis

The performance videos were analyzed offline. Trials that contained wrong grips, changing grips after holding the handle, or letting the handle go before reaching the target positions were excluded from the behavioral and neurophysiological analyses. The reaction time, reach time, and rotation time were pre-processed by excluding the extreme values (outside of mean ± three standard errors). On average, two final-perturbed trials, three initial-perturbed trials, and 20 non-perturbed trials were rejected due to the extreme values. It has been argued that manual laterality is hardly evident in planning the goal-directed prehensile movements (Seegelke et al., 2014 for review). Therefore, the left-hand and right-hand trials were pooled together in both behavioral and neurophysiological analyses. To determine the effect of *perturbation*, repeated-measures ANOVAs were performed separately on participants' averaged reaction, reach, and rotation times.

EEG signals were analyzed with the Matlab toolbox EEGlab (Delorme & Makeig, 2004) and ERPlab (Lopez-Calderon & Luck, 2014). The signals were offline band-pass filtered at 0.1–30 Hz. Re-referencing was conducted with linked mastoid electrodes. An 800 ms epoch was selected time-locked to the secondary stimulus. A baseline voltage over the first 100 ms intervals preceding stimuli onset was used for baseline correction. Ocular artifacts were corrected using the Gratton algorithm (Gratton et al., 1983). The peak-to-peak moving window method was engaged for artifact detection (200 ms window; 50 ms step). Epochs containing peak-to-peak amplitudes above the threshold of ±50 μV within the moving window were rejected. The epochs were also visually double-checked for artifacts that would not have been detected by the algorithm. Finally, 10% of the trials in the final-perturbed condition, 10% in the initial-perturbed condition, and 11% in the non-perturbed condition were rejected due to artifacts.

We compared the early ERP components P2 and N2, as well as the P3 component and the late slow-wave potentials from 500 to 700 ms in the epoch. For the P2, N2, and P3, the amplitudes were quantified as the peak in the time windows 150–200 ms, 200–250 ms, and 250–500 ms respectively. The amplitudes were compared among the midline electrodes (Fz, FCz, Cz, CPz, & Pz) because of the maximum amplitudes located in the central areas (Leuthold & Jentzsch, 2002; Luck et al., 1990). Repeated measures ANOVAs were performed on the amplitudes in the corresponding time windows with the factors *perturbation* (final-perturbed, initial-perturbed, non-perturbed) and *electrode* (Fz, FCz, Cz, CPz, Pz). As to the late slow-wave potentials, mean amplitudes were obtained and compared in 100 ms step windows (500–600, 600–700). The comparisons were performed among nine regions of interest (ROI) to assess the scalp distribution of ERP effects. The nine ROIs were anterior-left (AL): AF7, F7, F5, F3; anterior-middle (AM): F1, Fz, F2; anterior-right (AR): AF8, F8, F6, F4; central-left (CL): C3, C5, CP3, CP5; central-middle (CM): FCz, Cz, CPz; central-right (CR): C4, C6, CP4, CP6; posterior-left (PL): PO7, PO5, PO3, O1; posterior-middle (PM): Pz, POz, Oz; posterior-right (PR): PO8, PO6, PO4, O2. We compared the amplitudes by using repeated measures ANOVAs with the factors *perturbation* (final-perturbed, initial-perturbed, non-perturbed), *left–right* (left, middle, right), and *front–back* (anterior, central, posterior).

For all the above-mentioned ANOVAs, Bonferroni corrections were applied to control the type I error due to multiple comparisons. Not all ANOVAs met the sphericity assumption, so the Greenhouse-Geisser correction was applied whenever the assumption was violated. The original degrees of freedom and the corrected p-values were reported. Generalized eta-squared (η_G^2) was used for evaluating the effect size.

Results

Behavioral results

Mean difficulty ratings for final-perturbed trials showed a score of 2.65 (*SD* = 1.20). While for the initial-perturbed trials, the average difficulty score was rated as 3.12 (*SD*

= 1.28). Paired *t*-test suggested participants considered the initial-perturbed trials were more complicated than the final-perturbed trials, $t(25) = -2.13$; $p < 0.05$.

Mean reaction, reach, and rotation times for different conditions were shown in Figure 3.3. The analysis of reaction times revealed a significant main effect for *perturbation*, $F(2,50) = 94.04$; $p < 0.001$; $\eta_G^2 = 0.218$. Post-hoc analyses indicated that the reaction times were significantly longer for initial-perturbed trials (947 ms) than final-perturbed trials (887 ms), $t(25) = 4.65$; $p < 0.001$. The reaction times needed in final-perturbed trials were also significantly longer than reaction times needed in non-perturbed trials (706 ms), $t(25) = 9.78$; $p < 0.001$.

For reach times, the ANOVA revealed a main effect for *perturbation*, $F(2,50) = 30.99$; $p < 0.001$; $\eta_G^2 = 0.048$. Reach times were significantly slower in the initial-perturbed condition (930 ms) than the final-perturbed condition (847 ms), $t(25) = 4.49$; $p < 0.001$. Moreover, reach times were also slower for final-perturbed trials than non-perturbed trials (811 ms), $t(25) = 3.59$; $p < 0.01$.

A significant main effect for *perturbation* was also found in the analysis of rotation time, $F(2,50) = 39.40$; $p < 0.001$; $\eta_G^2 = 0.077$. The handle was moved slower in initial-perturbed trials (832 ms), as compared to final-perturbed trials (677 ms), $t(25) = 6.46$; $p < 0.001$, and non-perturbed trials (709 ms), $t(25) = 7.30$; $p < 0.001$. Rotation time was not different between final-perturbed and non-perturbed trials, $t(25) = -2.54$; $p = 0.053 > 0.05$.

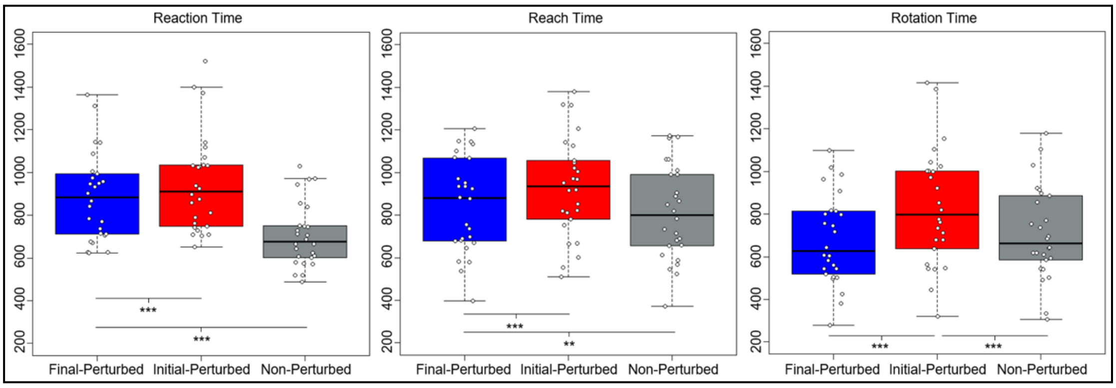

Figure 3.3 ***Timing of behavior.***

*Box plots representing reaction times (left), reach time (middle), and rotation time (right) for the Final-Perturbed (blue), the Initial-Perturbed (red), and the Non-Perturbed (grey) conditions. Time is shown in milliseconds. ** $p < 0.01$; *** $p < 0.001$.*

Neurophysiological results

P2 (150–200 ms) With the factors *perturbation* (final-perturbed, initial-perturbed, non-perturbed) and *electrode* (Fz, FCz, Cz, CPz, Pz), the ANOVA of the mean P2 amplitude yielded a significant interaction effect for *perturbation*electrode*, $F(8,200)= 4.16$; $p < 0.01$; $\eta^2_G = 0.014$. The main effects for *perturbation*, $F(2,50) = 6.46$; $p < 0.01$; $\eta^2_G = 0.079$, and electrode, $F(4, 100) = 25.16$; $p < 0.001$; $\eta^2_G = 0.111$, were also significant.

To interpret the significant interaction effect, repeated measures ANOVAs were made for the amplitudes at each electrode site separately. These analyses revealed a significant perturbation effect at Fz [$F(2,50) = 11.84$; $p < 0.001$; $\eta^2_G = 0.147$], FCz [$F(2,50) = 6.33$; $p < 0.01$; $\eta^2_G = 0.096$], and Cz [$F(2,50) = 4.70$; $p < 0.05$; $\eta^2_G = 0.078$], but not at CPz and Pz (all *F*s < 2.95, ns). The P2 amplitude at each electrode can be seen in Figure 3.4 (B). Further analyses revealed that the P2 amplitude at Fz was significantly larger in both the initial-perturbed condition (4.27 μV) and the final-perturbed condition (3.42 μV), as compared to the non-perturbed condition (1.83 μV), $t(25) = 4.50$; $p < 0.001$, and $t(25) = 3.22$; $p < 0.05$. No P2 difference was found between the initial-perturbed and the final-perturbed conditions at Fz, $t(25) = -1.73$; $p > 0.05$. At FCz, P2 amplitude was significantly larger for initial-perturbed trials (3.80 μV) than non-perturbed trials (1.93 μV), $t(25) = 3.49$; $p < 0.01$. Stronger P2 was also found for initial-perturbed trials (2.92 μV) at Cz, as compared to non-perturbed trials (1.45 μV), $t(25) = 2.87$; $p < 0.01$. No other significant effects were found in the further analyses (all *t*s < 2.03; ns).

N2 (200–250 ms) A significant interaction effect for *perturbation*electrode* was found in the ANOVA of N2 amplitude, $F(8,200) = 17.66$; $p < 0.001$; $\eta^2_G = 0.027$. The main effect for *perturbation* was also significant, $F(2,50) = 26.60$; $p < 0.001$; $\eta^2_G = 0.246$. Further analyses revealed strong perturbation effects for all electrodes, all *F*s >10.60; all *p*s < 0.001 (see Table A3 in the Appendix). N2 amplitude was significantly larger for the non-perturbed condition than the other perturbed conditions at all the electrodes (all *t*s > 2.46; all *p*s < 0.021). A significant amplitude difference between the final-perturbed (0.07 μV) and the initial-perturbed (−0.96 μV) conditions was only found at Pz, $t(25) = 2.38$; $p < 0.05$, and the amplitude difference was not significant at the remaining electrode sites (all *t*s < 1.65; ns).

P3 (250–500 ms) As for the P3 amplitude, we also found a significant interaction for *perturbation*electrode*, $F(8,200) = 3.61$; $p < 0.05$; $\eta_G^2 = 0.005$, a significant main effect for *perturbation*, $F(2,50) = 68.53$; $p < 0.001$; $\eta_G^2 = 0.261$, and a significant main effect for *electrode*, $F(4,100) = 13.77$; $p < 0.001$; $\eta_G^2 = 0.044$. Further analyses found significant perturbation effects for all the electrodes, all *F*s > 35.88; all *p*s < 0.001 (see Table A4 in the Appendix). Post hoc revealed P3 amplitudes were larger for the perturbed trials than the non-perturbed trials at all the electrodes, all *t*s > 6.37; all *p*s < 0.001, whereas no difference was found between the two perturbed conditions at any electrode site (all *t*s < 1.25; ns).

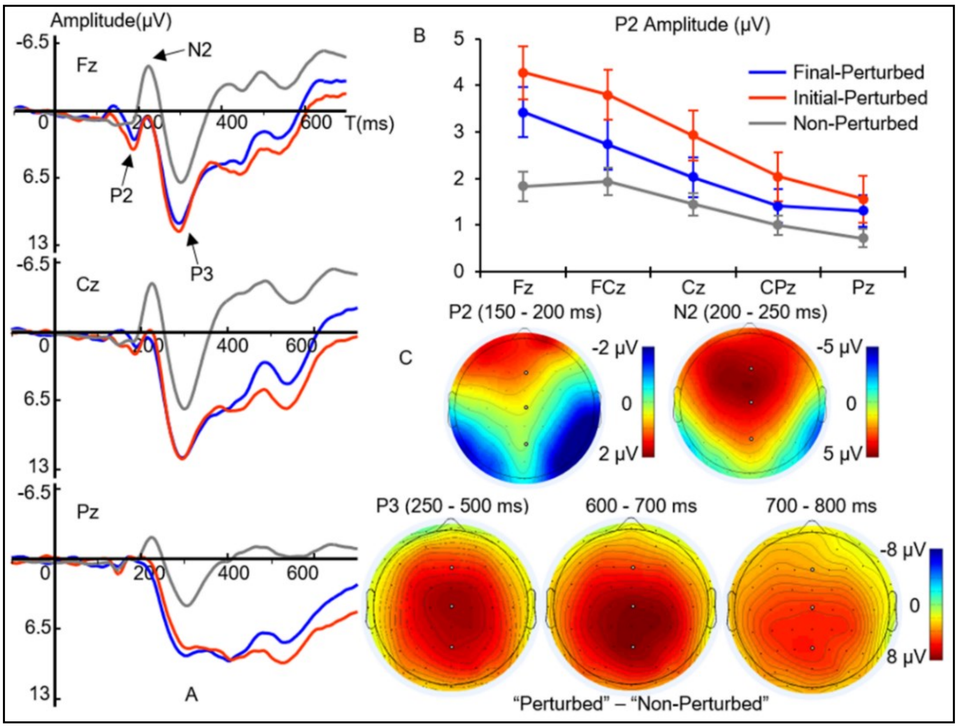

Figure 3.4 ERPs time-locked to the secondary stimulus.

***(A)** The grand-averaged ERPs time-locked to the secondary stimulus at the electrode Fz, Cz, and Pz. **(B)** The peak amplitude of P2 over the midline electrodes. The error bars represent standard errors. **(C)** Topographical plots represent the difference between the Perturbed conditions (averaged) and the Non-Perturbed condition. The mean amplitudes are used to draw the plots.*

Slow-wave potentials (500–700 ms) With the factors *perturbation* (final-perturbed, initial-perturbed, non-perturbed), *left–right* (left, middle, right), and *front–back* (anterior, central, posterior), the ANOVA for the amplitude of slow-wave potentials in 500–600 ms yielded a significant 3-way interaction effect (*perturbation*left–right*front–back*), $F(8,200) = 2.97$; $p < 0.05$; $\eta_G^2 = 0.001$. The 3-way interaction means that the ERP amplitude differences among the different perturbation conditions are not the same in magnitude for the various combinations of the factors *left–right* and *front–back*. The significant interaction permits the separate comparison of the different perturbation conditions in the various ROI. ANOVAs were performed for each ROI to determine if there was a significant difference based on the factor *perturbation* and in which ROI the difference was present. From the ANOVAs, we found that the difference among perturbation conditions was significant at all the ROIs, all Fs > 10.48; all ps < 0.001. Further post hoc analyses revealed the mean amplitude of slow waves in the perturbed trials was more positive than the non-perturbed trials at all the ROIs, all ts > 3.39; all ps < 0.01 (see Table A5 in the Appendix). However, in the perturbed trials, the slow waves for the initial-perturbed condition were not more positive than the final-perturbed condition at all the ROIs. Significant difference was found mainly in the left central-posterior ROIs, which were the AM-ROI, $t(25) = -2.79$; $p < 0.05$, the CL-ROI, $t(25) = -3.49$; $p < 0.01$, the CM-ROI, $t(25) = -3.15$; $p < 0.01$, the PL-ROI, $t(25) = -3.02$; $p < 0.05$, and the PM-ROI, $t(25) = -2.85$; $p < 0.05$. The slow waves in the initial-perturbed condition were more positive than the final-perturbed condition over the left central-posterior areas. No other significant difference was found in further analyses. Difference waves between the final-perturbed and the initial-perturbed conditions ("initial-perturbed"–"final-perturbed"), as well as the topographic maps, were shown in Figure 3.5.

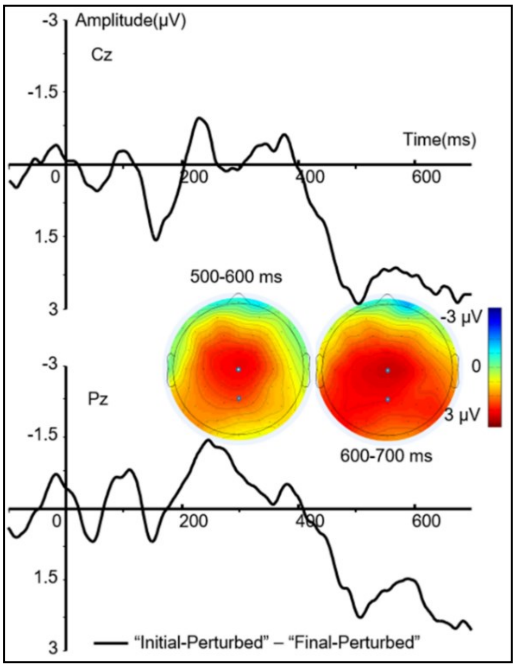

Figure 3.5 Difference waves between the Final-Perturbed and the Initial-Perturbed conditions.

ERP difference waves ("Initial-Perturbed"–"Final-Perturbed") time-locked to the secondary stimulus at the centro-parietal electrodes (Cz, and Pz). Topographical plots illustrate the distributions of the difference waves in the corresponding time windows.

The ANOVA of mean amplitudes for the slow-wave potentials in 600–700 ms also revealed a significant 3-way interaction for *perturbation***left–right***front–back*, *F*(8,200) = 2.52; $p < 0.05$; $\eta_G^2 = 0.001$. In further analyses, ANOVA was applied to each ROI separately to determine the *perturbation* effect. Consistent with the slow waves in 500–600 ms, we also found a significant difference among the different perturbation conditions in all the ROIs, all *F*s >6.32; all *p*s < 0.01. In most of the ROIs, more positive activities were found for the perturbed conditions than the non-perturbed condition, all *t*s > 2.87; all *p*s < 0.05. In the AR-ROI, the amplitude difference between the final-perturbed condition and the non-perturbed condition was not significant, *t*(25) = 2.55; $p > 0.05$, whereas the mean amplitude was more positive for the initial-perturbed condition than the non-perturbed condition, *t*(25) = 2.87; $p < 0.05$. Besides, the slow waves in the initial-perturbed trials also showed more positivity than those in the final-perturbed trials over the central-posterior ROIs as well as the AM-ROI, all *t*s > 3.28; all *p*s < 0.01(see Table A6 in the Appendix). No difference was found between the initial-perturbed and the final-perturbed trials in both of the lateral anterior ROIs (AL, AR). The topographic maps for the difference waves between the initial-perturbed and the final-perturbed trials were shown in Figure 3.5.

Discussion

With the help of ERPs, we investigated the motor re-planning processes behaviorally and on the neurophysiological level. It was asked how participants adapt to perturbations in either final or initial action goals. By using a modified “S1–S2” paradigm, unexpected perturbations in initial or final goals were introduced during the preparation of grasp-to-rotated movements, and participants had to correct their motor plans to adapt to the perturbations. The results revealed that perturbations in action goals did interfere with movement preparation and execution. Compared to non-perturbed trials, slower reaction times and execution times were observed in goal-perturbed trials. Perturbed action goals also evoked larger anterior P2s, P3s, and late positive slow-wave potentials. Within the goal-perturbed trials, slower reaction times and execution times were found for the initial-perturbed than the final-perturbed trials. Even though no amplitude difference was found for the anterior P2, the anterior N2, and P3, a more positive slow-wave potential (500–700 ms time-locked to the secondary stimulus) was found for initial-perturbed trials, as compared to final-perturbed trials.

Action goal perturbation vs. No perturbation

The first aim of the study was to explore whether the unexpected perturbations in the initial or final action goals interfere with movement preparation. As predicted, reaction times, which were defined as the duration from the imperative signal to movement onset, were found slower for both perturbed trials than non-perturbed trials. The result is in line with previous findings that compared to the baseline (standard motor planning), longer preparation times are needed when individuals re-planned their movements (Kraemer et al., 2011; Leuthold, 2003; Leuthold & Jentzsch, 2002; Nazarali et al., 2009; Vidal et al., 1995). Both goal-perturbed conditions involve an extra process (re-planning), as compared to the non-perturbed condition (baseline), and the extra process requires longer times to initialize the movement.

Reach times, which were defined as the duration from movement onset to grasping, were also longer for the goal-perturbed trials. It is consistent with previous findings (Hughes et al., 2012). The prolonged reach time for the perturbed trials can be explained by the increased cognitive demand for motor re-planning. It was claimed by Westerholz et al. (2013) that motor planning might overlap with the reaching period temporally in grasp tasks. During reaching to handle, participants might still configure their movement commands to ensure a correct grip posture. In perturbed trials (especially initial-perturbed trials), participants were focused on the possibility of making a wrong grip. Unexpected changes in action goals interrupted their pre-planned movements (which were generated before the imperative signal), and they had to implement new motor plans under time pressure (they were instructed to move as soon as possible). However, in non-perturbed trials, the reaching action and the grip posture were all pre-planned before the imperative signal with relatively less time pressure (at least 1000 ms). Therefore, more grip configurations in reaching may be needed for the goal-perturbed than the non-perturbed trials.

Rotation times, which were defined as the duration from grasping to reaching the target position, were also influenced by the goal perturbations. However, only the perturbations in the initial goals significantly prolonged the rotation time, and rotation times did not differ significantly between final-perturbed and non-perturbed trials. This might be attributed to different movement adaptations between the final goal and the initial goal perturbations. Detailed explanations can be seen in the following section.

