Neurophysiological correlates and cognitive components of motor and action control

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1 GENERAL INTRODUCTION

One of the most important concepts in motor control is the degrees of freedom problem (Bernstein, 1967). The problem describes that there are nearly infinite movement possibilities a person can choose from when deciding how to execute a specific movement. Bernstein's idea was, that if the information-processing-system was involved in the production of all decisions about the movements of single muscles of one action, it would be hard to imagine how all of the brain activity required for a simple movement can be explained. Every joint can be moved independently with at least one degree of freedom. The joints are moved by muscles, which consist of hundreds of motor units, which have to be controlled. It would be impossible for the central nervous system if it had to control all of these degrees of freedom separately through conscious decisions (Greene, 1972; Whiting, 1984). Following Bernstein's view (1967), motor coordination can resolve indeterminacy caused by redundant peripheral degrees of freedom. With increasing degrees of freedom, it is then necessary to have more control over the construction of the movement. The degrees of freedom problem asks the question of why we choose to execute the movement in the way we do. This problem applies also to partial body movements; many movement options are available for reaching, grasping, and transporting objects from one location to another.

One possible explanation for why we choose to execute a movement in the way we do is efficiency (Rosenbaum, 2010). That means, we choose to execute movements in the way we consider the most efficient. Acting in an efficient way requires anticipation of the upcoming movement and its effect. Thus, motor control requires cognitive components to work efficiently. Movements of the body are not just physical processes (movements of the muscles and joints) but strongly interconnected to cognitive processes. One could even say that the goal of every cognitive process - may it be perception, learning, or memory - is behavior and, thus, a motor action. Even processes that seem purely cognitive, like calculating numbers, require a motor action to write down the result, communicate it, or use it. Cognition without any kind of motor action may be pointless, stressing the importance of motor processes.

Thus, motor control has its application in almost all fields of life. The focus of this work lies on the cognitive and information processing level, exploring behavioral and neurophysiologic mechanisms underlying the planning and control of manual action. To advance our understanding of the link between motor control and cognition, we investigated the neural basis of manual object manipulations.

While the degrees of freedom problem is concerned with the biomechanical constraints and redundancies of action planning, other theories tackle action planning on the level of mental representations. Among the most influential of these theories is the ideomotor approach, which emphasis the strong link between motor control and cognition. The present thesis focuses on this link as well, so cognitive approaches like ideomotor theory and further concepts integrating representation of actions are described below providing a theoretical foundation. Then a summary of the most important results concerning behavioral experiments about the cognitive aspects of motor control is given. As we are interested in neurophysiological indicators underlying the mentioned cognitive approaches, neurophysiological methods are introduced and results about existing grasp related neurophysiologic research are summarized. This chapter closes with a short overview of the remainder of the present thesis.

1.1 Frameworks for action control

Most of the behaviors people perform are intended to achieve a certain purpose. How is the mind able to use the body to achieve its goals? One framework for action planning is the ideomotor theory, which suggests that actions are represented by their perceivable effects.

Ideomotor theory originated in the 19th century (Stock & Stock, 2004; Herbart, 1816, 1825; Lotze, 1852; Harless, 1861; Laycock, 1840, 1845; Carpenter, 1852). James emphasized ideomotor theory in his *Principles of Psychology* (1890, 1950) and brought it to the attention of many psychologists. The idea behind ideomotor theory is that internal representations of actions and the actions themselves are tightly linked. Perceptual events tend to generate actions for which the feedback is similar to already experienced action effects. The core character of ideomotor accounts is that actions are represented in terms of their sensorial effects, which can be classified in different manners. Another characteristic of ideomotor accounts is immediacy between perception and action, which means that no intermediate processing steps are required from idea to motor preparation. It has been suggested that planning an action is guided by an anticipatory representation of its perceptual consequences (Greenwald, 1970; Prinz, 1997).

One of the latest and frequently quoted accounts of an ideomotor theory is the theory of event coding (TEC; Hommel et al., 2001). It can be described as an elaboration of the common coding principle (Prinz, 1997). TEC (Hommel et al., 2001) was based on the close relation between action and perception. It incorporates anticipatory processes used to produce an action. TEC suggests a common representational domain for perception and action, which pertains the cognitive antecedent of the action.

Hommel (2009) describes TEC as a general framework that explains how perceived (stimuli) and produced events (responses) are cognitively represented and how their representations interact to generate perception and action. TEC makes the claim that the cognitive representations of perceived events and produced actions do not differ, as actions are represented by codes of their perceptual consequences. Hence, it's named theory of event coding. According to TEC, the ideomotor approach provides a good basis for this consideration. The same representation can provide the anticipation of an upcoming perception just like the selection of an action according to its expected outcome (Hommel, 2009). "TEC makes an attempt to explain that and how human action is anticipatory in nature, how anticipations emerge through experience, and how the anticipation of action effects comes to regulate human behavior. In particular, we have seen that anticipations serve at least two purposes: the selection of appropriate actions and the evaluation of action outcomes in the context of a particular goal" (Hommel, 2009). Ideomotor theory and TEC (Hommel, 2009) emphasize the importance of the goal and of anticipated sensory effects for action control. Both perspectives share "the basic idea that voluntary movements may be planned, performed, and stored in memory by representations of anticipated effects" (Schack, 2004).

As mentioned, complex movements require the control of a great number of degrees of freedom. According to Bernstein (1975), the anticipation of a movement effect is the first and decisive step for movement organization. After the anticipation of the movement effect, a model of the needed future is generated. All movement control and monitoring processes can be related to this model (Bernstein, 1967, 1975). For each goal-directed action, the degrees of freedom have to be transformed into the targeted movement effects (Bernstein, 1971). Bernstein developed a hierarchical model, which described how these transformation processes work together on different independent levels.