On the neurophysiological level and consistent with our hypothesis, the anterior P2 was enlarged in perturbed trials compared to non-perturbed trials. Similar results were observed by Golob et al. (2002) in a button press task and Recio et al. (2014) in a facial expression task. Larger anterior P2s are often observed for the stimuli with higher task relevance (Potts, 2004; Potts et al., 2006) or the stimuli indicating more complex responses (Van Elk, Crajé, et al., 2010; Van Elk, Van Schie, et al., 2010). The enlarged P2 reflects individuals' allocation of attention to the task-relevant stimulus. In Figure 3.4, an obvious P2 component can be seen in both perturbed conditions but not in the non-perturbed condition. Participants received a perturbed cue in both perturbed conditions, and the changed cue triggered the motor re-planning. Therefore, the P2 may reflect attention redirection to the changes in visual cues. However, as a baseline, the non-perturbed condition does not involve cue-changes, and there should be no obvious P2 components.

Unexpectedly, the anterior N2 was larger for non-perturbed than goal-perturbed trials. It is generally believed that the N2 component is a mismatch detector and an executive control indicator (Folstein & Van Petten, 2008; Wang et al., 2000). Previous studies found a larger anterior N2 for the re-planning condition than the baseline condition (Leuthold & Jentzsch, 2002; Recio et al., 2014), and the enlarged N2 was interpreted to indicate the movement inhibition in motor re-planning. However, we found a larger N2 amplitude for the non-perturbed (baseline) condition than for the perturbed (re-planning) conditions. The enlarged anterior N2 in the non-perturbed condition can be attributed to the monitoring of the movement plan. In our instruction, participants were instructed to "not plan the movement after the button-release", and the instruction was used to prevent participants from releasing the button after the imperative signal and then planning the movement. So, in non-perturbed trials, participants might try to retain their movement before they released the button to ensure a correct reaction (grip posture). The retention process (double-check) may evoke the anterior N2, which is an indicator for monitoring (Folstein & Van Petten, 2008). However, in goal-perturbed trials, participants re-planned their movement to adapt to the goal changes. The anterior N2 here seems to reflect the movement inhibition in re-planning. Based on the previous findings (Kopp et al., 1996; Ramautar et al., 2004, 2006; Vidal et al., 1995), the anterior N2 is regularly accompanied by an anterior P3 in the stop-signal task or motor re-planning task. Since robust anterior P3s were also found in goal-perturbed trials, therefore, anterior N2s may probably overlap with the increasing P3, which may reduce the N2 amplitude.

As predicted, P3 amplitudes for the perturbed conditions were larger than the non-perturbed condition. The P3 effect was found in both anterior and posterior areas. The larger anterior P3 in perturbed trials may reflect the movement inhibition in motor re-planning (Albert et al., 2013; Kopp et al., 1996; Ramautar et al., 2004, 2006). Participants had to inhibit their pre-planned movement in perturbed conditions, and the increased inhibition entailed an enlarged anterior P3. Besides, the enlarged anterior P3 can also be attributed to infrequent secondary stimuli. Compared to the non-perturbed condition, the secondary stimuli in the perturbed conditions are infrequent. The infrequent stimuli usually evoke larger anterior P3 than the frequent stimuli (Comerchero & Polich, 1999; Polich, 2007). Considering N2 results, we argue that the anterior P3 is more likely to be explained by the movement inhibition instead of the stimulus infrequency.

As for the enlarged posterior P3 (or P3b), it may indicate the increased cognitive demand for implementing a new movement in the perturbed conditions. Previous studies revealed a larger centro-parietal P3 for motor re-planning (Recio et al., 2014; Trewartha et al., 2013). The posterior P3 has been associated with processes involved in updating the mental representation of stimulus context in working memory (Donchin & Coles, 1988; Duncan-Johnson & Donchin, 1979; Polich, 2007; Squires et al., 1975). Compared to non-perturbed trials, goal-perturbed trials required participants to implement a new motor plan to adapt to the changes. So, the increased posterior P3 in the perturbed trials is proposed to reflect participants' updating of the new (changed) action goal information in working memory for preparing a new movement.

Furthermore, we found a slow-wave potential (500–700 ms time-locked to the onset of the secondary stimulus) that was more positive-going in perturbed trials than non-perturbed trials. The difference waves are mainly distributed over the centro-parietal areas (see the topographic maps in Figure 3.4). These results are similar to the previous findings that late (at least 400 ms after the cue) centro-parietal positivity was increased for motor re-planning than the baseline (Golob et al., 2002; Leuthold & Jentzsch, 2002; Recio et al., 2014). In accordance with these findings, the human parietal cortex has been claimed to contribute to the adjustment of prehensile movements (Tunik, Frey, &

Grafton, 2005; Tunik et al., 2008; Vingerhoets, 2014). Other research reported that the left dorsal premotor cortex (PMd) and the left supramarginal gyrus (SMG) jointly contribute to motor re-planning (Hartwigsen et al., 2012). So, the enlarged posterior slow waves here may reflect the increased centro-parietal activities and corresponding cognitive efforts for implementing a new motor plan.

Initial goal perturbation vs. Final goal perturbation

The second aim of the study was to investigate the functional roles of initial and final action goals in the re-planning of goal-directed manual actions. Participants rated the difficulty for final-perturbed trials with 2.65, whereas for initial-perturbed trials with 3.12 on a scale from 1 (easy) to 6 (difficult). Participants considered the initial-perturbed condition is more difficult than the final-perturbed condition, and it confirms our assumption that adjusting the movement to adapt to the changes in the initial goals needs more effort than the changes in the final goals.

Consistent with our hypothesis, the reaction time for initial-perturbed trials was slower than final-perturbed trials. It has been claimed that reaction times reflect planning processes before the movement onset (Botwinick & Thompson, 1966; Elliott et al., 2010). The prolonged reaction time may have indicated a more complicated motor re-plan processing in the initial-perturbed condition. The changes in the initial goals required participants to re-plan all the pre-planned actions (grip and rotation). However, the changes in final goals required participants to re-plan part of the pre-planned actions (rotation only), and the pre-planned grip posture could be reused since the initial goal was constant. In this regard, compared to the final-perturbed condition, more cognitive efforts are needed to reorganize the movement in the initial-perturbed condition, which results in longer reaction times.

The reach time was slower for initial-perturbed than final-perturbed trials. The prolonged reach time can also be attributed to the difficulty of the motor re-planning in the initial-perturbed condition. Participants might still plan their grasping movements when their hand was approaching the handle (Westerholz et al., 2013). Another explanation could be the participants' increased awareness of potential grip errors. Although the error rates were similar for both goal-perturbed conditions, unexpectedly perturbed initial goals might focus participants' attention on the grip posture in comparison to perturbed final goals. This might increase participants' awareness of potential wrong grips, which could slow down reaching action.

The rotation time was also significantly slower in initial-perturbed trials than final-perturbed trials. This result was not predicted because rotation movements are precisely the same in different conditions, and the previous finding has also suggested that perturbations in action goals did not significantly slow down the movement execution time (Hughes et al., 2012). The prolonged rotation time for initial-perturbed trials can also be attributed to participants' increased awareness of potential grip errors. The unexpectedly changed initial goal might focus participants' attention on grip postures, and participants might always confirm their grips to avoid errors, even after the grips had been made. However, in the final-perturbed condition, given that the required grip postures were not changed. Therefore, participants did not have to pay much attention to the pre-planned grips.

We did not find significant differences between the initial-perturbed and final-perturbed conditions on the amplitude of the anterior P2, the anterior N2, and the P3 components. This may suggest that there seems to be no difference between the different goal perturbations in the feature processing of changed cues (anterior P2, Golob et al., 2002; Potts, 2004; Potts et al., 2006) and the inhibition of prepared movements (anterior N2/P3, Kopp et al., 1996; Leuthold & Jentzsch, 2002; Ramautar et al., 2006) during the motor re-planning.

However, the mean amplitude of the late slow waves (500–700 ms time-locked to the secondary stimulus) differed significantly between the goal-perturbed conditions. The mean amplitude of the slow waves was more positive for the initial-perturbed than the final-perturbed trials. From the statistical results and the topographic maps in Figure 3.5, it can be seen that the amplitude difference is mainly distributed over the centro-parietal areas. Similar centro-parietal slow-wave activities have also been reported by previous studies with motor re-planning tasks (Golob et al., 2002; Leuthold & Jentzsch, 2002; Recio et al., 2014; Tunik et al., 2008).

Tunik et al. (2008) allocated these centro-parietal activities to the left aIPS by source estimation. It has been claimed that the aIPS is a critical node with the cortical network for the higher-order dynamic control of manual actions (Tunik et al., 2007). The aIPS has also been related to the movement representations for goal-directed manual actions (Hamilton 2006; Baumann 2009) and the integration of related action goals to generate a new motor plan (Tunik et al., 2008). In addition, TMS studies revealed the virtual lesions of the aIPS interfered with the correction of manual actions (Cohen et al., 2009; Le et al., 2014; Tunik et al., 2005). In our data, considering the spatial distribution of difference waves, we argue the enlarged centro-parietal slow waves may reflect the increased aIPS activities. The result may further indicate that compared to final goal perturbations, initial goal perturbations seem to bring about a more difficult motor re-planning, that is, more cognitive efforts are needed for integrating the perturbations to new motor plans.

Alternatively, the late slow waves can also be explained by the engagement of working memory for generating new movements. Emerged after the P3 (temporally), the parietal positive slow waves have been associated with working memory by previous research, and more positive parietal slow waves were found for the tasks which involved more massive working memory load (Can et al., 2017; García-Larrea & Cézanne-Bert, 1998; McEvoy et al., 1998; Rösler et al., 1985). Therefore, the increased parietal positive slow waves may also indicate the increased working memory demands for the motor re-planning in the initial-perturbed trials, as compared to the final-perturbed trials. Considering temporal information, as well as the N2/P3 results, the increased working memory demands seem to be devoted to implementing a new motor plan (Spiegel et al., 2013) instead of inhibiting pre-planned movements.

Taking the behavioral and neurophysiological results together, we may argue that the motor re-planning in response to a perturbed initial goal may need more cognitive efforts than a perturbed final goal. The increased demand for cognitive efforts seems to be employed to implement a new motor plan rather than to inhibit pre-planned movements. The results support our hypothesis that implementing a new movement is more cognitively demanding for the perturbation of initial goals than final goals. It seems to be similar to the hysteresis phenomenon in sequential or repetitive movement tasks (Rosenbaum & Jorgensen, 1992; Schütz et al., 2017). The motor hysteresis emphasizes that a former motor plan is at least partially reused for planning an ongoing movement, which is believed to be efficient in saving cognitive costs for the current motor planning (Schütz et al., 2011, 2017). In our case, participants re-planned all of their prepared actions (grip and rotation) when initial goals were perturbed. However, when final goals were perturbed, participants only corrected the rotation action and reused the grip action (which had been planned before). The reuse saves cognitive costs and results in a more efficient motor re-planning to adapt a final goal perturbation than an initial goal perturbation.

However, we did not include a third perturbation condition in which both the initial and the final action goals were changed, for the sake of controlling the length of the experiment. To reduce the participants' expectancy of the goal perturbations, we set the ratio of perturbed/non-perturbed to 1/3. So three times more non-perturbed trials would be needed if we add a third perturbation condition, which would significantly prolong the experiment duration. It would be interesting for researchers to add the "both-perturbed" condition in future studies, which may also provide more direct evidence for the above-mentioned "hysteresis-like" assumption.

In conclusion, the results of the present study indicate that more cognitive efforts are needed for re-planning the grasp-to-rotate movement when the initial or final action goals have been perturbed unexpectedly. Moreover, the motor re-planning with a perturbed initial goal seems to be more cognitively demanding than the re-planning with a perturbed final goal. Given the behavioral and neurophysiological results, we argue the increased cognitive efforts for the initial goal perturbations are more likely employed for implementing a new motor plan instead of inhibiting the prepared movements.

Initial and Final Action Goals in Movement Correction

Chapter 4

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Abstract

In this experiment, we explored how unexpected perturbations in the initial (grip posture) and the final (target position) action goals influence the movement execution and the neural mechanisms underlying the movement corrections. Participants were instructed to grasp a handle and rotate it to a target position according to a given visual cue. After participants started their movements, a secondary cue was triggered, which indicated whether the initial or final goals had changed (or not) while the electroencephalogram (EEG) was recorded. The results showed that the perturbed initial goals significantly slowed down the reaching action compared to the perturbed final goals. In the event-related potentials (ERPs), a larger anterior P3 and a larger central-distributed late positivity (600–700 ms) time-locked to the perturbations were found for the initial than for the final goals. Source analyses found stronger left middle frontal gyrus (MFG) activations for the perturbed initial goals than for the perturbed final goals in the P3 time window. These findings suggest that perturbations in the initial goals have stronger interferences with the execution of grasp-to-rotate movements than perturbations in the final goals. The interferences seem to be derived from both inappropriate action inhibitions and new action implementations during the movement correction.

Introduction

In everyday life, manual actions such as grasping can be produced effortlessly even if the external environment gets changed unexpectedly. Whenever an ongoing prehensile action is no longer suitable for the current situation, individuals constantly correct it to comply with new task demands. The movement correction reflects a compensatory motor control mechanism, which comprises a series of efficient cognitive processes such as a rapid online comparison between the contextual and motoric information (incompatibility detection), a suppression of prepared but inappropriate actions (issued action inhibition), and then the initialization of appropriate actions (novel action implementation) (Quinn & Sherwood, 1983; Spiegel, Koester, & Schack, 2013; Tunik, Frey, & Grafton, 2005; Venkataramani, Gopal, & Murthy, 2018). These processes take place and can be completed in a concise period after the change happens, even if the movements can be relatively complex (Ikudome, Nakamoto, Yotani, Unenaka, & Mori, 2015; Teixeira, Chua, Nagelkerke, & Franks, 2006; Teixeira, Dos Santos Lima, & Marília Franzoni, 2005). With the help of these efficient processes, movement correction facilitates humans to survive from the potential dangers and also supports individuals to interact adaptively with the dynamic world.

It has been implicated that the frontoparietal network is recruited in movement corrections. The network involves the pre-supplementary motor area (pre-SMA), the supplementary motor area (SMA), the anterior cingulate cortex (ACC), the inferior frontal gyrus (IFG), the premotor cortex (PMC), the intraparietal sulcus (IPS), the superior parietal lobule (SPL), and the supramarginal gyrus (SMG) (Buch, Mars, Boorman, & Rushworth, 2010; Hartwigsen et al., 2012; Hartwigsen & Siebner, 2015; Iannaccone et al., 2015; Mars, Piekema, Coles, Hulstijn, & Toni, 2007; Nakamoto, Ikudome, Yotani, Maruyama, & Mori, 2013; Neubert, Mars, Buch, Olivier, & Rushworth, 2010; Tunik et al., 2005; Tunik, Rice, Hamilton, & Grafton, 2007; Tunik, Ortigue, Adamovich, & Grafton, 2008; Ullsperger, Danielmeier, & Jocham, 2014). Among them, the prefrontal cortical areas such as the pre-SMA, the ACC, and the IFG have been associated with detecting the incompatibilities between the contextual and motoric information, as well as inhibiting ongoing but inappropriate actions (Iannaccone et al., 2015; Kropotov, Ponomarev, Hollup, & Mueller, 2011; Wang, Ulbert, Schomer, Marinkovic, & Halgren, 2005). Previous event-related potential (ERP) studies (Leuthold & Jentzsch, 2002; Vidal, Bonnet, & Macar, 1995) reported mid-frontal N2 and P3 components were elicited when a pre-planned response was successfully corrected, and the following source analyses found that these components were mainly derived from the ACC and pre-SMA. Transcranial magnetic stimulation (TMS) studies (Lee et al., 2016; Nakamoto et al., 2013; Tunik, Lo, & Adamovich, 2008) also reported that virtual lesions in the IFG or pre-SMA impaired the performance of individuals' movement adjustments. The ventral portion of the PMC (PMv) was also involved in the inhibition of a pre-planned action during movement correction (Buch et al., 2010). Meanwhile, the dorsal portion of the PMC (PMd) was employed for updating a pre-planned movement, which is not merely involved in inhibiting the issued inappropriate actions, but also initiating the appropriate actions (Hartwigsen et al., 2012; Hartwigsen & Siebner, 2015; Ward et al., 2010). The parietal cortical areas, such as the IPS and SPL, were relevant to planning and controlling goal-directed reaching or grasping movements (Culham, Cavina-Pratesi, & Singhal, 2006; Tunik et al., 2007). In the correction of manual actions, the anterior portion of IPS (aIPS) is responsible for updating goal-related information and implementing new actions (Rice, Tunik, & Grafton, 2006; Tunik et al., 2005; Tunik, Ortigue, et al., 2008), whereas the SPL is mainly engaged in the real-time adjustments of the movement (Striemer, Chouinard, & Goodale, 2011; Tunik, Ortigue, et al., 2008).

In previous studies, researchers have often focused on the movement corrections compensating for the perturbations in the recruitment of the movement effector (such as from one finger to another finger) (Hartwigsen et al., 2012; Hartwigsen & Siebner, 2015; Leuthold & Jentzsch, 2002; Pellegrino, Tomasevic, Herz, Larsen, & Siebner, 2018; Verbruggen, Aron, Stevens, & Chambers, 2010; Vidal et al., 1995) or the changes in the physical properties (shape, size, orientation) of the target object (Castiello, Bennett, & Chambers, 1998; Castiello, Bennett, & Paulignan, 1992; Castiello, Bennett, & Stelmach, 1993; Paulignan, Jeannerod, MacKenzie, & Marteniuk, 1991; Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991; Tunik et al., 2005; Tunik, Ortigue, et al., 2008). For example, in a reach-to-grasp task (Tunik, Ortigue, et al., 2008), participants were instructed to pincer-grasp a wooden cuboid on the narrow side (1 cm) if it was horizontally oriented, or on the wide side (5 cm) if it was vertically oriented. The cuboid was always horizontally oriented before the movement onset, but in 25% of trials, it went to vertical orientation as soon as participants started to move. Tunik et al. (2008b) found that the unexpected perturbations in orientation had considerable effects on reach-to-grasp kinematics. The final metacarpophalangeal (MCP) joint angle and the peak MCP angle were significantly larger for the perturbed than the unperturbed trials. The time to peak MCP was also significantly delayed in the perturbed trials, and the adaptive responses occurred around 271 ms after the perturbation.

Individuals correct their movements not only in response to the perturbations in the movement effectors or target objects, but also to compensate for the perturbations in the anticipated action effects (action goals) (Hughes & Seegelke, 2013; Hughes et al., 2012). In a grasp-to-place task (Hughes et al., 2012), with a modified "S1–S2" paradigm, participants were asked to grip a horizontal cylinder (either overhand or underhand, free choice) and placed the left or right end of the cylinder into a target disk according to the visual stimulus (final action goal, S1). As soon as the participants started their movements, a secondary stimulus (S2) was triggered, which indicated whether the intended action goal was perturbed (20% of trials) or not (80% of trials).

Hughes et al. (2012) found that when the intended action goals were perturbed, participants corrected their initial grasp postures during reaching to ensure a comfortable hand posture at the end of the object placing (end-state comfort), which resulted in a longer reach time and a shorter time to peak velocity during reaching. The corrections occurred either early (30% of the normalized reach time) or late (46% of the normalized reach time) in the reaching phase. Nevertheless, these studies (Hughes & Seegelke, 2013; Hughes et al., 2012) have been limited to the perturbations in the final action goals. Apart from the final action goal, the initial action goal (grip posture) is also crucial in planning and controlling grasping movements.

Rosenbaum et al. (2007) have proposed that manual actions are organized with a hierarchical motor plan, in which both the initial goal (start posture) and final goal (end posture) are located at the top level, and all the transitions between the initial and the final goals are located at the lower levels. Besides, compared to the final goal, the initial goal acts as an immediate task demand in the execution of grasping movements, whereas the final goal acts as a remote (further) task demand. Therefore, if the unexpected perturbation in the initial goals occurs during reaching, it would have a stronger interference with motor execution than a perturbation in the final goals because the initial goal is the immediate (direct) action effect for reaching. However, it has also been argued that the final action goals are more important for planning and executing grasping movement than the initial goals (Rosenbaum, Vaughan, Barnes, & Jorgensen, 1992; Westerholz, Schack, & Koester, 2013; Yu, Schack, & Koester, 2021), and initial grasp postures are selected on the bases of final action effects (Cohen & Rosenbaum, 2004; Hughes et al., 2012). Since there has been little discussion on the movement corrections with a perturbed initial goal, it is still difficult to conclude whether the perturbed initial goals have stronger interference with motor execution than the perturbed final goals or not.

In this study, we sought to investigate how unexpected perturbations in initial or final action goals influence the execution of grasp-to-rotate movements. To address this issue, we induced an unexpected perturbation in either the initial or final action goal with the modified S1-S2 paradigm. Participants were cued by a visual stimulus (S1) with specified initial and final goals. As soon as participants started their movements, a secondary stimulus (S2) was triggered, which indicated whether the anticipated initial and final goals were perturbed or not. When the goals were perturbed, participants were asked to correct their movements to comply with the corresponding perturbations. Electroencephalography (EEG) was recorded during the movement execution. ERP and the subsequent source analyses were employed to distinguish the neural mechanisms underlying the movement corrections to adapt to the perturbations in the initial or the final goals.

On the basis of previous studies (Golob, Pratt, & Starr, 2002; Hughes et al., 2012; Leuthold & Jentzsch, 2002; Tunik, Ortigue, et al., 2008; Vidal et al., 1995), we hypothesized that the perturbations in the action goals interfere with the motor execution, which can be characterized as longer reach times, stronger N2 (incompatibility detection), stronger P3 (issued action inhibition), and larger late slow waves (new action implementation) in the goal-perturbed conditions versus the non-perturbed condition. Moreover, we also assumed that the perturbed initial goals have a stronger interference with the motor execution than the perturbed final goals, due to the fact that the initial goal (how to grip the handle) is the immediate demand for the grasping action and an unexpected change in immediate demands may have a stronger interference than a change in future demands (final goals). In this regard, we further hypothesized that reach times might be longer for the movement correction to adapt to perturbed initial goals than perturbed final goals. Neurophysiologically, we expected a stronger anterior P3, as well as more positive late slow waves, for the trials with perturbed initial goals than with perturbed final goals, which may reflect (prepared) action inhibitions (P3) and (new) action implementation (slow waves) in movement re-planning.

Method

Participants

Twenty-four volunteers were initially recruited for this experiment. Four of them with less than 30 artifact-free correct trials in any condition were discarded, resulting in a final sample of 20 participants (mean age = 24.30 years; *SD* = 2.32; 11 females). All participants were right-handed (mean score = 90, Edinburgh Handedness Inventory, Oldfield, 1971). All participants were with normal or corrected-to-normal vision and had no history of psychiatric or neurological impairments. This study was approved by the ethics committee at Bielefeld University (EUB), and all participants gave their written informed consent under the Declaration of Helsinki.

Apparatus and stimuli

The setup of the grasp-to-rotate task is shown in Figure 4.1. The graspable part was a handle (cylinder, 16 cm in length, 3 cm in diameter) that had a yellow stripe at one end and a blue stripe at the other end. The handle was attached to a disk (28 cm in diameter), which could be rotated clockwise or counterclockwise. On the disk, a pointing marker was placed next to the yellow end of the handle, and it was used to indicate the handle direction. Outside of the disk, eight target markers were fixed in the dial display. During the experiment, the rotation apparatus was always settled where its center faced the shoulder of the participant's grasping arm, and the distance was calibrated to each participants' arm size for preventing expansive movements. A start button was placed in front of the participants, and the distance was also calibrated to each participant. The distance between the button (center) and the rotation apparatus was constant for each participant (35 cm between the centers).

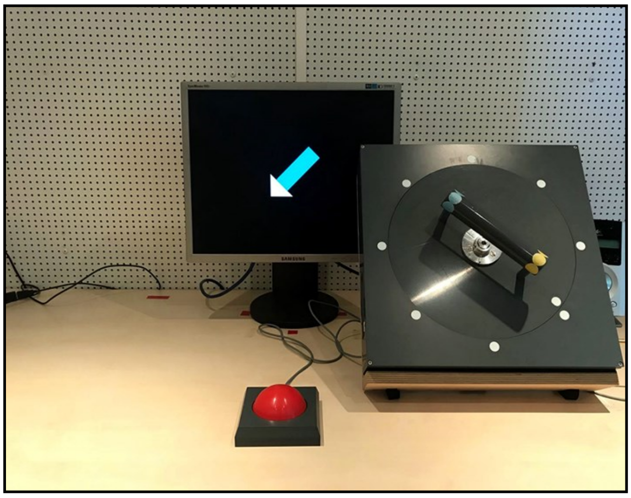

Figure 4.1 Front view of the experimental setup.

A 19-inch TFT monitor was placed behind the rotation apparatus, and it was about 75 cm away from the participants. Color arrows were employed as the visual stimuli, and they were presented by Presentation (Neurobehavioral Systems). The color (yellow or blue) indicated that participants should grip the handle with their thumbs toward the corresponding stripe. The direction of the arrow (eight directions identical with the eight target markers) indicated that participants should rotate the handle (pointing marker) to the pointed target marker. Besides, the direction was always perpendicular to the handle's initial orientation, and participants were instructed to make 90-degree rotations only.

Experimental paradigm

In this experiment, participants were instructed to grip the handle (initial goal) and rotate it to a target position (final goal). To introduce the movement correction, we used a modified S1–S2 paradigm. With the first stimulus (S1), the initial and final goals were given by a colored arrow, and participants were instructed to respond to it. As soon as participants started their movements, another colored arrow was triggered as the secondary stimulus (S2), and it was either the same as or different from the first one. Participants were instructed to finish the movement with the new stimulus if it got perturbed. Thus, different S2s divided the experiment into three conditions (see Figure 4.2): (1) Final-Perturbed (FP). The arrow direction changed to the opposite, but the color stayed the same. (2) Initial-Perturbed (IP). The color changed (yellow to blue or blue to yellow), but the direction stayed the same. (3) Non-Perturbed (NP). Both color and direction stayed the same (no change).

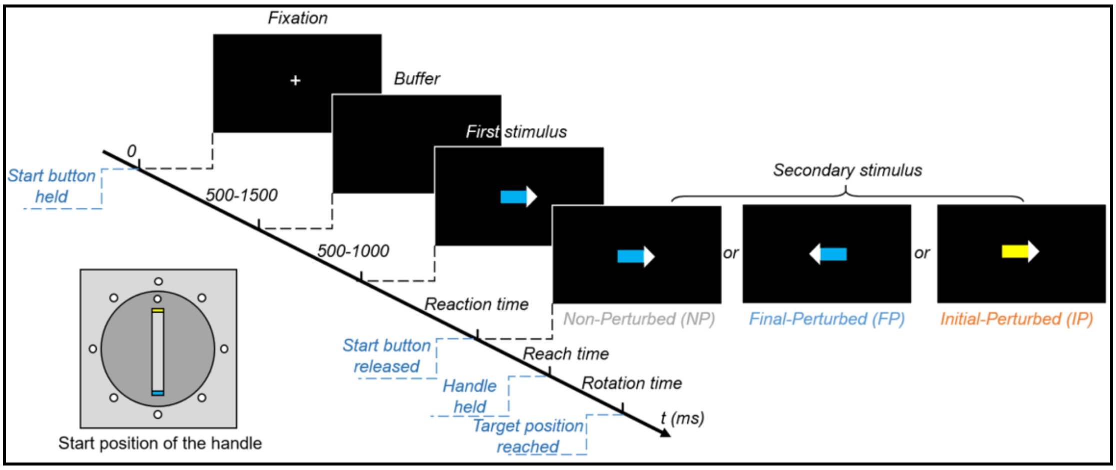

Figure 4.2 Time course of the task events.

The time course of events during the experimental task with the example of a trial with the handle starts at the 12 o'clock position. The trial started with a fixation cross with a variable time interval, followed by a buffer. After that, the first stimulus (S1) appeared, and it indicated the initial goal (blue) and final goal (3 o'clock direction) of the coming movement. A secondary stimulus (S2) was triggered as soon as participants started their movement. In the NP condition (left), the S2 was as same as the first. In the FP condition (middle), the final goal was perturbed (from 3 o'clock to 9 o'clock), but the initial goal stayed. In the IP condition (right), the initial goal was perturbed (from blue to yellow), but the final goal stayed. The S2 stayed on the screen until the handle reached the target position.

Procedure

After the EEG preparations, participants were guided to a shielded room and seated comfortably at the experimental desk. A written instruction was provided to the participants. The stimulus changes were not mentioned in the instruction for reducing the expectancy effect, and participants were only instructed to react to the stimulus, which was showing on the screen. All of the questions regarding the task were answered.

The experimental trial started with a voluntary button press. Then the handle automatically moved to the start position by the motor inside of the apparatus. The start positions were randomly assigned to each marker, and every marker had the same number of trials. After participants held the start button, a fixation cross was presented at the center of the screen with a variable duration from 500 to 1500 ms. After the fixation, a black screen was presented as a buffer for a variable duration from 500 to 1000 ms. Then the first stimulus was presented. Participants were asked to respond to it as soon as possible. Once the participants released the button, an S2 was presented. Participants had to correct their movements if the stimulus got changed. The S2 disappeared when the handle reached the target position. The next trial came after another button press. If the start button was released before the first stimulus, error feedback was presented, and the next trial came after it. To minimize the ocular artifacts, participants were instructed to keep their gaze at the center of the screen during motor planning and execution.

The experiment began with a practice section. All trials in this section were non-perturbed trials. After the practice, participants started eight experimental blocks, and each block contained 48 trials. Two-minute breaks were given between the blocks. To avoid the laterality of the brain activations due to hand use, we asked participants to perform the tasks with both hands (one hand for the first four blocks, and then change to the other hand). The starting hand (left/right) was counterbalanced. After the first four blocks, the rotation apparatus was moved to the other side and recalibrated. Half of the trials were gripped with the thumb toward the yellow stripe, and the rests were gripped with the thumb toward the blue stripe. Besides, half of the trials were rotated clockwise, and the others were rotated counterclockwise. The grips and rotation directions were randomly assigned to the trials. Additionally, to minimize participants' expectancy, we set the ratio of "FP: IP: NP" to 1:1:6, that is, 48 FP trials, 48 IP trials, and 288 NP in total. After the experiment, subjective difficulty ratings (from 1 to 6, from easy to difficult) for different perturbed conditions were queried. It took around 2 hours to finish the experiment.

Behavioral and electrophysiological recordings

Participants' performance was recorded by a video camera. The time points of releasing the start button, gripping the handle, and reaching the target position were detected by the micro-switches in the apparatus. The reaction time (from the first stimulus onset to movement onset), reach time (from movement onset to gripping the handle), and rotation time (from gripping the handle to reaching the target position) were calculated with these time points.

The electroencephalography (EEG) data were collected with a 64-channel ANT amplifier and the acquisition software ASA (ANT, Netherlands) at a sampling rate of 512 Hz. Recordings were made from 64 Ag/AgCl electrodes, which were positioned in accordance with the international 10–10 system. Electrooculography (EOG) was also recorded by two bipolar electrodes placed above and below the right eye and lateral to both eyes. The impedance of all electrodes was less than five kΩ, and AFz was selected as the recording ground. All signals were band-pass filtered (DC–138 Hz) and average-referenced.

Data analysis

Behavioral data

Based on the performance videos, trials with wrong grips or changing grip during rotation were excluded from the behavioral and neurophysiologic analyses. Besides, trials with extreme (outside of mean ± three standard errors) reaction time, reach time, or rotation time were also excluded. On average, participants executed the task correctly in 85% of the FP trials, 84% of the IP trials, and 93% of the NP trials. The remaining 15%, 14%, and 7% of trials, respectively, were rejected. Since we did not find any significant main or interaction effects involving "hand used" in behavioral timings, we pooled the left- and right-hand trials together in analyses. Repeated-measures ANOVAs were performed separately on participants' averaged reaction times, reach times, and rotation times to determine the within-subject effect for *perturbation* (FP/IP/NP).

ERPs

EEG signals were offline analyzed with the toolbox EEGlab (Delorme & Makeig, 2004) and ERPlab (Lopez-Calderon & Luck, 2014). All signals were band-pass filtered (0.1–30 Hz) and re-referenced with linked mastoid electrodes. Two analysis epochs were extracted from the continuous signals. Epoch time-locked to S2 (as well as movement onset) included the time interval from −1400 to 1000 ms. Epoch time-locked to grasping included the time interval from −2900 to 300 ms. Baseline correction was performed with the first 300 ms of the epochs. Gratton regression (Gratton, Coles, & Donchin, 1983; Miller, Gration, & Yee, 1988) was employed to correct the ocular artifacts. Any trials containing peak-to-peak amplitudes above 100 μV within a moving window (200 ms window; 50 ms step) were automatically removed. The remaining trials were visually double-checked for artifacts that would not have been detected by the moving window algorithm. On average, there were 34 FP trials, 35 IP trials, and 232 NP trials left for averaging the ERPs in the epoch time-locked to S2, and there were 33 FP trials, 34 IP trials, and 227 NP trials left for averaging the ERPs in the epoch time-locked to grasping.

In the epoch time-locked to S2, a robust P3 (300–600 ms) and stronger late positive slow waves (600–1000 ms) were found for the goal-perturbed conditions (FP, IP), as compared to the NP condition. For the P3 component, the amplitude was quantified as the mean amplitude from 390 to 440 ms (the average peak latency was 415 ms). For the slow waves, mean amplitudes were measured and compared in 100 ms step windows. Both the P3 and slow waves were accessed among nine regions of interest (ROI) to assess the scalp distribution. The ROIs were anterior-left (AL): AF7, F7, F5, F3; anterior-middle (AM): F1, Fz, F2; anterior-right (AR): AF8, F8, F6, F4; central-left (CL): C3, C5, CP3, CP5; central-middle (CM): FCz, Cz, CPz; central-right (CR): C4, C6, CP4, CP6; posterior-left (PL): PO7, PO5, PO3, O1; posterior-middle (PM): Pz, POz, Oz; posterior-right (PR): PO8, PO6, PO4, O2. Repeated-measures ANOVAs with the factor *perturbation* (FP/IP/NP), *left-right* (left/middle/right), and *front-back* (anterior/central/posterior) were performed on the mean amplitudes of the electrodes (in corresponding ROIs).

In the epoch time-locked to grasping, we only focused on the slow waves before grasping. According to the previous findings (Van Schie & Bekkering, 2007; Westerholz et al., 2013; Westerholz, Schack, Schütz, & Koester, 2014), the analysis time window was set as −500–0 ms. Similar to the previous epoch, the mean amplitudes of the slow waves time-locked to grasping were also compared in 100 ms step windows. Mean amplitudes of the above-mentioned nine ROIs were compared by repeated-measures ANOVAs with the factor *perturbation* (FP/IP/NP), *left–right* (left/middle/right), and *front–back* (anterior/central/posterior) to determine the perturbation effect and its scalp distribution.

For the above-mentioned ANOVAs, Greenhouse-Geisser correction was applied whenever the sphericity assumption was violated. The original degrees of freedom and the corrected p-values were reported. Generalized eta-squared (η_G^2) was used for evaluating the effect size. Post hoc multiple comparisons among means were made with Bonferroni t-tests.

Source analysis

In a subsequent analysis, the three-dimensional cortical distributions of the averaged ERPs (in different conditions) were analyzed with the standardized low-resolution brain electromagnetic tomography analysis software (sLORETA) (Pascual-Marqui, 2002). The sLORETA partitions the intracerebral volume in 6239 grey matter voxels with a spatial resolution of 5 mm, and the standardized scalp current density at each voxel is then calculated in a realistic head model (Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002) with the probabilistic MNI152 template (Mazziotta et al., 2001).

In order to identify possible differences in the brain electrical activity between the goal-perturbed conditions (FP vs. IP), statistical non-parametric mapping (SnPM) (Nichols & Holmes, 2003) was employed for computing the averaged intracerebral current density distribution at the time intervals showing significant differences based on a non-parametric log-F-ratio statistic on the three-dimensional sLORETA images (number of randomizations = 5000). The SnPM corrected for multiple comparisons. Voxels with significant differences ($p < 0.05$) between the perturbed conditions were located in specific brain regions with Brodmann areas (BA) and the MNI coordinates.

Results

Subjective difficulty ratings

Participants rated the subjective difficulty of FP trials as 3.20 ($SD = 1.36$) on a scale from 1 (easy) to 6 (difficult). For the IP trials, the average difficulty was rated as 3.35 ($SD = 1.18$). The paired t-test yielded that the subjective difficulty was not significantly different between the goal-perturbed conditions, $t(19) = 0.65$; $p > 0.05$.

Timing

The averaged reaction, reach, and rotation times for different conditions were shown in Figure 4.3. For the reaction time, we did not find a significant difference among the different conditions (FP/IP/NP), $F(2,38) = 2.69$; $p > 0.05$.

For the reach time, we found a significant main effect for *perturbation*, $F(2,38) = 132.52$; $p < 0.001$; $\eta_G^2 = 0.533$. Post hoc analyses revealed that the reach time was longer in the IP condition (1515 ms) than the FP condition (1359 ms), $t(19) = 3.80$; $p < 0.01$, and a longer reach time was also found for the FP condition than the NP condition (875 ms), $t(19) = 11.81$; $p < 0.001$.

For the rotation time, we also found a significant main effect for *perturbation*, $F(2,38) = 7.13$; $p < 0.01$; $\eta_G^2 = 0.021$. Post hoc analyses yielded that rotation times were significantly longer for the IP condition (641 ms) than for the FP condition (593 ms), $t(19) = -3.73$; $p < 0.01$. However, the difference between the NP condition (624 ms) and the FP condition was not significant, $t(19) = 2.26$; $p > 0.05$, and neither was the difference between the NP condition and the IP condition, $t(19) = -1.37$; $p > 0.05$.

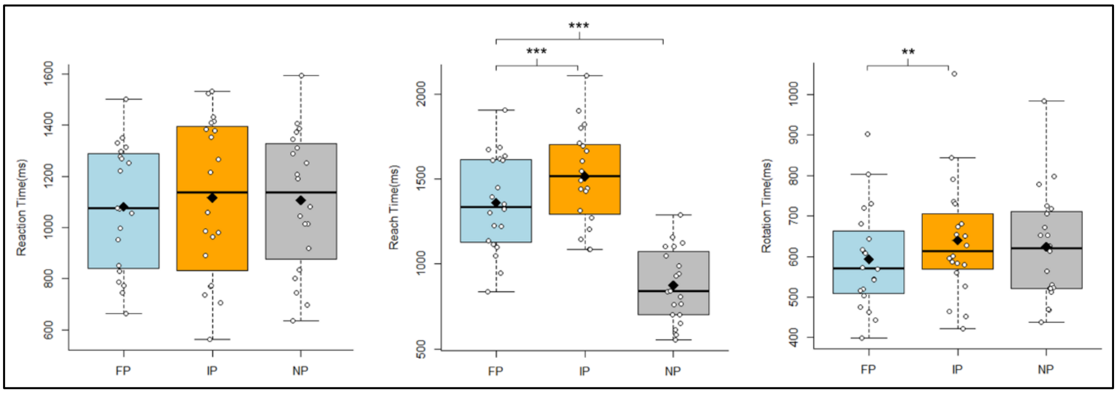

Figure 4.3 Timing of behavior.

*Averaged reaction time, reach time, and rotation time for the Final-Perturbed (blue), the Initial-Perturbed (orange), and the Non-Perturbed (grey) conditions (N = 20). The error bars represent standard errors. The "***" represents the difference between the two conditions is extremely significant (p <0.001), and the "**" represents the difference between the two conditions is very significant (p <0.01).*

ERP results

Epoch time-locked to S2

P3 With the factor *perturbation* (FP/IP/NP), *left–right* (left/middle/right), and *front–back* (anterior/central/posterior), the ANOVA of P3 amplitude yielded significant interaction effects for *perturbation*front–back*, $F(4,76) = 9.83$; $p < 0.001$; $\eta_G^2 = 0.015$, *perturbation*left–right*, $F(4,76) = 25.24$; $p < 0.001$; $\eta_G^2 = 0.010$, and *left–right*front–back*, $F(4,76) = 9.98$; $p < 0.001$; $\eta_G^2 = 0.007$. We also found significant main effects for *perturbation*, $F(2,38) = 39.27$; $p < 0.001$; $\eta_G^2 = 0.268$, and *left–right*, $F(2,38) = 20.16$; $p < 0.001$; $\eta_G^2 = 0.017$. Further analyses revealed that in the anterior ROIs, P3 amplitude was larger in the IP condition (11.53 μV) than the FP condition (8.10 μV), $t(19) = 3.22$; $p < 0.01$, and the P3 in FP condition was also larger than the NP condition (0.80 μV), $t(19) = 6.87$; $p < 0.001$. However, in the central and posterior ROIs, the amplitude differences between the IP and FP conditions were not significant, all ts < 1.62; all ps > 0.34, but the P3 amplitudes were larger in the goal-perturbed conditions (FP, IP) than the non-perturbed condition (NP), ts > 4.72; all ps < 0.001 (see Table A7 in the Appendix for more details). Moreover, the P3 amplitudes were also larger in the goal-perturbed conditions (FP, IP) than the non-perturbed condition (NP), ts > 5.94; all ps < 0.001, over the left, middle, and right ROIs. Nevertheless, the amplitude differences between the IP and FP conditions were not significant, all ts < 1.46; all ps > 0.46. No other significant effects between the FP and IP conditions were found in the further analyses.

Slow waves For the ERP slow waves from 600 to 700 ms, the ANOVA revealed a significant interaction effect for *perturbation*left–right*, $F(4,76) = 8.71$; $p < 0.001$; $\eta_G^2 = 0.002$, and a significant interaction effect for *front–back*left–right*, $F(4,76) = 6.16$; $p < 0.001$; $\eta_G^2 = 0.004$. The main effects for *perturbation*, $F(2,38) = 36.12$; $p < 0.001$; $\eta_G^2 = 0.110$, *front–back*, $F(2,38) = 11.70$; $p < 0.001$; $\eta_G^2 = 0.018$, and *left–right*, $F(2,38) = 17.87$; $p < 0.001$; $\eta_G^2 = 0.013$, were also significant. To explain the significant interaction for *perturbation*left–right*, we conducted further analyses, and the results revealed that the amplitudes of the slow waves were larger for the FP and IP conditions than the NP condition in the left, middle, and right ROIs, all ts > 4.95; all ps < 0.001 (see Table A8 in the Appendix for more details). However, the amplitude difference between the IP and FP conditions was only significant in the middle ROIs. In the middle ROIs, the mean amplitude of the slow waves was larger in the IP condition (7.85 μV) than the FP condition (5.27 μV), $t(19) = 2.52$; $p < 0.05$. The difference waves between FP and IP conditions, as well as the topographic maps of the difference waves, were shown in Figure 4.5.

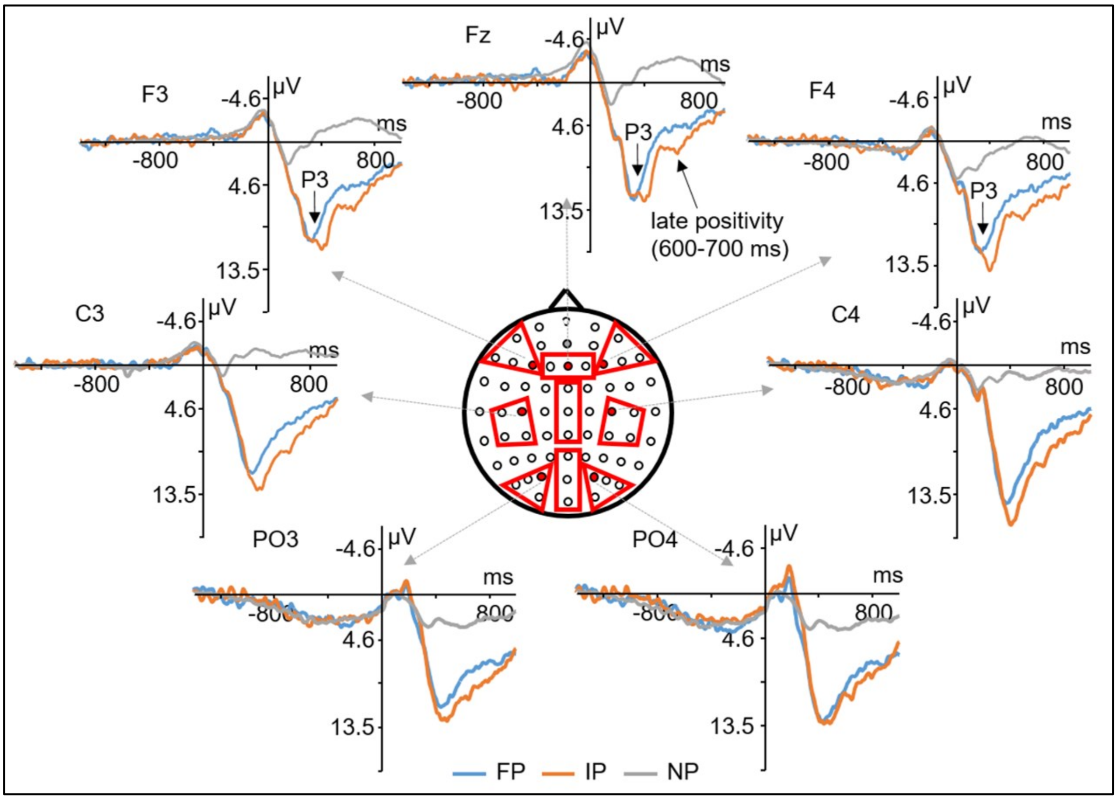

Figure 4.4 Grand-averaged ERP waveforms time-locked to the secondary stimulus.

The grand-averaged ERP waveforms (N = 20) time-locked to the secondary stimulus(S2), for the Final-Perturbed condition (blue), Initial-Perturbed condition (orange), and Non-Perturbed condition (grey), from one anterior-left electrode (F3), one anterior-middle electrode (Fz), one anterior-right electrode (F4), one central-left electrode (C3), one central-right electrode (C4), one posterior-left electrode (PO3), as well as one posterior-right electrode (PO4).

For the slow waves in the time windows from 700 to 800 ms, from 800 to 900 ms, and from 900 to 1000 ms, all the ANOVAs revealed significant main effects for *perturbation*, all Fs > 6.55; all ps < 0.01. Nevertheless, the interaction effects for *perturbation*front–back*, *perturbation*left–right*, and *perturbation*front–back*left–right* were all not significant in these time windows (see Table A9 in the Appendix for more details). Post hoc analyses revealed that the mean amplitudes of the slow waves were more positive for the goal-perturbed conditions (FP, IP) than the non-perturbed condition in all the time windows, all *t*s > 2.89; all *p*s < 0.05, whereas the mean amplitudes were not different significantly between the FP and IP conditions, all *t*s < −1.43; all *p*s > 0.48 (see Table A10 in the Appendix for more details).

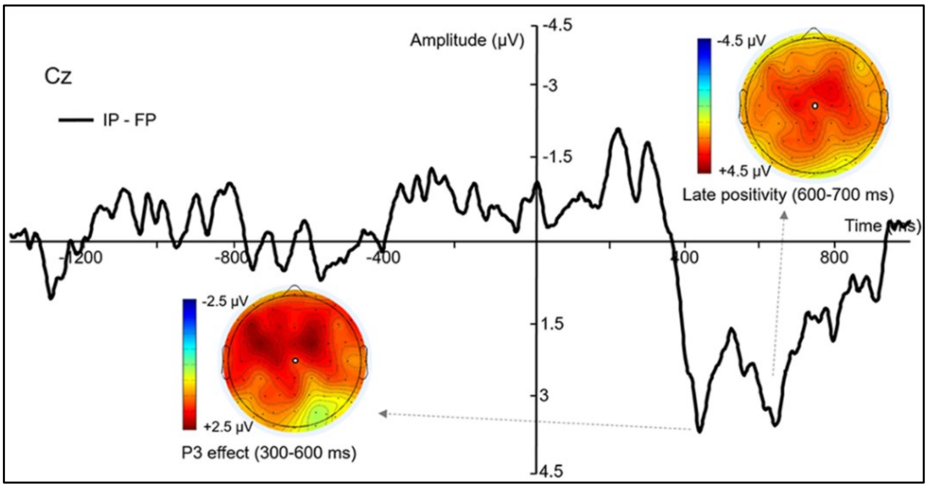

Figure 4.5 The ERP difference waves time-locked to the secondary stimulus.

ERP difference waves ("Initial-Perturbed"–"Final-Perturbed") time-locked to the onset on the secondary stimulus (S2) at the central-middle electrode (Cz). Topographical maps of the difference waves in the P3 (300–600 ms) and late positivity (600–700 ms) time intervals are also showed.

Epoch time-locked to grasping

For the epoch time-locked to grasping, we compared the slow waves from −500 to 0 ms in 100 ms step windows. For the time window from −500 to −400 ms, the ANOVA yielded a significant main effect for *perturbation*, $F(2,38) = 3.79$; $p < 0.05$; $\eta_G^2 = 0.014$, a significant main effect for *front–back*, $F(2,38) = 3.79$; $p < 0.05$; $\eta_G^2 = 0.014$, a significant main effect for *left–right*, $F(2,38) = 29.89$; $p < 0.001$; $\eta_G^2 = 0.031$, and a significant interaction effect for *front–back* left–right,* $F(4,76) = 4.23$; $p < 0.05$; $\eta_G^2 = 0.005$. Post hoc analyses found that the slow waves were more positive in the FP (4.86 µV) than the NP (2.70 µV) condition, $t(19) = 2.73$; $p < 0.05$. However, the amplitude difference was not significant between either the FP and IP conditions, $t(19) = 1.05$; $p > 0.05$, or the IP and NP conditions, $t(19) = 1.68$; $p > 0.05$.

For the slow waves in the time windows from −400 to −300 ms, from −300 to −200 ms, from −200 to −100 ms, and from −100 to 0 ms, the ANOVAs found no significant main effects for, all Fs < 2.09; all $ps > 0.14$, no significant interactions for *perturbation*front–back*, all Fs < 1.24; all $ps > 0.30$, no significant interactions for *perturbation*left–right*, all Fs < 1.35; all $ps > 0.27$, and no significant interactions for *perturbation*front–back*left–right*, all Fs < 1.00; all $ps > 0.37$ (see Table A11 in the Appendix for more details).

Figure 4.6 Grand-averaged ERP waveforms time-locked to grasping at electrode POz.

Grand-averaged ERP waveforms (N = 20) recorded at electrode POz, time-locked to grasping, for the Final-Perturbed condition (blue), Initial-Perturbed condition (orange), and Non-Perturbed condition (grey). Average time points (dash lines) for the first stimulus presentation (S1), the secondary stimulus presentation/movement onset, and handle grasping are marked (shaded areas beside the dash lines indicate the standard deviations).

Source analysis

For the averaged time window between 390 and 440 ms time-locked to S2 (corresponding to the P3 peaks), a significantly higher cortical activation for the IP in contrast to the FP conditions was found in the following cortical areas: the left middle frontal gyrus (MFG; BA9; x = −30, y = 40, z = 35, and x = −30, y = 40, z = 30), and the left superior frontal gyrus (SFG; BA9; x = −35, y = 45, z = 30), see Figure 4.7. The maximum difference was located at the left MFG, *log-F* = 0.663, $p < 0.05$ (*log-F* threshold = 0.650).

For the averaged time window between 600 and 700 ms time-locked to S2 (corresponding to the late positivity from 600 to 700 ms), we found that the cortical activation difference between the goal-perturbed conditions was mainly located at the cingulate gyrus (BA24; x = −10, y = 0, z = 45), and the medial frontal gyrus (MFG; BA6; x = −5, y = −25, z = 70). However, the activation difference in neither of the areas reached the significance level: all *log-F*s < 0.470, all *p*s > 0.05 (*log-F* threshold = 0.488).

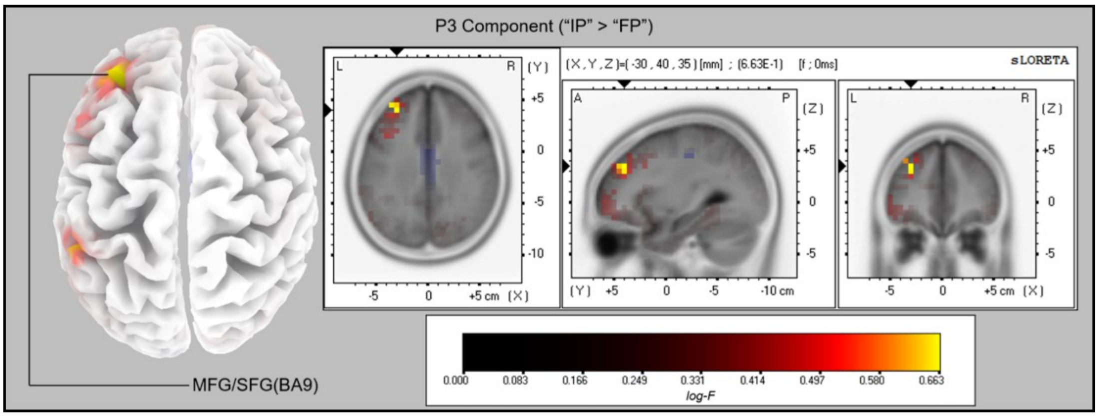

Figure 4.7 Results of the source analysis ("Initial-Perturbed" > "Final-Perturbed") in the time window of the P3 component (300–600 ms)

The images have been obtained after statistical non-parametric mapping (SnPM), and they represent the voxels in which the Initial-Perturbed > Final-Perturbed contrast was significant ($p < 0.05$, log-F threshold = 0.650) in the time window of the P3 component. Significantly activated voxels are indicated by yellowish colors.

Discussion

In this experiment, we examined how unexpected perturbations in initial or in final action goals interfere with the execution of grasp-to-rotate movements and the neural mechanisms underlying the adjustments in response to the goal perturbations. The results revealed that compared to a perturbed final goal, a perturbed initial goal significantly slowed down the movement execution. Moreover, a larger frontal P3 and larger central-distributed late positivity (600–700 ms) time-locked to the perturbations were found for the initial than for the final goals. Further source analyses suggested increased cortical activations in the left middle frontal gyrus (MFG, BA9) and left superior frontal gyrus (SFG, BA9) were found for the perturbed initial goals than the perturbed final goals in the P3 time window. Taking together, these findings suggest that the influence of perturbed initial and final action goals in the execution of grasp-to-rotate movements differs, and the unexpected perturbations in the initial goals seem to have stronger interference with motor execution than the final action goals.

Participants rated the subjective difficulty in the FP condition with 3.20 and in the IP condition with 3.35, on a scale from 1 (easy) to 6 (difficult). Even though the participants rated the IP condition slightly harder than the FP condition, the difference was not significant. Participants perceived similar subjective difficulties for the goal perturbations. It seems to be in line with our accuracy results that participants executed the task correctly in 85% of trials in the FP condition and in 84% of trials in the IP condition. These indicate that task difficulty did not differ between the perturbation conditions and, hence, task difficulty is unlikely to be related to any effects found between the FP and IP conditions.

As predicted, the reaction times (from fist stimulus onset to movement onset) were not different among the conditions (FP/IP/NP). It has been suggested that reaction times usually reflect the motor planning processes before the movement onset (Botwinick & Thompson, 1966; Elliott et al., 2010). In our experiment, reaction times reflect the movement preparations in response to the first stimulus, whereas the first stimuli are all the same across the different conditions (without any perturbations). Therefore, reaction times should be similar across different conditions.

Consistent with the previous findings (Hughes et al., 2012), as well as our hypothesis, the reach times (from movement onset to grasping) in the goal-perturbed conditions (FP, IP) were significantly slower than the non-perturbed condition (NP). The prolonged reach time reflected the movement corrections compensating for the perturbations in action goals. More importantly, we found that reach times were significantly slower in the IP than in the FP condition. It seems to indicate that the perturbations in the initial action goals have stronger interference with the correction of manual actions as compared to the perturbations in the final action goals, and the stronger interference slows down the reaching movements.

For the rotation time (from grasping the handle to arriving at the target marker), we did not find a significant difference between the FP and NP conditions. Also, the rotation times in the IP condition were not significantly different from the NP condition. That is consistent with previous studies (Hughes & Seegelke, 2013; Hughes et al., 2012), which revealed that object manipulation is not influenced by the perturbation of action goals.

Interestingly, we found that the rotation times were significantly slower in the IP than in the FP condition. A possible explanation might be a prolonged rotation time in the IP condition, which reflected the participant's increased awareness of potential grip errors. The initial goal (how to grip) was changed after the movement onset, and it made participants drive more attention toward their grip postures. So participants might always have “double-checked” their postures to avoid a potential error, even after the handle had been gripped.

With a bar transportation task, Westerholz et al. (2013) found that the transport times (durations between grasping and bar-on-target) were slower when the initial goals were emphasized (compared to when the final goals were emphasized), even though the same movements were performed in both goal-emphasized conditions. The “initial-emphasized” seems to be similar to the current IP condition in which participants may focus on the perturbed initial goals, and the “final-emphasized” seems to be similar to the current FP condition in which participants may focus on the perturbed final goals. Moreover, in another study with a similar grasp-to-rotate task (Yu et al, under review), we also found that the rotation times were slower when the initial goals were perturbed unexpectedly (during movement preparation), as compared to when the final goals were perturbed unexpectedly. Therefore, the prolonged rotation times might be attributed to the increased awareness of potential grip errors.

As for the ERPs, we did not find the expected N2 effect between the goal-perturbed and the non-perturbed conditions. From the grand-averaged ERPs (time-locked to the secondary stimulus) shown in Figure 4.4, we can hardly tell an obvious N2 component around 200 ms over the anterior area (except for a slight negative-going oscillation). The reduction of anterior N2 can be attributed to the overlapping of N2 and P3 components. Because the probabilities of the different S2s were unequal, large anterior P3s were evoked in the goal-perturbed trials. The large P3s may overlap and reduce the observed N2 amplitude. Besides, Kraemer et al. (Kraemer, Knight, & Muente, 2011) also reported that as compared to stopping a response, changing a response did not elicit an anterior N2 component.

As predicted, we found that the amplitude of the P3 component (time-locked to S2) was significantly larger for the goal-perturbed conditions (FP, IP) than the non-perturbed condition (NP). This is consistent with previous findings that movement corrections elicited stronger P3s than the movement execution without correction (Leuthold & Jentzsch, 2002; Recio, Shmuilovich, & Sommer, 2014; Vidal et al., 1995). The increased P3 activities in the goal-perturbed conditions reflect the inhibitory processes to stop inappropriate actions compensating for the perturbations in action goals.

More importantly, the P3 amplitude was larger in the IP than in the FP condition over the anterior ROIs. From the topographic map shown in Figure 4.5, we can see the amplitude difference maximizes over the left and middle frontal areas. That is also further confirmed by the source analyses results that activations of the left middle frontal gyrus (MFG, BA9) and left superior frontal gyrus (SFG, BA9) were significantly higher in the IP than the FP condition. It has been reported that in the go/nogo task (Albert, López-Martín, Hinojosa, & Carretié, 2013; Benikos, Johnstone, & Roodenrys, 2013; Eimer, 1993; Falkenstein, Hoormann, & Hohnsbein, 1999; Falkenstein, Koshlykova, Kiroj, Hoormann, & Hohnsbein, 1995; Gajewski & Falkenstein, 2013; Kok, 1986), the stop-signal task (Boecker, Gauggel, & Drueke, 2013; Dimoska, Johnstone, & Barry, 2006; Oldenburg, Roger, Assecondi, Verbruggen, & Fias, 2012; Ramautar, Kok, & Ridderinkhof, 2004, 2006; Smith, Johnstone, & Barry, 2008; Wessel & Aron, 2015), and the movement re-planning tasks (Leuthold & Jentzsch, 2002; Recio et al., 2014; Vidal et al., 1995), larger P3s were evoked over the frontal and central areas when the responses had been inhibited or corrected in comparison to those that were normally executed. Besides, previous neuroimaging studies also suggest the middle frontal gyrus (MFG) in the left hemisphere is involved in inhibitory processing, and stronger MFG activations were found when a pre-planned response was inhibited (Blasi et al., 2006; Brass, Zysset, & Von Cramon, 2001; Brown, Vilis, & Everling, 2008; Rae, Hughes, Weaver, Anderson, & Rowe, 2014; Rubia et al., 2001; Sebastian et al., 2013). Moreover, the left dorsolateral prefrontal cortex (DLPFC), which lies in the left MFG, has been associated with inhibiting the stereotyped responses (Kadota et al., 2010) or processing incongruous object-action combinations (Balconi & Vitaloni, 2012). Therefore, the enlarged P3 amplitude and the stronger activations of the left MFG in the IP condition compared to the FP condition may indicate that perturbations in initial goals induce a stronger inhibition process during the movement correction, in which participants are trying to stop the inappropriate actions to prevent potential errors.

It is interesting that we only found different cortical activations in the left hemisphere between the FP and IP conditions, even though both left- and right-hand movements were performed and averaged in our study. It seems to be consistent with the idea that the left hemisphere is specialized for motor planning (Frey, 2008; Haaland, Harrington, & Knight, 2000; Janssen, Beuting, Meulenbroek, & Steenbergen, 2009;

Janssen, Meulenbroek, & Steenbergen, 2011; Martin, Jacobs, & Frey, 2011).A recent fMRI study (Mayer et al., 2020) also suggested that the left hemisphere (left-SMA) plays a critical role in interhemispheric inhibition and motor planning. However, several studies (Mars et al., 2007; Nakamoto et al., 2013; Neubert et al., 2010) have reported that several right-hemisphere regions, such as the right-SMA, are associated with motor inhibitions and movement selections during motor re-programming (re-planning). It is still hard to conclude whether brain lateralization exists in motor re-planning or not. For future research, it might be of interest to focus on brain lateralization in motor re-planning.

For the late slow waves (600–1000 ms) time-locked to S2, we found that the mean amplitudes were significantly larger in the goal-perturbed conditions (FP, IP) than the non-perturbed condition (NP), which is also consistent with our hypothesis. The enlarged slow waves may reflect the increased cognitive efforts involved in the action implementations or action reorganizations during the movement corrections. Between the different perturbation conditions, we only found the mean amplitudes were significantly larger for the IP than the FP condition in the time window from 600 to 700 ms (time-locked to S2). The amplitude difference was only found in the middle ROIs. Besides, from the topographic map in Figure 4.5, we can see the difference waves maximize over the frontocentral areas (the primary motor cortex). Further source analyses also yielded a higher but not significant at the cingulate gyrus for IP than FP. Moreover, from the averaged ERP waveforms in Figure 4.4, we can also tell a prominent positive ERP component in the IP condition, which peaks around 600 ms after S2 onset. This late positivity is reminiscent of the P600 effect obtained in language studies, which reflects the processing of structured representations at the syntactic level (Bach, Gunter, Knoblich, Prinz, & Friederici, 2009; Frisch, Kotz, Von Cramon, & Friederici, 2003; Gouvea, Phillips, Kazanina, & Poeppel, 2010; Hagoort & Brown, 2000; Kaan, Harris, Gibson, & Holcomb, 2000; Osterhout & Holcomb, 1992; Van Herten, Kolk, & Chwilla, 2005). The P600 is elicited when there is a syntactic violation in a sentence, and it is characterized for the reanalysis or repair of the sentence structure. Some studies have also reported that the P600 was evoked by the violation of action (Kuperberg, 2007; Maffongelli et al., 2015) or music structures (Koelsch, Gunter, Wittfoth, & Sammler, 2005; Patel, Gibson, Ratner, Besson, & Holcomb, 1998). Therefore, the enlarged P600-like positivity elicited by the perturbed initial goals may reflect a restructuring or reorganization processing of the ongoing movements. In the IP condition, participants have to adjust their ongoing reaching movements before grasping to ensure a correct grip posture. However, in the FP condition, participants can still use their pre-planned (ongoing) reaching movements because the initial action goal is not changed.

For the slow-wave potentials before grasping (from −500 to 0 ms time-locked to grasping), we only found a significant amplitude difference between the FP and the NP conditions in the time window from −500 to −400 ms, and the slow-wave potentials were more positive in the FP than the NP condition. However, the difference between the FP and the IP was not significant, neither was the difference between the IP and the NP. Considering the temporal overlapping of the epochs (time-locked to S2 and time-locked to grasping), the enlarged slow-wave potentials for the FP condition in the time window (−500–−400ms) might be attributed to the movement correction processes (the late positivity potentials in the epoch time-locked to S2). It is worth noting that the difference in slow waves might also be attributed to eye movements. Even though we instructed participants to fix their gazes during movement and corrected the ocular artifacts by Gratton regression (Gratton et al., 1983; Miller et al., 1988), the (potential) residual effects might still remain (especially) in a large analysis epoch, which could influence (partially) the slow-wave amplitude. Therefore, the slow-wave effect between FP and NP conditions might also be caused by the residual effects of eye movement. It is still an open question, which deserves further research.

In the time windows from −400 to 0 ms time-locked to grasping, no significant difference was found for the slow-wave potentials among the different conditions (FP/IP/NP). It seems to suggest that participants adjust their movements as soon as they perceived the perturbations, and the movement corrections may have been finished at least 400 ms before grasping. It is in line with the movement kinematics data in the previous study (Hughes et al., 2012) that movement correction to adapt to a perturbed (final) action goal occurred in the first half of the reach time. More importantly, the similar slow-wave potentials before grasping between the FP and the IP also indicate that the (neuro-) cognitive processes before grasping are the same for both goal-perturbed conditions, which may exclude the possibility that participants corrected their movements only after they gripped the handle in the FP condition.

Limitations of the present study should be taken into consideration. Even though none of the participants reported (in the post questionnaire) a strategy that they planned all of the four possible grasp-to-rotate movements before they release the start button, it still could be a limitation for our experimental design (the corrections of the upcoming movements are predictable) and it may affect our results (such as the reaction times). For future research, it would be interesting if unpredictable changes can be involved. Besides, to control the length of the experiment, we did not include a third "perturbed" condition in which both initial and final action goals are perturbed. Future research may consider implementing this in order to provide a more comprehensive picture of goal perturbations in manual actions.

Taking the behavioral and neurophysiological results together, we found that the re-planning times, as well as the cortical activities, differed between the corrections of manual actions with perturbed initial goals and perturbed final goals. The perturbed initial goals have a stronger interference with the execution of the grasp-to-rotate movement than the perturbed final goals, and the interference seems to arise from both action inhibition (stopping inappropriate actions) and action implementation (generating new actions). To our knowledge, this is one of the first studies to distinguish the online corrections of manual actions with perturbed initial and final action goals, as well as the first study to differentiate cerebral activity underlying overt goal-related manual actions executed with an unexpectedly perturbed initial and final action goal. Our findings also emphasized the importance of the initial action goals (grip postures) in the execution and online correction of manual actions, and individuals correct their ongoing manual actions mainly based on the immediate task demands, rather than future task purposes.

General Discussion

Chapter 5

Instead of external stimuli, most manual actions used in everyday life are voluntarily triggered by certain internal motivations or desires, namely action goals. Individuals intentionally start a movement for a goal and terminate it when the desired goal (state) is achieved. Most of the previous studies only focused on a single action, such as button-pressing, reaching, pointing, or grasping, and accordingly, in these studies, the action goals were mostly manipulated as the last position or object involved in the task. However, manual actions can be more complicated than a single action. Multiple single actions can be tightly combined into a multi-step action in which single actions are arranged following a specified (temporal or spatial) manner. In our daily life, most manual actions involved in object manipulation are not merely limited to reaching toward an object but also contain grasping and some further actions for achieving the action goal, such as grasp a glass for drinking and grip a piece of toast for eating. In this regard, the "last position or object" seems to be not enough for characterizing the action goal for manual actions, and the immediate grasp demands (how to grip the object) are always neglected. Hence, the functional roles of the initial (grip posture) and the final (task purpose) action goal are still not fully understood.

The current dissertation sought to look into the roles of the initial and the final action goal in multi-step manual actions (object manipulations). A series of three EEG/ERP experiments were carried out to study the initial and the final action goal, as well as the neurophysiological mechanisms underlying the action goals, in the planning, the re-planning, and the online correction stages of grasp-to-rotate movements.

By presenting the initial and the final action goals separately in different sequences, the first experiment (Chapter 2) studied how individuals coordinate the action goals (top-down vs. bottom-up) during the preparation of manual actions. Results mainly revealed that larger anterior P2s but smaller anterior N2s were found for final goals as compared to initial goals. However, these component differences were only significant when the goals were presented as the first cue of the stimulus sequence. The findings of the first experiment suggest that the final task goals are more critical than the initial grip postures in planning manual actions, and the action goals seem to be coordinated in a "top-down" way that task purposes are processed before the selection of grip postures.

By using a modified “S1–S2” paradigm, the second experiment (Chapter 3) investigated the motor re-planning processes in adjusting to the unexpected changes in either initial or final action goals during the movement preparation. Results yielded that perturbations in initial goals significantly slowed down the motor re-planning, as compared to perturbations in final goals. Perturbed initial goals elicited a larger centroparietal positivity (during 500–700 ms time-locked to the perturbation) than perturbed final goals, but the mean amplitudes of anterior P2, anterior N2, and P3 were not significantly different between the initial and final goal perturbations. These results indicate that the re-planning costs (cognitive efforts) induced by initial goal perturbations are higher than final goal perturbations, and the increased re-planning costs (initial perturbations compared to final perturbations) are more likely to be utilized in the implementation of a new action (plan) instead of the inhibition of the pre-planned actions.

The third experiment (Chapter 4) further explored the motor re-planning processes in response to the changes in the initial or final action goals. Different from the second experiment, this experiment focused on the motor re-planning that occurred during the movement execution, that is, online correction. Results showed that the re-planning time was significantly longer for the initial goal perturbation than the final goal perturbation. Moreover, initial goal perturbations elicited a larger anterior P3 and a larger central distributed late positivity (600–700 ms) time-locked to the perturbations than for the final goal perturbation. Source analyses revealed that increased cortical activations in the left middle frontal gyrus (MFG, BA9) were found for the perturbed initial goals compared to the perturbed final goals in the P3 time window. These findings suggest that perturbations in initial goals have stronger interferences with the movement execution compared to perturbations in final goals, and the interferences seem to be derived from both inappropriate action inhibitions and new action implementations, that is, initial goal perturbations require more cognitive efforts than final goal perturbations in both movement inhibition and new movement implementation.

Collectively, the findings of the current dissertation illustrate that both initial and final action goals are important in manual action planning and control. The EEG/ERP findings further confirm that the frontoparietal cortical network is highly involved in manual action planning and control. Nevertheless, the results also suggest that the functional roles of initial and final goals in manual actions are somewhat different. Compared to initial goals, final goals seem to hold a leading position in planning manual actions. Yet, when correcting a pre-planned action (motor re-planning), changes in initial goals seem to be more urgent than changes in final goals.

Final action goals are leading manual action planning

In the first study of the current dissertation (Chapter 2), the functional roles of initial and final action goals in intentional manual action planning were investigated with a separated cue (goal) paradigm. Initial (grip posture) and final (task purpose) action goals were presented in either hierarchical (final–initial, "top-down") or chronological (initial–final, "bottom-up") way during the preparation of a specified (fixed grip postures) or free-choice (grip postures) grasp-to-rotate movement.

Results yielded that participants tended to select the habitual grips (thumb toward the rotation pointer) for most of the free-choice trials, but the percentage of the habitual grips significantly decreased when the target position located at the lower part of the rotation disk (around 6 o'clock), which is in line with the end-state comfort effect (Rosenbaum et al., 1990). ERP results revealed that a larger anterior P2 was evoked by final goals than initial goals when participants got only partial information about the goals, which seems to reflect that final goals are more task-relevant than initial goals in manual action planning. Meanwhile, a larger anterior N2 and frontal negativity were elicited by initial goals than final goals, which seems to indicate that processing an initial goal without a final goal is an unfamiliar way to plan a goal-directed manual action.

In sum, the results of the first study confirm the idea that final task purposes are more important than initial grip postures in motor planning (Rosenbaum & Jorgensen, 1992; Westerholz, Schack, & Koester, 2013 for ERPs), and the initial and final action goals are more likely to be organized in a "top-down" (hierarchical) manner during the preparation of goal-directed manual actions, that is, final action goals are leading the planning of manual actions.

Although the grip selections in the free-choice trials illustrated a strong tendency of thumb-toward bias (Rosenbaum, Vaughan, Barnes, & Jorgensen, 1992) in which participants tended to select the grips that enable their thumb direction to be aligned with the target at the end, the percentage of the habitual grips significantly decreased when the target position located at the lower part of the rotation disk (position 4, 5, and 6; see table A12 in the appendix for more details). The averaged percentage of the habitual grips for each target position is plotted in Figure 5.1. The decrease at the lower positions indicates that participants tended to avoid the uncomfortable (thumb-down) postures at movement end, for both left and right hand, even if the start postures are awkward. Such a tendency is consistent with the end-state comfort effect (Rosenbaum, Chapman, Weigelt, Weiss, & van der Wel, 2012; Rosenbaum et al., 1990).

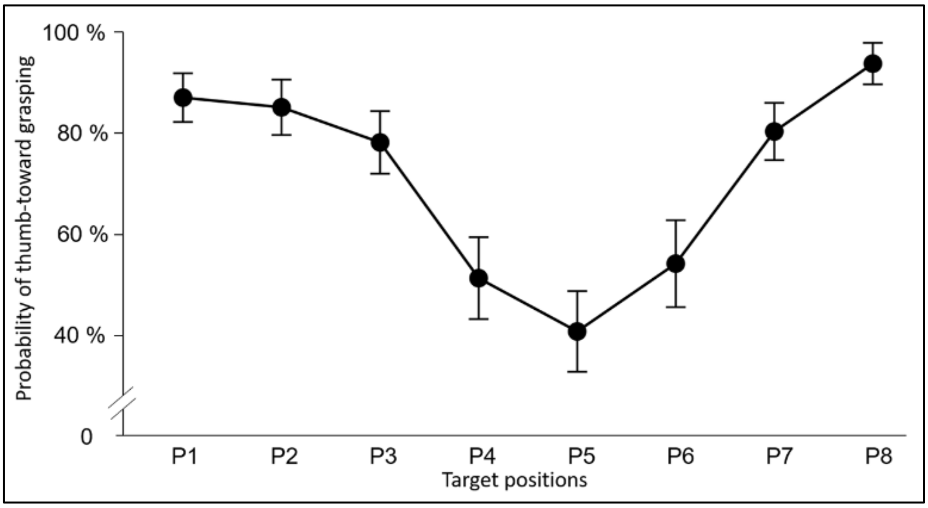

Figure 5.1 Averaged percentage of the habitual grips for each target positions in free-choice trials of study 1 *(error bars stand for 95% confidence intervals)*

The end-state comfort effect illustrates that the initial grip postures (initial action goals) are usually selected to ensure the actor to have comfortable hand postures in the end (final action goals), that is, the selection of initial goals is affected by the final goals. Previous behavioral findings (Belardinelli, Stepper, & Butz, 2016; Cohen & Rosenbaum, 2004; Herbort & Butz, 2015; Rosenbaum et al., 1990; Seegelke, Hughes, & Schack, 2011; Weigelt & Schack, 2010), as well as kinematic data (Ansuini, Santello, Massaccesi, & Castiello, 2006; Hughes et al., 2012; Zhang & Rosenbaum, 2008), have already suggested that initial grasp postures are selected for achieving the final task goal effortlessly.

For example, Hughes et al. (2012) tested participants with a bar-transfer task in which the cued action goals (final goals) might have changed unexpectedly. In the task, participants were instructed to grasp a horizontal bar, and then move it to a target plate vertically according to the specified orientation given by the cue. In some trials, the cue was perturbed as soon as participants started their movement. Results yielded an end-state comfort tendency in the non-perturbed trials that participants tended to select the grips to ensure comfortable (thumb-up) postures in the end. However, when the cue got perturbed unexpectedly, participants were found to correct their (grip) movements during reaching to achieve a comfortable placing posture, which was characterized by longer reaching times and shorter times to peak velocity in reaching. The end-state comfort effect emphasizes the importance of final action goals in the planning of manual actions, that is, final action goals are more crucial than initial grip postures in motor planning (Rosenbaum & Jorgensen, 1992; Westerholz et al., 2013).

The ERP results of the first study confirm the importance of final goals in motor planning on the neurophysiological level. The anterior P2 results indicate that final goals are more task-relevant than initial goals when the goal information is incomplete. Moreover, final goals[5]also evoked the largest anterior P2 (compared to other conditions) for the free-choice trials with the cue sequence "initial–final". The results further emphasize the importance of final goals in motor planning. In this condition (initial–final, free-choice), no effective initial goals were given until the final goals were presented, so the given final action goals presented here contained the most relevant information for planning the upcoming movements (compared to the stimuli in other conditions). Taking together, these results support the previous idea that final goals are more important than initial grips in motor planning (Rosenbaum & Jorgensen, 1992; Westerholz et al., 2013), with neurophysiological data.

Furthermore, the N2 and frontal negativity effects suggest that the "bottom-up" (initial–final, chronological) way to process the action goals seems to be contradictory to the preferred way that individuals organized the goals. People seem to coordinate the initial and final action goals in the "top-down" (final–initial, hierarchical) way that final action goals are processed before the initial action goals. The results seem to be in line with the results of previous studies (Van Schie & Bekkering, 2007; Westerholz et al., 2013; Westerholz, Schack, & Koester, 2014). Motor planning was faster for movements with the emphasized final action goals, as compared to movements with the emphasized initial action goals (Van Schie & Bekkering, 2007; Westerholz et al., 2013). Westerholz

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[5] The final goals in this experimental condition (free-choice, initial–final) refer to the second cue presented to participants. That means at that moment (second cue onset), participants received complete information at once. See the texts in Chapter 2.

et al. (2014) reported that different neural activities (mid-frontal slow-wave potentials) were found between the free- and specified- (final) goal movements, whereas no differences were found for the neural activities between the free- and specified-grip (initial goal) movements. The results seem to be in line with the ideomotor ideas that the what-decision of voluntary manual actions are planned and executed based on the mental representation of the action goals (task purpose, final goal) and not on the movement itself (grip posture, initial goal). The N2 and frontal negativity results further confirm the leading role of final action goals in motor planning.

The idea that final action goals are leading the manual action planning is also broadly consistent with the fundamental assumption of the ideomotor theory of action. The ideomotor ideas suggest that voluntary actions are selected and initiated by the anticipated action effects (Hoffmann, Stoecker, & Kunde, 2004; Hommel, Müsseler, Aschersleben, & Prinz, 2001; Koch, Keller, & Prinz, 2004; Pfister, Melcher, Kiesel, Dechent, & Gruber, 2014). For manual actions, in contrast to reaching or grasping (which ends with anticipated initial goals), the endmost task purposes (anticipated final goals) are the action effects that individuals would like to achieve. The initial goals (how to grip the object) seem to a mean or an intermediate state for individuals to achieve the final goals (how to use the object). Taking the grasp-to-drink movement as an example, the glass can be held with many different types of (grip) postures, but the final purposes of the action are the same, that is, bringing the water into the month. The final goal represents the most essential action effect that individuals have to achieve when planning a goal-directed manual action, and the initial goal seems to be an intermediate action effect that individuals anticipate for achieving the essential effect (final goal) in an easier way (i.e. end-state comfort effect). Therefore, for manual actions, the initial goal is mostly processed, selected, and anticipated (if possible) after individuals have an anticipated final goal (effect) in mind during the motor planning.

In sum, the findings of the first study confirm that final goals are more critical than initial grip postures when planning a goal-directed manual action on a neurophysiological level. On this level, the initial and final action goals are coordinated in a hierarchical (“top-down”) way that final goals are processed before the initial goals during the movement preparation.

Initial action goals are critical for motor re-planning

The second (Chapter 3) and the third (Chapter 4) study of the current dissertation focused on the role of initial and final action goals in re-planning manual actions. Similar experimental paradigms (modified "S1–S2") were employed in these studies, and participants had to re-plan (correct) their action (or action plan) to adapt to the unexpected perturbations in either initial or final goals. In the second study, the goal perturbations appeared during the motor planning (1000–1500 ms after the first cue), whereas in the third study, the perturbations appeared during movement execution (as soon as participants initiated their movements). The main behavioral and neurophysiological findings in the second and the third study are listed in Table 5.1.

Table 5.1 A summary of the main results in study 2 and study 3

	Study 2	Study 3
Re-planning time[6]	IP > FP (reaction time)	IP > FP (reach time)
Execution time	IP > FP > NP (reach time) IP > FP = NP (rotation time)	IP = NP > FP (rotation time)
Anterior P2 amplitude	IP = FP > NP	--[7]
Anterior P3 amplitude	IP = FP > NP	IP > FP > NP
Posterior P3 amplitude	IP = FP > NP	IP = FP > NP
Late slow-wave potentials (mean amplitude)	IP > FP > NP (500–700 ms)	IP > FP > NP (600–700ms)

Note: "IP" stands for the Initial-Perturbed condition. "FP" stands for the Final-Perturbed condition. "NP" stands for the Non-perturbed condition. The ">" means significantly larger, and the "=" means no significant difference.

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[6] Re-planning time is not applicable for NP condition (because there were no goal perturbations).

[7] There was no obvious anterior P2 evoked by perturbed action goals. See texts as well as figures in Chapter 4 for more details.

These results suggest that more re-planning costs arise for correcting the prepared actions (or prepared action plans in the second study) to adapt to a perturbed initial action goal than to a perturbed final action goal. That means the prepared initial action (grip posture) and final action (object manipulation) seem to be organized chronologically as the elements in the motor plan. In this regard, the pre-planned action goals (both initial and final) seem to be integrated with a serial or temporal sequence (grasp–manipulate) in motor plans. Therefore, when re-planning is needed for changing a prepared action (plan), perturbations in initial goals might be more urgent than perturbations in final goals. Initial action goals are the immediate task demand in motor re-planning, whereas final action goals are the remote task demand in motor re-planning. Changes in immediate task demands (initial goals) are more urgent than in remote task demands (final goals) when individuals have to re-plan (correct) a prepared action (plan).

Behaviorally, both studies revealed that re-planning times were longer in order to adapt to the changes in initial action goals, as compared to the changes in final action goals. The prolonged times seem to reflect the motor re-planning processes in which individuals inhibit their prepared action (or motor plan) and then implement a new one (Quinn & Sherwood, 1983; Spiegel, Koester, & Schack, 2013). Neurophysiologically, ERPs provide a fine-grained perspective on the temporal dynamics of motor re-planning processes, which can hardly be provided by behavioral timing results. The inhibition and implementation processes can be distinguished by different evoked components in the course of motor re-planning. The anterior P2 is associated with the process that individuals evaluate the task-relevance of perceived stimuli (Potts, 2004; Potts, Martin, Burton, & Montague, 2006; Potts, Patel, & Azzam, 2004). The larger anterior P2s evoked by the goal perturbations may reflect the evaluation of the cue changes. The anterior P3, together with the anterior N2 (only in study 2), are associated with the inhibition of the prepared actions (or motor plans). It has been reported that a larger frontal P3 component can be always found when prepared responses are stopped before or during execution (Albert, López-Martín, Hinojosa, & Carretié, 2013; Kopp, Mattler, Goertz, & Rist, 1996; Ramautar, Kok, & Ridderinkhof, 2004, 2006; Smith, Jamadar, Provost, & Michie, 2013; Smith, Johnstone, & Barry, 2008). Additionally, both studies found that goal perturbations evoked larger slow-wave potentials (centro-parietal positivity) than the baseline condition (non-perturbed). A similar centro-parietal positivity has been found in the previous motor re-planning study (Tunik, Ortigue, Adamovich, & Grafton, 2008), and the slow-wave potentials seem to represent neural activities involved in the implementation of new actions.

The findings of the second and the third experiments suggest that when individuals re-plan their movements in response to a goal perturbation, the immediate task demand (initial goal) seems to be more critical than the remote task demand (final goal). Our behavioral timing results may have indicated that re-planning in response to the initial goal perturbation requires more cognitive efforts, as compared to re-planning in response to the final goal perturbation. When cued action goals were perturbed during the movement preparation (study 2), different neural activities between the initial and the final goal perturbations were only found for the late slow-wave potentials. The anterior P3 amplitudes were similar between the initial and the final goal perturbations. However, when cued action goals were perturbed during the movement execution (study 3), a significantly larger anterior P3, as well as a larger centro-parietal positivity, were yielded for the initial than for the final goal perturbations. Further source localization analysis also found that stronger cortical activations in the left prefrontal area (MFG, BA9) were found for the initial than the final goal perturbations during the P3 time window. It has been claimed that left MFG has been involved in the inhibition of pre-planned movements (Brass, Zysset, & Von Cramon, 2001; Brown, Vilis, & Everling, 2008; Smith et al., 2013). That is, much stronger motor inhibitions seem to be needed in motor re-planning when the initial goal perturbation occurred temporally closer to the hand-object interaction (grasping). In sum, these neurophysiological results further suggest that the increased cognitive efforts (between the initial and the final goal perturbations) seem to be mainly devoted to the implementation (instead of the inhibition, evidenced by the similar N2/P3 amplitudes between the goal perturbations) when the goal perturbations occurred during the movement preparation (study 2) and to both inhibition (anterior P3) and implementation (P6-like late positivity potentials) when the goal perturbations occurred during the movement execution (study 3).

When correcting a pre-planned manual action, a change in grip postures (initial goals) may lead to an entirely new action. However, a change in task purposes (final goals) may only induce a partially new action because part of the pre-planned action (grips) can be reused. In our studies, participants had to correct all of their prepared movements (grasping and rotation) in response to the unexpected perturbations in the initial goals, whereas when they corrected the actions in response to the unexpected perturbations in the final goals, they could reuse the pre-planned grasping and modify the rotation movement. In this regard, re-planning costs might be saved when correcting actions to adapt to a changed final goal.

It seems to be similar to the hysteresis phenomenon found in sequential or repetitive manual action tasks (Rosenbaum et al., 2012; Schütz, Weigelt, Odekerken, Klein-Soetebier, & Schack, 2011). The hysteresis phenomenon refers to a tendency that individuals may reuse at least part of the former motor plan when planning an ongoing similar manual action, and such kind of reuse is believed to be efficient in saving cognitive costs for the current motor planning (Cohen & Rosenbaum, 2004; Schütz et al., 2011; Schütz, Weigelt, & Schack, 2016, 2017). When the final goals get changed unexpectedly, individuals may still use part of the pre-planned action (grip) so that it could save them some cognitive costs in motor re-planning.

To sum up, the findings of the re-planning studies (study 2 and study 3) emphasize the importance of initial action goals in correcting a pre-planned manual action. Our results may indicate that the initial and the final action goals are represented chronologically in a motor plan so that correcting the initial grip postures is more cognitively demanding than correcting the final task purposes in re-planning a manual action.

The frontoparietal network for manual actions

It has been claimed that the frontoparietal cortical network plays an essential role in the preparation and execution of goal-directed manual actions (Cisek & Kalaska, 2010; Fogassi et al., 2005; Koester, Schack, & Westerholz, 2016; Majdandžić et al., 2007; Martin, Jacobs, & Frey, 2011; Turella & Lingnau, 2014). The frontal areas (such as PMC, SMA, and IFG) and the parietal areas (such as aIPS, SPL, and SMG) have been proved to jointly contribute to the manual action planning and control (Bozzacchi, Giusti, Pitzalis, Spinelli, & Di Russo, 2012; Hartwigsen et al., 2012; Hartwigsen & Siebner, 2015; Koester et al., 2016; Majdandžić et al., 2007; Tunik, Ortigue, Adamovich, & Grafton, 2008; Van Schie & Bekkering, 2007; Ward et al., 2010; Westerholz et al., 2013). For example, by using repetitive TMS over the SMG and dorsal PMC in the left hemisphere, Hartwigsen et al. (2012) found that online repetitive

TMS of the left SMG significantly increased the error rate when participants were asked to re-plan their movement, regardless of the left dorsal PMC function. However, the online repetitive TMS of SMG significantly slowed down motor performance when the re-planning was executed successfully, but only after the dorsal PMC was dysfunctional. The results show that the dysfunction of dorsal PMC might increase the functional relevance of SMG for motor re-planning, so the time needed for movement corrections was prolonged after the dysfunction of dorsal PMC. It can be inferred from the results that the left SMG and left dorsal PMC jointly contribute to the re-planning of motor actions.

The neurophysiological results of the current dissertation supported the idea that the frontoparietal cortical network is highly associated with the preparation and execution of goal-directed manual actions. Both frontal and parietal neural activities were found in all three experiment during the motor planning and re-planning.

In the motor planning task (study 1), the anterior P2, the anterior N2, and the late posterior slow waves were found when participants were processing the given cues for movement planning. The anterior P2 reflects the stimulus evaluation processing that participants were evaluating the relevance of the given cues (action goals) for planning the upcoming movement. The largest P2 amplitude can be found over the central areas, regardless of the experimental conditions (see waveforms and topographic maps in Figure 5.2). In a previous study, Van Elk et al. (2010) also observed a frontocentral distributed P2 component when participants were planning a grasp-to-rotate movement. They further localized the P2 component at the dorsal posterior cingulate cortex (dPCC), which is proposed to couple the visual information to an appropriate motor plan (Vogt, Vogt, & Laureys, 2006).

The anterior N2 in our study 1 reflects the conflict processing caused by the initial action goals when the initial goals are presented before the final goals, which is incompatible with the familiar way to process the action goals. It has been reported by many studies that the mismatch N2 is localized to the anterior cingulate cortex (ACC, Folstein & Van Petten, 2008; Iannaccone et al., 2015; Kanske & Kotz, 2010; Ramautar, Kok, & Ridderinkhof, 2004; Tillman & Wiens, 2011).

The late posterior slow waves in our study 1 seem to reflect the parietal engagement during the movement preparation. Similar posterior slow waves were found by previous studies during motor planning (Bozzacchi et al., 2012) and movement execution (Koester & Schack, 2016; Tunik et al., 2008; Van Schie & Bekkering, 2007; Westerholz et al., 2013). Tunik et al. (2008) localized the posterior slow waves at the anterior intraparietal sulcus (aIPS), which has been suggested to represent the action goals for intentional grasping movement (Rice, Tunik, & Grafton, 2006).

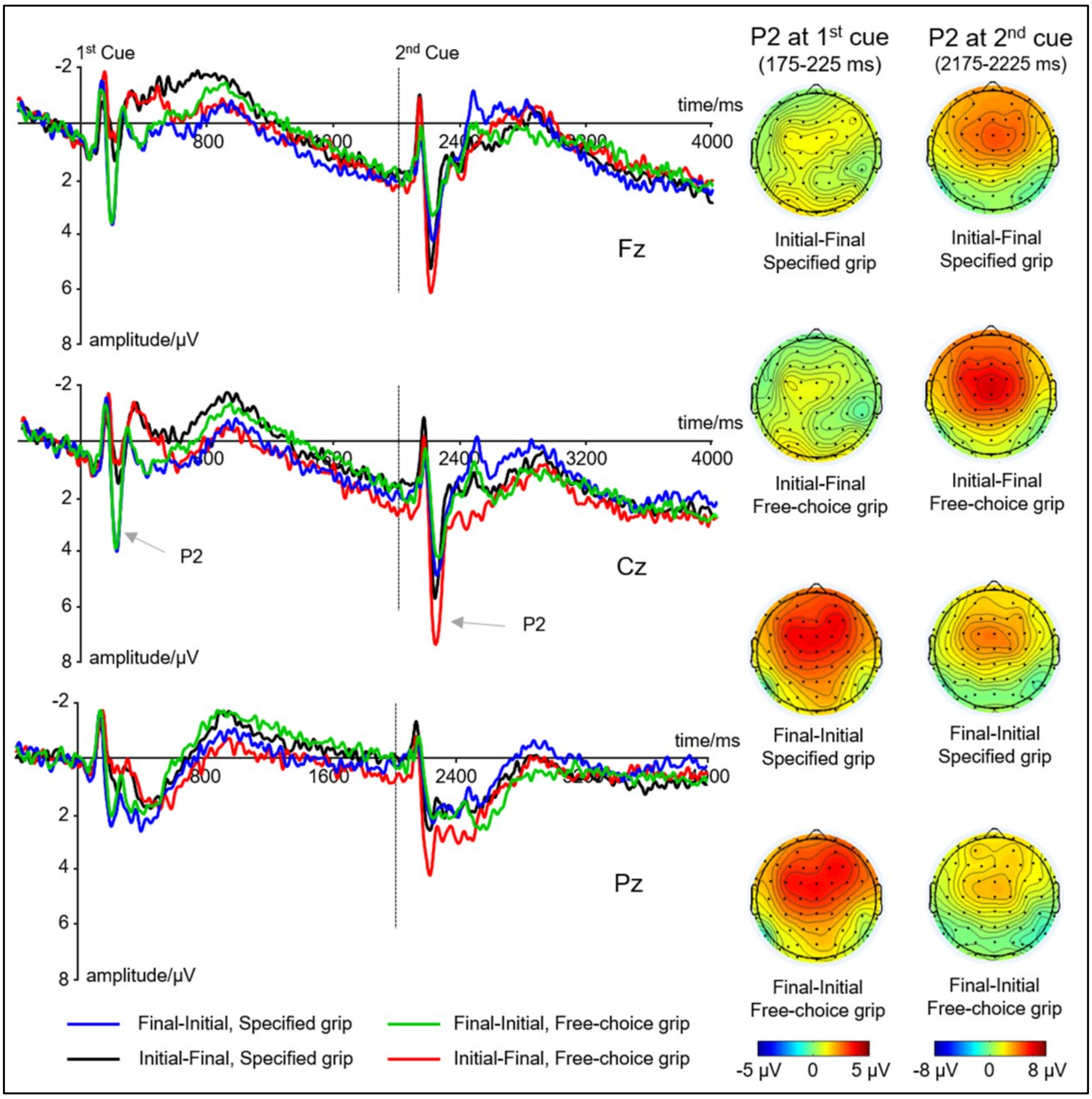

Figure 5.2 ERP waveforms (time-locked to the first cue) for study 1

Grand-averaged ERP waveforms for different experimental conditions, time-locked to the first cue for study 1 at the electrode Fz, Cz, and Pz. Topographic maps illustrate the spatial distribution of the P2 mean amplitude (in the corresponding time window) for different experimental conditions (left column for the P2 at the first cue, and right column for the P2 at the second cue).

In the motor re-planning tasks (study 2 and 3), the anterior P2, P3 (both anterior and posterior), and the late centro-parietal positivity were found when participants were correcting their actions (or action plans) in response to the cue perturbations. Similar to the P2 in the motor planning task (study 1), the anterior P2s in the motor re-planning tasks also reflect the processing that participants were evaluating the task-relevance of the stimulus (Potts, 2004; Potts, Patel, & Azzam, 2004; Van Elk et al., 2010). The anterior P3 component has been claimed to reflect the movement inhibition during motor re-planning (Albert, López-Martín, Hinojosa, & Carretié, 2013; Gajewski & Falkenstein, 2013; Kropotov, Ponomarev, Hollup, & Mueller, 2011; Leuthold & Jentzsch, 2002; Smith, Johnstone, & Barry, 2008), and it has been localized at the ACC and the supplementary motor area (SMA) by previous studies (Albert et al., 2013; Leuthold & Jentzsch, 2002). The posterior P3 component, as well as the late centro-parietal positivity, seem to reflect the parietal activities that are involved in the implementation of a new action (plan). In both study 2 and study 3, the posterior positivity was found for the movement re-planning conditions. Similar late posterior positivity was also found in the movement correction task by Tunik et al. (2008). In that study, the posterior positivity during motor re-planning was localized at the aIPS, and it was believed to reflect the integration of action goals and an emerging motor plan (Tunik et al., 2008), that is, transferring action goals into motor plans.

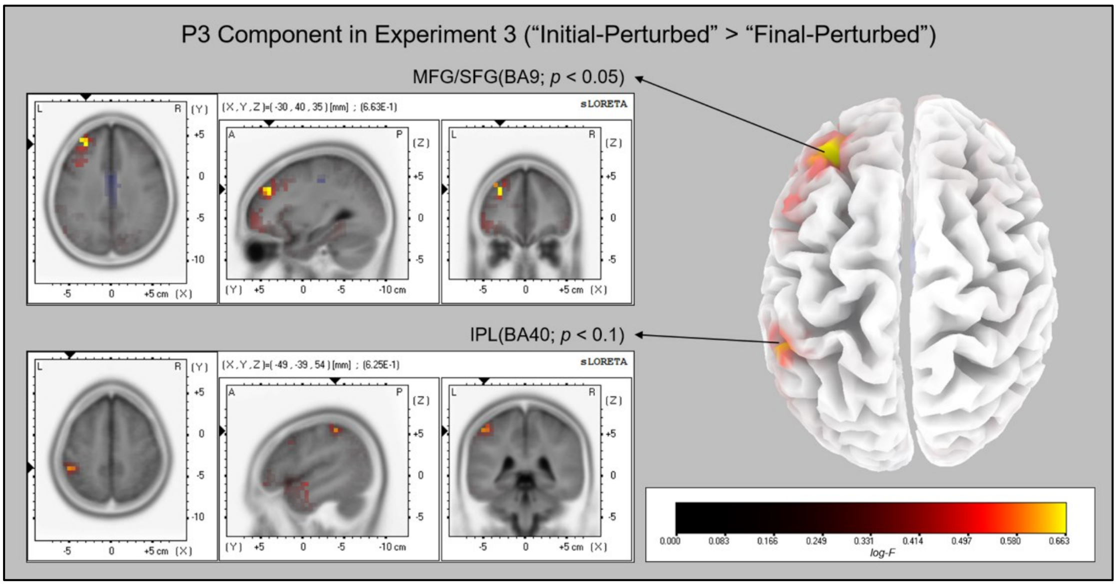

Figure 5.3 Different cortical activations (IP > FP) in the P3 time window for study 3

The images have been obtained after statistical non-parametric mapping (SnPM), and they represent the voxels in which the "Initial-Perturbed"> "Final-Perturbed" contrast was significant (p < 0.05) or nearly significant (p < 0.1) in the time window of the P3 component. (log-F threshold = 0.650;p < 0.05)

It is noteworthy that in the third study, source analyses were conducted to clarify the different cortical engagements during the movement corrections between the perturbed initial and the perturbed final goals. Statistical analyses (statistical non-parametric mapping, SnPM) yielded that in the P3 time window, cortical activations were significantly different over the left frontal area, MFG (BA9). Moreover, different cortical activations were also found in the same time window over the left inferior parietal lobule (IPL, BA40), but the difference showed only a trend toward significance ($p < 0.1$). Although the activations in the left IPL are not significant, these source analyses are consistent with the idea that frontal and parietal cortices jointly contribute to the online movement corrections (Hartwigsen et al., 2012; Hartwigsen & Siebner, 2015).

The neurophysiological results of study 3 also emphasize the engagement of the prefrontal cortex (PFC) in planning and control intentional manual actions. The PFC has long been believed to play an important role in higher-level cognitive functions (Koechlin, Corrado, Pietrini, & Grafman, 2000a; Miller & Cohen, 2001; Tanji & Hoshi, 2001, 2008), and it is the brain region that “orchestrates thought and action in accordance with internal goals” (Miller & Cohen, 2001). Neuroanatomical and neuroimaging studies have revealed that there are many structural (anatomical) and functional connections within (the different portions of the PFC) as well as between the PFC and broad areas in the cortical and subcortical structures (Miller & Cohen, 2001; Tanji & Hoshi, 2001). Due to the numerous neural connections, PFC acts as an essential node for polysensory information processing and integration, working and short-term memory, emotional processing, associative learning, and cognitive control functions, such as inhibition (Barbas, 2000; Koechlin, Corrado, Pietrini, & Grafman, 2000b; Miller & Cohen, 2001; Mushiake, Saito, Sakamoto, Itoyama, & Tanji, 2006; Tanji & Hoshi, 2008). Moreover, PFC is also associated with behavioral selection and decision, especially when behavior must be guided by internal states or intentions, namely goal-directed actions (Koechlin et al., 2000b; Miller & Cohen, 2001; Svoboda & Li, 2018; Tanji & Hoshi, 2008). In the affordance competition hypothesis (Cisek, 2007; Cisek & Kalaska, 2010), PFC is suggested to be the cortical area that receives information from other areas (temporal cortex and basal ganglia) and then evaluates the behavioral relevance of the received information. Based on the relevance evaluations, PFC selects the relevant actions (or action rules) and transfers them to PMC for further motor planning.

The anterior P2 (P2a) time-locked to action goals in the first and second study could also be believed to reflect PFC's relevance evaluation functions proposed by the affordance competition hypothesis (Cisek, 2007; Cisek & Kalaska, 2010). It has been claimed that the P2a reflects stimulus relevance and can be localized at prefrontal areas (Potts, 2004; Potts, Martin, Burton, & Montague, 2006; Potts et al., 2004). In a later study (Van Elk et al., 2010), the anterior P2 has been localized at the dorsal posterior cingulate cortex (dPCC), which also lies in the frontal part of the brain. However, given that we have not conducted a source analysis for the anterior P2 component in the first and the second study, it can only be assumed that the anterior P2s in the first and second study may be localized at the PFC. It might be interesting for future research to investigate more detailed localizations for the anterior P2 in motor planning and re-planning tasks.

Meanwhile, the anterior N2 and anterior P3 time-locked to the goal perturbations in the second and third study may reflect PFC's inhibition functions in motor re-planning. It has been reported that larger frontal N2 and anterior P3 are elicited when individuals re-plan or correct a pre-planned action, and the N2 and P3 components reflect the inhibition processing when individuals are trying to stop their pre-planned actions (Leuthold & Jentzsch, 2002; Nakamoto & Mori, 2012; Recio, Shmuilovich, & Sommer, 2014). Localizations of these components indicated that the source of the N2 and P3 might be the SMA, the ACC, and the rIFG (Folstein & Van Petten, 2008; Iannaccone et al., 2015; Leuthold & Jentzsch, 2002). These neurophysiological results emphasize the role of PFC in re-planning manual actions, that is, inhibiting the prepared actions.

In summary, the current dissertation confirms that the frontoparietal cortical network is critical for the planning and execution of goal-directed manual actions. The prefrontal areas are more likely to be involved in inhibiting pre-planned actions, and the central and parietal areas are more likely to be associated with implementing a new action.

Laterality in manual action planning and control

Laterality is an important as well as an interesting topic in motor control studies, especially in the studies related to manual actions. It has been reported that about 90% of people prefer to use the right hand as their predominant hand when performing unimanual actions (Corballis, 1997; Helbig & Gabbard, 2004; Oldfield, 1971). The handedness and laterality seem to be not limited to humans, other species, such as non-human primates (Corballis, 1997; Warren, 1980), parrots (Hopkin, 2004), and even octopuses (Hopkin, 2004), have been also found to have a preferred hand or body part when reaching for something.

The laterality in manual actions is mainly focused on two aspects, manual asymmetries (laterality in physical movements) and brain asymmetries (laterality in the brain activities). It has been reported less execution time, higher peak velocities, and greater end-point accuracy were observed in right-handers when performing aiming and pointing movements with their dominant right hand (Elliott & Chua, 1996; Elliott, Lyons, Chua, Goodman, & Carson, 1995; Elliott et al., 1993; Helsen, Starkes, Elliott, & Buekers, 1998). Similar manual asymmetries have been found in the execution of grasping movements as well (Flindall, Doan, & Gonzalez, 2014; Seegelke et al., 2011; Seegelke, Hughes, & Schack, 2014; Vainio, Ellis, Tucker, & Symes, 2006). Investigations into manual asymmetries are not limited to the level of motor execution but have also been extended to the motor planning level. Seegelke et al. (2011) have reported that no differences in grasp posture selections (end-state comfort satisfaction) between the dominant and non-dominant hands were found when right-handers were asked to rotate a cylinder 180-degree. Moreover, the reaching time was also similar for the dominant and the non-dominant hand when 180-degree rotation was needed. Similar performance between the dominant and the non-dominant hand in grasp posture planning during unimanual manipulation tasks has also been reported by other studies (Herbort & Butz, 2011; Hughes & Franz, 2008; Hughes, Reißig, & Seegelke, 2011; Hughes, Seegelke, & Schack, 2012). In a review paper, Seegelke et al. (2014) found little evidence for hand-based performance differences in grasp posture planning (selections) during object manipulation tasks in healthy adults, that is, there seem to be no manual asymmetries in grasp posture planning.

The results of the present studies confirmed the idea that there seem to be no manual asymmetries in grasp posture planning. In the first study, we asked participants to perform the grasp-to-rotate movement with both hands. No significant difference was found in the selection of grip postures (thumb-toward, thumb-away) between the left- and the right-hand movements when participants were cued to perform a free-choice grasping (see Chapter 2 for more details).

To examine the manual asymmetries in motor planning, we further analyzed our reaction times with additional factor *laterality* (left/right) in all of our three studies. Results revealed that neither significant main effects nor significant interaction effects for the factor *laterality* were found in the reaction time results of our studies (see Table A13–A15 in the Appendix), which is in line with the previous study (Hughes & Franz, 2008). Altogether, our results may suggest that there seem to be very few manual asymmetries in planning the manual actions involved in object manipulation.

In terms of movement execution, our timing results also yielded that the reach and the rotation times among the studies were similar between the different hands (see Table A13–A15 in the Appendix). Seegelke et al. (2011) also reported no significant reaching time difference between the left- and the right-hand movements. In this study, Seegelke et al. (2011) found no significant main effect for hand use but a significant interaction between hand use and target location (left/right side) in transport times. Transport times were significantly shorter for movements to the ipsilateral target for both the left and hand hands (the movement distances are different). So, it may not be an effect of laterality but an effect of different transport distances. However, in our case, the rotation device was always placed at the same side of the grasping hand (same distance) and the rotation degrees were always the same so that the execution times (reach, rotation) in our studies are not influenced by target side, as well as the movement distance. Therefore, we did not find significant effects for the factor *laterality* in the reach and rotation times of our studies. In another study with bimanual bar transfer task, Hughes and Franz (2008) found no significant laterality effect in their reach and transfer times, which is consistent with our further analyses.

Taking together, in our grasp-to-rotate tasks, laterality in hand use seems not to be a factor that may be interfered with the behavioral timing results. Therefore, in their studies, we pooled left- and right-hand movement trials together in the behavioral analyses.

As for the brain asymmetries, it has been argued by previous researchers that the left hemisphere seems to be dominant for motor planning and motor control in humans (Janssen, Beuting, Meulenbroek, & Steenbergen, 2009; Janssen, Meulenbroek, & Steenbergen, 2011; Martin et al., 2011; Sabaté, González, & Rodríguez, 2004). By involving both left- and right-handers, behavioral studies (Janssen et al., 2009, 2011) have also reported that both left- and right-handed participants showed stronger end-state comfort tendencies for their right hand compared to their left hand, which supports the left-hemisphere-dominance in motor planning on the behavioral level. Martin et al. (2011) found equivalent activation increases in left ventral PMC regardless of hand dominance in both left- and right-handers. In another study (Floegel & Kell, 2017), left lateralization occurred in the intraparietal sulcus (IPS) during the online control of a virtual avatar (by grip force). Moreover, Tunik et al. (2008) also localized the sources of the centro-parietal potentials they found during the motor re-planning to the aIPS and SPL in the left hemisphere.

Some of the previous studies only employed right-hand movements, so that the contralateral cortices may get activated (as they should be) during the motor planning and execution, which may bias the "left laterality" for motor planning. To minimize the effect of hand use, we asked our participants to perform with both hands and pooled both hands trials together in ERP analyses. In the motor planning study (study 1), we did not find significant effects for the factor *left–right* in the analyses of (mean) slow-wave amplitudes during the motor planning (see Table A1–A2 in the Appendix). Moreover, in our study 1, the topographic maps of the early ERP components (P2, N2, and P3; see Figure 2.6, Figure 2.7, and Figure 5.2) did not show an obvious left-hemisphere asymmetry. Since we only compared the amplitude of the mid-line electrodes for the early ERP components in the statistical analyses, it is hard to conclude that whether the asymmetries do exist or not. It would be interesting for researchers in the future.

In our motor re-planning studies (study 2 and study 3), we did not find obvious (clear-cut) brain asymmetries for the ERP components (from the topographic maps). Interestingly, when we localized the different cortical activations between the different goal-perturbed conditions (final-/initial-perturbed), a significant cortical activation difference was only found in the left-MFG during the P3 time window (300–600 ms). Even though we instructed our participants to perform the movements with both hands and pooled the data from both hands together, the different cortical activations were only found in the left hemisphere. The result may suggest that more left hemisphere cortices are involved in the motor re-planning process.

However, it seems to be premature to say that the left hemisphere is dominant for motor re-planning. Previous neuroimaging studies (Mars et al., 2007; Nakamoto et al., 2013; Neubert et al., 2010) have reported that several right-hemisphere regions, such as the right-SMA or right-IFG, are involved in motor re-planning as well. For example, with the help of the TMS, Nakamoto et al. (2013) found that virtual lesions over the right-IFG may diminish the superiority of fastball experts in movement correction tasks (compared to novices) by impairing their inhibitory functions. Therefore, it may be difficult to conclude whether brain lateralization does exist in motor re-planning or not with current findings. It might be of interest for researchers to focus on brain lateralization in motor re-planning in the future.

Habit in manual action planning and control

Habit is also an interesting topic in manual action control, especially for the studies involving object manipulation and tool use. When individuals grasp an object for further manipulation, both habitual (stimulus-driven) system and intentional (goal-directed) system are employed by the central nervous system (Balleine, 2005; Balleine & O’Doherty, 2010; Dickinson & Balleine, 1994; Dickinson & Charnock, 1985; Dolan & Dayan, 2013; Millslagle, Hines, & Smith, 2013; Yin & Knowlton, 2006). The habitual system associates stimuli with responses that were rewarding in the past (past reinforcement), whereas the intentional system selects actions dependent on the match of anticipated action outcomes and current needs (Dolan & Dayan, 2013; Herbort & Butz, 2011).

Even though most manual actions are controlled by the intentional system, the habitual system may also play an important role in grasping if there are no specific demands required in generating the motor plan. In this regard, when grasping an object for manipulation, individuals tend to hold the object with their thumb toward the “effector part”. For example, grasp a knife with the thumb toward the blade, and grip a hammer with the thumb toward the metal part. In a grasp-to-rotate task, Rosenbaum et al. (1992) found that participants tended to hold the bar with their thumb directed toward a pointer, which was marked on one end. Such a tendency has been termed as the thumb-toward bias (Rosenbaum et al., 1992), and it has been found in later studies (Belardinelli et al., 2016; Herbort & Butz, 2011; Herbort, Mathew, & Kunde, 2017; Rosenbaum, Van Heugten, & Caldwell, 1996; Westerholz, Schack, Schütz, & Koester, 2014; Yu, Schack, & Koester, 2021). Herbort and Butz (2011) have suggested that the thumb-toward might be controlled by the "habitual system" that people habitually grasp with the thumb toward the effector part of an object if there are no specific demands for grip selection (free-choice). Moreover, another study (Westerholz, Schack, Schütz, et al., 2014) has also suggested that grasping a handle with habitual posture (thumb-toward) is faster in the preparation as well as execution of the grasp-to-rotate movement, as compared to grasping with non-habitual posture (thumb-away).

To minimize the effects of grasping habit, we controlled it by having and averaging both habitual and non-habitual grasping trials in our studies. Participants performed the same number of habitual and non-habitual trials in each experimental condition (except for the free-choice conditions in the first study), and the habitual and non-habitual trials were also fully randomized in our studies.

In our first study (Chapter 2), a tendency of thumb-toward was found for the grip postures in free-choice trials. Participants tended to hold the handle habitually (thumb toward the pointing marker) when there was no specified requirement for grip selections. Such a tendency is in line with the previous findings (Rosenbaum et al., 1992; Westerholz, Schack, Schütz, et al., 2014).

To determine the effect of grasping habit in our behavioral results, we further analyzed the behavioral timings of our first study (in both specified and free-choice conditions) with the additional factor *habit*[8] (habitual/non-habitual). The further analyses yielded significant main effects for the factor habit, and the reaction, reach, and rotation times were significantly shorter for the habitual than for the non-habitual grasping (see Figure A1 in the Appendix). Similar results were found in the previous study (Westerholz, Schack, Schütz, et al., 2014).

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[8] The habit we used for further analyses refers to the actual grip postures that participants adopted in the grasping movements (regardless of the free-choice/specified grip requirements).

We have also conducted additional analyses for the behavior timing results in our study 2 and study 3, with the factor *habit* (habitual/non-habitual grasping) and *perturbation* (initial-/final-/non-perturbed). These analyses yielded similar *habit* effects for the preparation and execution times. Reaction times, reach times, and rotation times were significantly faster for movements with habitual grasping with non-habitual grasping in both study 2 and study 3 (see Figure A2 & A3 in the Appendix for more details), which is consistent with the additional analyses in our study 1, as well as the results reported by Westerholz et al. (2014).

Altogether, the results of these additional analyses confirm that the habitual system plays an important role in the planning and execution of manual action. The results further suggest that planning and executing manual actions with non-habitual grasping seems to be more difficult (cognitively), as compared to manual actions with habitual grasping.

Furthermore, since the grasping habit was not our main topic, the studies were not designed for analyzing the different neural mechanisms underlying habitual and non-habitual grasping (due to the insufficient number of trials for ERP analysis after adding the factor *habit*). Besides, only a few previous studies focused on the neuro-cognitive mechanisms underlying the grasping habit in manual actions. It would be interesting for researchers to conduct further studies on the neural mechanisms of the grasping habit in the future.

Implication and perspectives

The current dissertation focused on the roles of the initial and the final goal, as well as the neurophysiological mechanisms underlying the goals, in intentional manual action planning and control. These studies extend our understandings of the anticipatory control of complex movements. To our knowledge, the dissertation is among the first neurophysiological study to test the coordination of initial and final goals in manual action planning. More specifically, the findings of the present dissertation make several important implications in theoretical and methodological considerations.

Firstly, our studies investigated the coordination of initial and final action goals in the planning and execution of manual actions, which supplements previous studies on manual action control. To our knowledge, it is the first to demonstrate the action goal coordination in manual actions. Moreover, the neurophysiological results also confirm the importance of final action goals (task purposes) in planning manual actions, which may provide us a more comprehensive picture of the end-state comfort phenomenon.

Secondly, our studies focused on the initial action goal (how to grip) in manual actions, which seems to be mostly overlooked by previous studies. The findings of the present dissertation underscore the importance of initial action goals in manual actions, especially in the re-planning (correction) of a prepared action.

Thirdly, from a methodological perspective, our studies also developed novel experimental paradigms, which can be used in future manual action studies. Both cue (goal) separation paradigm (Chapter 2) and goal perturbation paradigm (Chapter 3 and 4) may be helpful for future manual action studies to investigate the anticipated effects in motor planning and control (such as end-state comfort). Moreover, our studies also further extended the application of the ERP technique in complex movement studies. Our findings confirm that ERPs can be employed in studies related to complex movements (such as grasping).

Apart from these theoretical and methodological implications, the present findings also provide some important practical perspectives, for scientists from other disciplines, such as cognitive robotics and sports training.

In the current dissertation, we explored the functional roles and neural mechanisms of the initial and final action goals in object-related grasping movements (manipulations). The findings of the current dissertation extended our knowledge of the "manual intelligence" (Maycock et al., 2010; Ritter, Haschke, Röthling, & Steil, 2011) from a neuro-cognitive perspective. Our studies confirmed both hierarchical (final–initial) and chronological (initial–final) ways are used in planning and controlling object-related manual actions. In motor planning, the grip postures and task purposes seem to be processed and organized in a hierarchical (final–initial) way, whereas, after the motor planning, the grip posture and task purpose seem to be represented chronologically (initial–final) in the motor plan. These findings may provide several insights into the possibilities for robotics researchers and engineers in designing a more human-like robot system. The hierarchical and chronological ways to process the initial and final action goals for humans can be transferred into the programming scripts or algorithms in cognitive robotics to build a smarter and more adaptive robot system (such as mechanical arms), especially for the robot systems that are designed for interacting with humans. The robot actions may follow the hierarchical manner when processing the grip selection and task purpose before the mechanical action initiation, that is, the robot actions should be intuitive for humans in case that they have to interact with humans.

Moreover, our results may also promote the cognitive robotics studies in another direction, that is, the research area of the brain-machine interface. From a neuro-cognitive perspective, we explored the neurophysiological features of action intentions in manual actions. Different from many previous studies, we employed the goal separation designs in with the action intentions are elaborated, with the initial (how to grip the object) and the final (how to use the object) action goals. Using both initial and final action goals seems to be more appropriate than using an overall goal in the studies that involve manual action planning and execution. In this regard, the robotics researchers are suggested to employ the more detailed (elaborated) initial and final action goals, instead of using only an overall movement intention, in their studies when training their participants as well as the robot systems in the object manipulation tasks.

Our results may also provide several insights into the training of grasp-related sports, such as climbing, wrestling, Judo, and so on. It has been reported that the selection of grasp postures plays an essential role in these sports (Ariyama, Shimamoto, & Nakanishi, 2017; Bläsing, Güldenpenning, Koester, & Schack, 2014; Calmet, Miarka, & Franchini, 2010; Piras, Pierantozzi, & Squatrito, 2014). Therefore, our findings may provide some insights for sports psychologists or coaches in training their athletes. The grip selection serves the task purpose when preparing the action, and trying to avoid (if possible) the changes in grip selections when a prepared movement has to be modified. Given that a limited number of studies has been conducted in such a direction, more attention might be focused on the grip selection studies in these above-mentioned sports.

In sum, by investigating the functional role and neurophysiological mechanisms of the initial and the final action goals separately in the planning and re-planning of manual actions, the current dissertation extends our knowledge on the anticipatory control of complex movements, as well as the neural representation of action goals in controlling complex movements. The results of the current dissertation may also provide researchers in other related areas (cognitive robotics, sports science) some inspiration for their studies.

Conclusion and Future Directions

Chapter 6

Object manipulations are essential in every aspect of our daily life. Many of our object interactions involve our hands. With the help of event-related potentials (ERP), the current dissertation investigated the functional roles of the initial (grip posture) and the final (task purpose) action goal, as well as the neurophysiological mechanisms underlying the goals. To this end, we investigated the multi-step goal-directed manual actions that are involved in object manipulations. Three studies were conducted to investigate the roles of the initial and the final action goals in the planning stage (Chapter 2), the re-planning stage (Chapter 3), and the online correction stage (Chapter 4) of object manipulations (grasp-to-rotate movements).

By presenting the initial and the final action goals separately in different sequences, the first study (Chapter 2) studied how individuals coordinate the action goals (top-down vs. bottom-up) during the preparation of the object manipulation. Results mainly revealed larger anterior P2s but smaller anterior N2s for final goals, as compared to initial goals. However, these component differences were only significant when the goals were presented as the first cue of the stimulus sequence. The findings of the first experiment suggest that the final task goals are more critical than the initial grip postures in planning manual actions, and the action goals seem to be coordinated in a "top-down" (hierarchical) way that task purposes are processed before the selection of grip postures.

Through a modified "S1–S2" paradigm, the second study (Chapter 3) investigated the motor re-planning in adjusting to the unexpected changes in either initial or final action goals during the movement preparation. Results yielded that perturbations in initial goals significantly slowed down the motor re-planning, as compared to perturbations in final goals. Perturbed initial goals elicited a larger centro-parietal positivity (during 500–700 ms time-locked to the perturbation) than perturbed final goals, but the amplitude of anterior P2, anterior N2, and P3 was not significantly different between the initial and final goal perturbations. The results indicate that the re-planning costs induced by initial goal perturbations are higher than final goal perturbations, and the increased re-planning costs seem to be utilized in planning a new action (action implementation) instead of inhibiting the pre-planned action.

Following the second study, the third study (Chapter 4) further explored the motor re-planning in response to the changes in initial or final action goals during the movement execution (online correction). Results also showed that the re-planning time was longer for the initial goal perturbation than the final goal perturbation. Moreover, a larger anterior P3 and a larger central distributed late positivity (600–700 ms) time-locked to the perturbations were found for the initial than for the final goal perturbation. Source analyses revealed that increased cortical activations in the left middle frontal gyrus (MFG, BA9) were found for the perturbed initial goals than the perturbed final goals in the P3 time window. The results imply that online corrections in response to perturbed initial goals are more “resource-demanding” as compared to perturbed final goals. Initial goal perturbations seem to require more cognitive efforts than final goal perturbations in both the inhibition of pre-planned actions and the implementation of new actions.

To conclude, the present dissertation demonstrates that:

1) Both initial and final action goals are crucial in the planning and control of manual actions related to object manipulation.

2) The frontoparietal cortical network is highly involved in manual action planning and control.

3) When planning the object manipulations, final action goals are more critical than the initial grip postures. The initial and final goals are coordinated in a “top-down” (hierarchical) manner during motor planning.

4) When re-planning or correcting the object manipulations, changes in the initial action goals seem to be more crucial (urgent) than changes in the final action goals. The anticipated initial and final action goals are more likely represented in a “bottom-up” (chronological) manner in a prepared motor plan for the upcoming multi-step manual action.

Considering that the limited number of previous studies focused on the topic of initial and final action goals, future investigations with other kinds of manual action tasks (i.e. grasp-to-transfer, sequential button pressing) are necessary to validate the conclusions that can be drawn from the current dissertation. Besides, it would be helpful if future research could employ unpredictable (i.e. random) initial and final action goals in study designs, by which the action goals could be separated in a better way.

In addition, the habit (grasping) effect in object manipulations (tool use) might also be an important and interesting topic for future research. Future studies may focus on the interference and interaction between the goal-directed (end-state comfort consideration) and the habitual (thumb-toward consideration) systems in grip selection. It is also an interesting topic for future research to explore the neurocognitive mechanisms underlying the grasping habit, as well as the interaction between the above-mentioned grip selection systems.

Given the fact that most of the studies mentioned in the current dissertation are individual actions that participants interacted with the objects individually. It would be interesting if future research could extend the initial and final goal topics to a social motor setting (i.e. joint action, joint end-state comfort, and actions in social interaction) in which participants interact with not only the objects but also others.

Overall, the present and such future studies will provide a more detailed and nuanced understanding of human manual actions and how individuals plan as well as control their goal-directed actions, which extends our current understandings about the "manual intelligence". The findings of the present and such future studies may also contribute to other related research areas (such as cognitive robotics, and sports training) by providing several theoretical and practical implications.

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Supplementary Materials

Appendix

Supplementary materials for Chapter 2

Table A1 ***100 ms-step analyses of the slow-wave amplitudes at the first cue (600–2000 ms)***

*F-Values for the ANOVAs with the factors cue sequence (CS), grip selection (GS), front–back (FB), and left–right (LR). * represents for $p < 0.05$; ** represents for $p < 0.01$; *** represents for $p < 0.001$; see also text in Chapter 2.*

	600–700	700–800	800–900	900–1000	1000–1100	1100–1200	1200–1300	1300–1400	1400–1500	1500–1600	1600–1700	1700–1800	1800–1900	1900-2000
CS	0.04	0.01	0.43	0.32	0.14	0.64	0.62	0.50	0.01	0.00	0.15	0.08	0.11	0.56
GS	0.30	0.03	0.02	0.03	0.05	0.07	0.04	0.65	0.53	0.14	0.06	0.03	0.58	0.57
FB	0.43	0.04	0.30	1.77	4.94*	14.22***	23.34***	23.20***	30.53***	32.84***	35.74***	42.43***	45.67***	45.38*
LR	0.27	0.71	1.43	2.24	2.56	1.40	1.00	0.98	0.72	0.04	0.29	0.00	0.11	0.86
CS*GS	7.33*	9.16**	7.45*	7.78**	9.16**	6.91*	6.18*	3.23	1.68	1.67	2.17	1.27	1.51	1.47
CS*FB	53.28***	39.08***	16.17***	15.56***	11.82***	15.11***	16.65***	11.47**	17.10***	11.36**	12.32**	11.26**	12.83**	8.31*
GS*FB	0.99	0.32	0.002	0.10	0.04	0.48	0.23	0.24	1.66	2.64	0.85	0.63	0.48	0.33
CS*LR	0.34	1.27	1.56	0.37	0.05	0.79	0.58	0.62	0.72	2.67	2.34	1.67	1.43	1.19
GS*LR	0.05	0.18	1.14	1.41	1.30	1.81	2.04	2.43	1.15	2.24	1.95	1.52	1.62	0.89
FB*LR	1.18	1.28	2.35	2.98	2.85	2.88	3.60	4.48	4.16	3.56	4.72*	2.79	1.67	0.97
CS*GS*FB	0.67	1.17	0.28	1.53	1.09	1.77	1.45	1.98	2.40	2.69	2.60	2.08	1.75	1.95
CS*GS*LR	0.00	0.07	0.52	0.18	0.00	0.05	0.24	0.34	0.71	0.03	0.51	0.62	0.38	0.36
CS*FB*LR	0.01	0.05	0.09	0.38	1.55	3.79	2.69	1.93	1.77	0.26	0.25	0.29	0.22	0.34
GS*FB*LR	0.15	1.24	0.16	0.02	0.00	0.06	0.49	0.06	0.08	0.01	0.25	0.98	1.75	1.67
CS*GS*FB*LR	3.62	3.93	4.46*	1.98	1.59	0.86	1.79	3.50	2.78	1.70	1.04	1.73	1.83	2.10

Table A2 **100 ms-step analyses of the slow-wave amplitudes at the second cue (2600–4000 ms)**

F-Values for the ANOVAs with the factors cue sequence (CS), grip selection (GS), front–back (FB), and left–right (LR). * *represents for p < 0.05;* ** *represents for p < 0.01;* *** *represents for p < 0.001; see also text in Chapter 2.*

	2600–2700	2700–2800	2800–2900	2900–3000	3000–3100	3100–3200	3200–3300	3300–3400	3400–3500	3500–3600	3600–3700	3700–3800	3800–3900	3900–4000
_CS_	0.00	0.00	0.19	0.45	0.01	0.36	0.04	0.05	0.00	0.05	0.03	0.03	0.04	0.01
_GS_	1.77	1.66	1.78	1.12	0.72	0.49	0.01	0.07	0.06	0.22	0.01	0.01	0.40	0.86
_FB_	1.20	0.01	0.12	1.43	3.56	**_5.21*_**	**_7.69*_**	**_9.63**_**	**_12.25**_**	**_14.66***_**	**_14.07***_**	**_13.53**_**	**_16.57***_**	**_19.51**_**
_LR_	0.28	0.35	0.19	0.18	0.15	0.13	0.00	0.01	0.04	0.04	0.20	0.72	1.00	1.02
_CS*GS_	**_5.22*_**	1.71	1.25	0.90	0.36	0.06	0.03	0.00	0.00	0.34	0.38	0.32	2.03	2.25
_CS*FB_	2.11	3.35	**_7.09*_**	**_10.70**_**	**_8.64**_**	**_13.64**_**	**_11.04**_**	**_4.55*_**	**_6.48*_**	**_7.94**_**	4.14	**_5.19*_**	2.44	2.15
_GS*FB_	1.77	0.79	0.29	0.47	0.68	0.39	0.88	0.81	0.27	0.23	0.15	1.11	0.72	0.60
_CS*LR_	0.28	0.54	0.21	0.46	0.63	0.09	0.05	0.00	0.08	0.07	0.00	0.01	0.05	0.45
_GS*LR_	1.67	1.59	1.72	2.36	2.99	2.91	2.25	2.49	1.50	0.98	1.26	0.90	0.97	0.77
_FB*LR_	0.71	0.70	0.91	0.86	1.03	0.84	0.57	0.36	0.36	0.49	0.44	0.09	0.20	0.07
_CS*GS*FB_	1.98	2.49	1.19	0.67	0.27	0.01	0.00	0.02	0.02	0.20	0.81	0.54	0.01	0.14
_CS*GS*LR_	0.79	0.24	0.47	0.65	0.20	0.08	0.21	0.08	0.02	0.83	0.71	0.64	0.25	0.16
_CS*FB*LR_	2.11	0.89	0.17	0.04	0.01	0.00	0.00	0.11	0.30	0.19	0.53	0.63	1.47	1.51
_GS*FB*LR_	2.39	2.06	2.43	2.67	2.65	3.39	3.07	2.98	2.14	2.06	1.35	1.36	2.15	1.39
_CS*GS*FB*LR_	0.60	0.07	0.24	0.52	0.04	0.15	0.00	0.09	0.01	0.01	0.61	0.52	0.14	0.00

Supplementary materials for Chapter 3

Table A3 **Simple effect analyses of perturbation for N2 amplitudes (200–250 ms).** * < 0.05; ** < 0.01; *** < 0.001.

Electrode	Perturbation	M(SD)	RM ANOVA		Post hoc analyses		
			$F_{(2, 50)}$	η^2_G	Contrast	$t_{(25)}$	Cohen's d
	FP	−0.37(4.13)			FP−IP	−0.24	−0.046
Fz	IP	−0.25(3.94)	29.86***	0.260	FP−NP	5.79***	1.136
	NP	−4.78(2.64)			IP−NP	6.43***	1.260
	FP	−0.47(3.95)			FP−IP	0.50	0.098
FCz	IP	−0.73(3.72)	32.70***	0.304	FP−NP	6.31***	1.238
	NP	−5.39(2.62)			IP−NP	6.40***	1.256
	FP	−0.39(3.36)			FP−IP	0.74	0.145
Cz	IP	−0.77(3.48)	28.57***	0.301	FP−NP	6.12***	1.200
	NP	−4.90(2.62)			IP−NP	5.85***	1.147
	FP	−0.10(3.03)			FP−IP	1.65	0.324
CPz	IP	−0.85(3.20)	19.63***	0.230	FP−NP	5.54***	1.086
	NP	−3.65(2.23)			IP−NP	4.17***	0.818
	FP	0.07(2.91)			FP−IP	2.38*	0.467
Pz	IP	−0.96(2.89)	10.60***	0.140	FP−NP	4.23***	0.829
	NP	−2.42(1.80)			IP−NP	2.46*	0.483

Table A4 **Simple effect analyses of perturbation for P3 amplitudes (250–500 ms).** * < 0.05; ** < 0.01; *** < 0.001.

Electrode	Perturbation	M(SD)	RM ANOVA		Post hoc analyses		
			$F_{(2, 50)}$	η^2_G	Contrast	$t_{(25)}$	Cohen's d
	FP	12.02(5.61)			FP−IP	−1.25	−0.246
Fz	IP	12.72(5.79)	35.88***	0.180	FP−NP	6.37***	1.249
	NP	7.30(4.20)			IP−NP	7.05***	1.383
	FP	13.79(5.64)			FP−IP	−0.82	−0.161
FCz	IP	14.27(5.49)	44.46***	0.221	FP−NP	7.11***	1.395
	NP	8.48(4.29)			IP−NP	8.21***	1.610
	FP	13.36(5.21)			FP−IP	−0.27	−0.053
Cz	IP	13.51(5.18)	55.46***	0.239	FP−NP	8.59***	1.685
	NP	7.68(4.36)			IP−NP	8.53***	1.673
	FP	12.08(4.37)			FP−IP	0.34	0.066
CPz	IP	11.91(4.73)	64.83***	0.310	FP−NP	9.66***	1.894
	NP	5.97(3.84)			IP−NP	8.63***	1.693
	FP	11.85(4.02)			FP−IP	0.56	0.109
Pz	IP	11.58(4.44)	80.30***	0.418	FP−NP	10.89***	2.135
	NP	4.79(3.23)			IP−NP	9.22***	1.808

Table A5 Statistics analyses for mean amplitudes of the slow waves in the time window from 500 to 600 ms time-locked to the secondary stimulus. ** < 0.05; ** < 0.01; *** < 0.001.*

ROI	**Perturbation**	***M(SD)***	**RM ANOVA**		**Post hoc analyses**		
			$F_{(2, 50)}$	$\eta^2{}_G$	***Contrast***	$t_{(25)}$	***Cohen's d***
AL	***FP***	2.18(4.29)	14.09***	0.110	***FP−IP***	−1.08	−0.211
	IP	2.69(4.97)			***FP−NP***	4.59***	0.901
	NP	−0.57(2.95)			***IP−NP***	3.83**	0.751
AM	***FP***	1.86(5.34)	24.69***	0.221	***FP−IP***	−2.78*	−0.545
	IP	3.36(5.63)			***FP−NP***	4.89***	0.958
	NP	−2.58(3.12)			***IP−NP***	5.42***	1.063
AR	***FP***	3.46(4.37)	10.48***	0.09	***FP−IP***	−0.67	−0.132
	IP	3.82(4.58)			***FP−NP***	3.95**	0.774
	NP	0.91(3.55)			***IP−NP***	3.39**	0.666
CL	***FP***	5.18(4.08)	69.08***	0.377	***FP−IP***	−3.49**	−0.685
	IP	6.69(4.31)			***FP−NP***	8.96***	1.756
	NP	−0.25(3.27)			***IP−NP***	9.94***	1.753
CM	***FP***	3.63(6.14)	54.30***	0.343	***FP−IP***	−3.15**	−0.689
	IP	5.90(5.49)			***FP−NP***	6.98***	1.368
	NP	−3.07(4.36)			***IP−NP***	8.70***	1.705
CR	***FP***	5.94(3.89)	59.89***	0.404	***FP−IP***	−2.41	−0.472
	IP	7.07(3.68)			***FP−NP***	8.30***	1.627
	NP	0.28(3.48)			***IP−NP***	8.48***	1.663
PL	***FP***	6.00(3.39)	58.56***	0.352	***FP−IP***	−3.02*	−0.592
	IP	7.26(3.83)			***FP−NP***	8.16***	1.601
	NP	1.62(2.74)			***IP−NP***	8.55***	1.677
PM	***FP***	6.69(3.97)	92.28***	0.427	***FP−IP***	−2.85*	−0.559
	IP	7.95(4.13)			***FP−NP***	10.79***	2.117
	NP	0.67(3.08)			***IP−NP***	10.53***	2.065
PR	***FP***	6.22(3.43)	47.74***	0.343	***FP−IP***	−1.79	−0.351
	IP	7.11(3.96)			***FP−NP***	8.21***	1.609
	NP	1.59(2.74)			***IP−NP***	7.53***	1.476

Table A6 Statistics analyses for mean amplitudes of the slow waves in the time window from 600 to 700 ms time-locked to the secondary stimulus. ** < 0.05; ** < 0.01; *** < 0.001.*

ROI	**Perturbation**	***M(SD)***	**RM ANOVA**		**Post hoc analyses**		
			$F_{(2, 50)}$	η^2_G	***Contrast***	$t_{(25)}$	***Cohen's d***
	FP	0.85(4.03)			***FP−IP***	−1.94	−0.380
AL	***IP***	1.70(4.22)	17.57***	0.125	***FP−NP***	4.27***	0.838
	NP	−1.74(3.54)			***IP−NP***	4.70***	0.921
	FP	−2.14(3.68)			***FP−IP***	−3.28**	−0.643
AM	***IP***	−0.63(3.98)	14.53***	0.177	***FP−NP***	3.05**	0.598
	NP	−4.79(3.68)			***IP−NP***	4.48***	0.878
	FP	1.69(4.12)			***FP−IP***	−1.05	−0.205
AR	***IP***	2.21(3.72)	6.32**	0.058	***FP−NP***	2.55	0.500
	NP	−0.06(4.09)			***IP−NP***	2.87*	0.563
	FP	2.60(3.83)			***FP−IP***	−5.12***	−1.004
CL	***IP***	4.82(4.32)	52.94***	0.279	***FP−NP***	6.14***	1.205
	NP	−1.18(4.02)			***IP−NP***	8.69***	1.704
	FP	−1.11(4.83)			***FP−IP***	−4.72***	−0.925
CM	***IP***	1.37(5.15)	31.84***	0.230	***FP−NP***	4.37***	0.858
	NP	−5.09(4.90)			***IP−NP***	6.82***	1.338
	FP	2.96(3.53)			***FP−IP***	−4.48***	−0.878
CR	***IP***	4.83(3.89)	34.71***	0.235	***FP−NP***	4.67***	0.916
	NP	−0.32(4.29)			***IP−NP***	7.23***	1.418
	FP	4.75(3.26)			***FP−IP***	−5.22***	−1.024
PL	***IP***	6.82(4.17)	40.61***	0.230	***FP−NP***	5.15***	1.010
	NP	1.97(3.62)			***IP−NP***	7.43***	1.456
	FP	4.40(4.09)			***FP−IP***	−4.07***	−0.799
PM	***IP***	6.30(4.76)	44.61***	0.251	***FP−NP***	6.24***	1.223
	NP	0.51(3.84)			***IP−NP***	7.71***	1.511
	FP	4.74(3.37)			***FP−IP***	−4.43***	−0.869
PR	***IP***	6.53(4.27)	47.74***	0.343	***FP−NP***	4.89***	0.690
	NP	2.06(3.56)			***IP−NP***	6.71***	1.315

Supplementary materials for Chapter 4

Table A7 ***Simple effect of perturbation for P3 amplitude in different front–back and left–right areas.*** ** < 0.05; ** <0.01; *** <0.001.*

Area		**RM ANOVA**		**Post hoc analyses**	
		$F_{(2,38)}$	η^2_G	*Contrast*	$t_{(19)}$
Front-back	***Anterior***	53.096***	0.283	***FP−IP***	−3.42**
				FP−NP	6.87***
				IP−NP	10.09***
	Central	46.38***	0.345	***FP−IP***	−1.62
				FP−NP	7.41***
				IP−NP	9.03***
	Posterior	16.53***	0.19	***FP−IP***	−0.48
				FP−NP	4.72***
				IP−NP	5.20***
Left-right	***Left***	32.28***	0.251	***FP−IP***	−1.61
				FP−NP	6.01***
				IP−NP	7.62***
	Middle	50.52***	0.357	***FP−IP***	−1.86
				FP−NP	7.63***
				IP−NP	9.49***
	Right	30.72***	0.249	***FP−IP***	−1.46
				FP−NP	5.94***
				IP−NP	7.40***

Table A8 ***Simple effect of perturbation for the mean amplitude of the slow waves during 600–700 ms in different left–right areas.*** ** < 0.05; ** <0.01; *** <0.001.*

Area		**RM ANOVA**		**Post hoc analyses**	
		$F_{(2,38)}$	η^2_G	*Contrast*	$t_{(19)}$
Left-right	***Left***	36.97***	0.125	***FP−IP***	−2.19
				FP−NP	6.10***
				IP−NP	8.30***
	Middle	41.28***	0.141	***FP−IP***	−2.52*
				FP−NP	6.30***
				IP−NP	8.82***
	Right	25.76***	0.085	***FP−IP***	−2.03
				FP−NP	4.95***
				IP−NP	6.98***

Table A9 Summary of the statistical results for the slow waves from 700 to 1000 ms (time-locked to the secondary stimulus). ** < 0.05; ** <0.01; *** <0.001.*

	Time windows		
	700–800 ms	*800–900 ms*	*900–1000 ms*
Perturbation [$F_{(2,38)}$]	22.08***	12.54***	6.55**
Front–back [$F_{(2,38)}$]	9.43**	9.66**	6.47**
Left–right [$F_{(2,38)}$]	22.82***	26.96***	24.38***
Perturbation*Front–back [$F_{(2,38)}$]	1.51	0.72	0.74
Perturbation*Left–right [$F_{(2,38)}$]	2.84	0.30	0.72
Front–back*Left–right [$F_{(4,76)}$]	6.13***	5.81**	4.90**
Perturbation*Front–back*Left–right [$F_{(4,76)}$]	0.84	0.80	1.62

Table A10 Summary of the post hoc results for the factor perturbation from 700 to 1000 ms (time-locked to the secondary stimulus). ** < 0.05; ** <0.01; *** <0.001.*

Contrast	Time windows		
	700–800 ms	*800–900 ms*	*900–1000 ms*
FP–IP	−1.43	−0.94	−0.44
FP–NP	4.90***	3.79**	2.89*
IP–NP	6.34***	4.73***	3.33**

Table A11 Summary of the statistical results for the ERP slow waves from −400 to 0 ms (time-locked to grasping). ** < 0.05; ** <0.01; *** <0.001.*

	Time windows			
	−400 – −300 ms	*−300 – −200 ms*	*−200 – −100 ms*	*−100 – 0 ms*
Perturbation [$F_{(2,38)}$]	2.09	1.17	1.57	1.99
Front–back [$F_{(2,38)}$]	6.91**	8.29***	9.87***	15.34***
Left–right [$F_{(2,38)}$]	33.14***	36.04***	33.27***	35.54***
Perturbation*Front–back [$F_{(2,38)}$]	0.27	0.69	1.24	0.65
Perturbation*Left–right [$F_{(2,38)}$]	0.92	1.31	1.35	0.73
Front–back*Left–right [$F_{(4,76)}$]	4.14*	3.77*	3.57*	4.48*
Perturbation*Front–back*Left–right [$F_{(4,76)}$]	0.64	0.98	1.00	0.82

Supplementary materials for Chapter 5

Table A12 Post hoc results for the averaged percentage of habitual grips in free-choice trials of study 1

Repeated measure ANOVA was applied to the averaged percentage of habitual grips in free-choice trials of the first study, with the factors Hand (left, right) and Position (P1–P8). Results only yielded a significant main effect for Position, F (7, 175) = 43.50; p < 0.001;$\eta_G^2 = 0.363$*. The results of post hoc analyses were listed in the following table. Note that P1–P8 represent the target positions corresponding to the target markers on the rotation device (clock-wisely).*

	P1	*P2*	*P3*	*P4*	*P5*	*P6*	*P7*	*P8*
P1		1	1	***<.001***	***<.001***	***<.001***	1	1
P2	1		1	***<.001***	***<.001***	***<.001***	1	1
P3	1	1		***<.001***	***<.001***	***<.001***	1	***0.033***
P4	***<.001***	***<.001***	***<.001***		0.755	1	***<.001***	***<.001***
P5	***<.001***	***<.001***	***<.001***	0.755		0.142	***<.001***	***<.001***
P6	***<.001***	***<.001***	***<.001***	1	0.142		***<.001***	***<.001***
P7	1	1	1	***<.001***	***<.001***	***<.001***		0.141
P8	1	1	***0.033***	***<.001***	***<.001***	***<.001***	0.141	

Table A13 Results of ANOVAs with the factor laterality for timings in study 1

Repeated measure ANOVAs were applied to the averaged reaction, reach, and rotation times with the factor cue sequence (final-initial; initial-final), grip selection (specified; free-choice), and laterality (left; right).

	Reaction time			*Reach time*			*Rotation time*		
	$F_{(1,25)}$	*p*	η^2_G	$F_{(1,25)}$	*p*	η^2_G	$F_{(1,25)}$	*p*	η^2_G
cue sequence	2.06	0.164	0.000	0.01	0.912	0.000	0.07	0.799	0.000
grip selection	0.001	0.971	0.000	26.41	**<.001**	0.016	13.41	**0.001**	0.013
laterality	0.01	0.761	0.001	0.30	0.586	0.001	0.12	0.729	0.000
cue sequence*grip selection	6.91	**0.014**	0.002	0.91	0.350	0.000	8.64	**0.007**	0.001
cue sequence*laterality	0.10	0.327	0.000	0.01	0.924	0.000	0.02	0.895	0.000
grip selection*laterality	3.25	0.083	0.000	0.11	0.742	0.000	0.16	0.698	0.000
cue sequence*grip selection* laterality	1.67	0.208	0.000	0.95	0.339	0.000	1.52	0.229	0.000

Table A14 Results of ANOVAs with the factor laterality for timings in study 2

Repeated measure ANOVAs were applied to the averaged reaction, reach, and rotation times with the factor goal perturbation (FP; IP; NP) and laterality (left; right).

	Reaction time			***Reach time***			***Rotation time***		
	F	***p***	η^2_G	***F***	***p***	η^2_G	***F***	***p***	η^2_G
goal perturbation	87.91	**<0.001**	0.175	37.52	**<0.001**	0.043	39.82	**<0.001**	0.053
laterality	1.44	0.241	0.010	0.20	0.662	0.001	0.02	0.884	0.010
goal perturbation *laterality	0.85	0.418	0.001	0.16	0.803	0.000	2.10	0.132	0.002

Table A15 Results of ANOVAs with the factor laterality for timings in study 3

Repeated measure ANOVAs were applied to the averaged reaction, reach, and rotation times with the factor goal perturbation (FP; IP; NP) and laterality (left; right).

	Reaction time			***Reach time***			***Rotation time***		
	F	***p***	η^2_G	***F***	***p***	η^2_G	***F***	***p***	η^2_G
goal perturbation	2.371	0.122	0.002	133.73	**<0.001**	0.505	8.20	**0.001**	0.020
laterality	0.86	0.366	0.009	0.03	0.875	0.001	4.19	0.055	0.019
goal perturbation *laterality	1.45	0.248	0.002	0.13	0.883	0.000	1.62	0.218	0.005

Figure A1 ***Behavioral timing results with the factor movement habit for the first study***

Averaged (N = 26) reaction time, reach time, and rotation time are showed in different cue sequences (Final-initial, FI; Initial-final, IF) and movement habits (habitual; non-habitual) conditions. RM ANOVAs were conducted with the factor cue sequence and movement habit for reaction, reach, and rotation times. Results revealed significant main effects for movement habit in reaction, reach, and rotation times (see below). No other significant effects were found in the ANOVAs. The error bars represent standard errors. Note: the habit refers to the grasping postures that participants actually adopted in the experiment, regardless whether the grip selections are free-choice or specified.

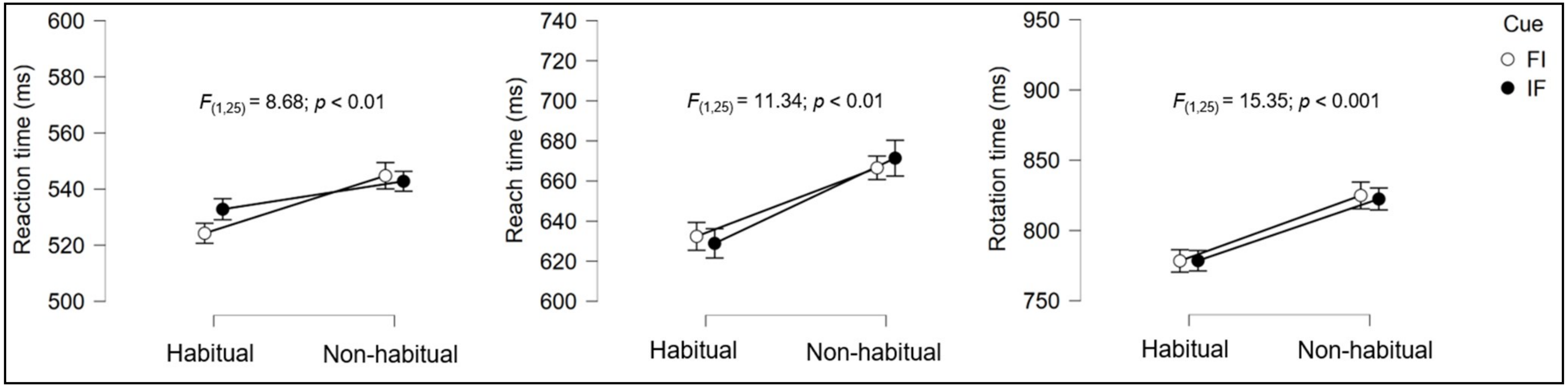

Figure A2 **Behavioral Figure A2 Behavioral timing results with the factor movement habit for the second study**

*Averaged (N = 26) reaction time, reach time, and rotation time are showed in different perturbations (FP; IP; NP) and movement habits (habitual; non-habitual). RM ANOVAs were conducted with the factor perturbation and movement habit for reaction, reach, and rotation times. Results yielded a significant interaction for perturbation*movement habit in reaction time. Further analyses found significant habit effects in the FP and the NP conditions, but not in the IP condition (see below, "***" represents p < 0.001; "n.s." represents p > 0.05). In the analysis of reach and rotation times, only significant main effects for movement habit were found (see below). The habit here refers to the grasping posture that participants performed. The error bars represent standard errors. Note: the habit here refers to the grasping postures that participants actually adopted in the experiment. Please note that in the IP condition, the instructed postures are different from the performed ones (because of the goal perturbation).*

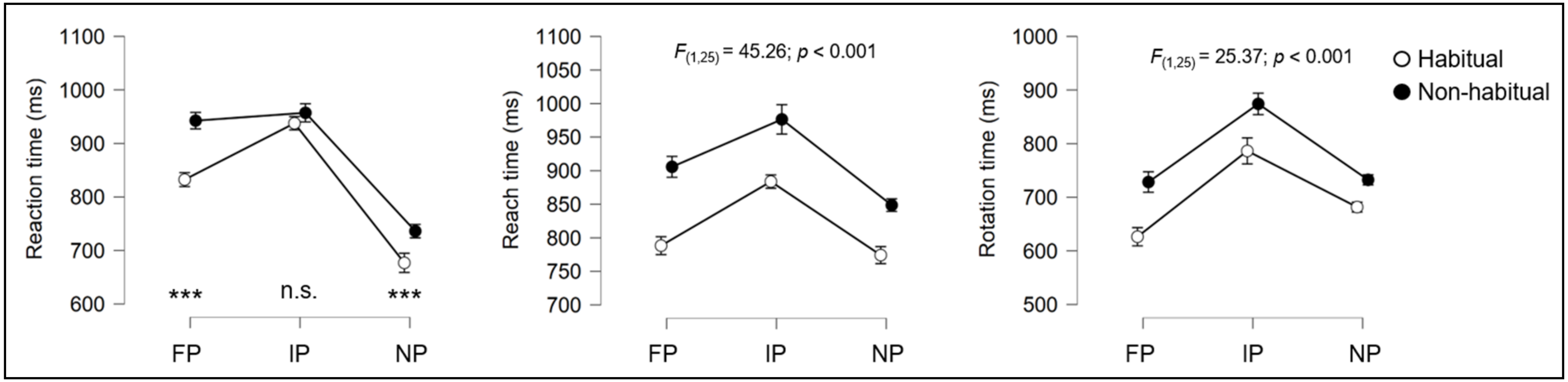

Figure A3 **Figure A3** **Behavioral timing results with the factor movement habit for the third study**

*Averaged (N = 20) reaction time, reach time, and rotation time are showed in different perturbations (FP; IP; NP) and movement habits (habitual; non-habitual). RM ANOVAs were conducted with the factor perturbation and movement habit for reaction, reach, and rotation times. Results only yielded a significant main effect for movement habit in reaction time (see below). The analysis of reach time found a significant interaction effect for perturbation*movement habit, and significant habit effects were found in all the perturbation conditions (see below, "***" represents p < 0.001; "**" represents p <0.01). The analysis of rotation time also yielded a significant interaction effect for perturbation*movement habit, and significant habit effects were found in all the perturbation conditions (see below, "***" represents p < 0.001; "**" represents p <0.01). The error bars represent standard errors. Note: the habit in reaction time refers to the cued postures because at that moment the goal perturbations did not come (see text in Chapter 4 for more details). The habit in reach time and rotation time refers to the grasping postures that participants actually adopted in the experiment. Please note that in the IP condition, the instructed postures are different from the performed ones (because of the goal perturbation).*