Which level has the leading role and which ones are subordinate depends on the task requirements and the mastery of specific skills related to the task. This means, that the functional relation of the levels is not fixed and regulation processes work only partially according to hierarchical principles. Rather, there is an interplay and interchange of information between the different levels. Bernstein (1996a, 1996b) distinguished five different levels named from level A to level E from bottom to top.

Level	Basic control function	Related neurophysiological structures
E	Symbolic activities	Cortical
D	Object related actions	Cortical, parietal-premotor
C (C1, C2)	Movements in space	
	C1: orientation in space	Cortical (pyramidal) and
	C2: object manipulation in space	Striatal (extrapyramidal)
B	Muscle synergies	Thalamo-pallidal
A	Muscle tone and posture	Rubro-spinal

Table 1.1: Levels of movement construction and their suggested neurophysiological structures according to Bernstein (1975, 1996a, 1996b).

Level E is the highest level and is responsible for the control of symbolic activities like giving a speech. This level is more of a symbolic system and not directly concerned with the control of corresponding movements themselves. Level D controls object related actions. Feedback on action effects is getting processed on level D by means of an action plan. The exact details of movements and necessary corrections are delegated to lower background levels. Level C is responsible for movements in space and is important for learning specific movement patterns. "The lower sublevel of space (C1) builds locomotions, transfer of objects, and so forth; the upper sublevel of space (C2) builds its accurate throws, strikes, hits, pointings, and so on" (Bernstein, 1996b, p. 155). Level B is responsible for the control of synergies, for example in rhythmic and cyclic movement patterns. Level A is responsible for the regulation of muscle tone and posture control. Level A has a background function during voluntary movements. Almost everything that happens on level A is involuntary and automatic.

Support for the organization of movement control on different levels has also been found on a neural level where it seems that neurophysiological structures are constructed hierarchically as well (Bernstein, 1975; Jeannerod, 1995; Kandel et al., 2013). Jeannerod (2004) states that "(motor) brain activity during action representation strongly suggests that the same areas are involved during different types of representations" (p. 388). These different types of representations belong to processes like "intending, imaging, observing/imitating, and performing an action" (Jeannerod, 1999, p. 10) and seem to "share, at least in part, common structural and functional mechanisms" (Jeannerod, 1999, p. 10). On the data he reviewed, Jeannerod (1999) concludes that several levels of processing are necessary "so that the level used for execution would be distinct from the level of the conscious representations. At the lower level, action-related signals are processed automatically for controlling execution and generating corrections when necessary. The state of the lower level influences the upper level where consciously accessible representations are generated" (p. 24).

The levels of Bernstein's model were matched to the following neurophysiological structures (Bernstein, 1975). Level A is supposed to be controlled mainly by the nucleus ruber and the rubrospinal tract. Level B is completely extrapyramidal and is defined by the interplay of thalamus and globus pallidus. Level C involves the extrapyramidal as well as the pyramidal motor system and the striatum being one of this level's most important structures. Level D was considered as a parietal-premotor level according to its location. This level is completely cortical, but can indirectly affect the pyramidal and extrapyramidal system.

Bernstein (1975) further mentions that sensory related systems are located in parietal areas of the cortex, while the frontal areas of the cortex are responsible for the planning and execution of movements. Thus, he describes the parietal areas as the sensory receiving end of an information system, while the frontal areas are involved in a creation process. He explicitly does not hypothesize that separate localizations exist for his model of the needed future (what has to be created) and a model for the past (what has been received). However, Bernstein (1975) considers it possible that one of the processes is mainly connected to parietal areas while the other is mainly connected to frontal areas.

While there are neurophysiological findings supporting a hierarchical organization of motor control, Bernstein himself called attention to the possibility of a subordinate cognitive level for complex movements, that he did not make detailed assumptions about. Schack (2004) elaborated Bernstein's idea on the construction of movement integrating cognitive components and their functional role in action organization and performance into a model of the cognitive architecture of complex movements. According to this model, the cognitive architecture of complex movements is organized over four hierarchical levels. These are a mental and a sensorimotor control level, as well as a mental and a sensorimotor representation level.

Processes on the level of mental control (Level IV) are initiated intentionally. On this level, intended action effects are coded into action goals. A further component of mental control are control strategies, like instructions and inner speech. The level of mental representation (Level III) is primarily a cognitive reference for the level of mental control (Level IV). The level of mental representation (Level III) is organized conceptually and is responsible for the transformation of the anticipated action goal into a suitable movement program. This level constitutes the basis for movement programming processes and its integration of temporal and spatial information. The major building blocks of the level of mental representation are Basic Action Concepts (BACs), which are generated and formed through movement experience. BACs tie together functional and sensory features of complex movements (Schack, 2004). They are connected to Level IV through functional features, which are derived from movement goals, and to the level of sensorimotor representation (Level II) through sensory features, referring to perceptual effects of movements. The level of sensorimotor control (Level I) is connected to the environment. In contrast to the level of mental control (Level IV), which is driven intentionally, the level of sensorimotor control (Level I) is driven perceptually. It is built on functional units, which are mainly representing perceptual effects. The level of sensorimotor representation (Level II) is where modality-specific information representing perceptual effects of movements are stored. Level I sums up levels A and B of Bernstein's model. Bernstein's level C is split into Levels II (C1) and III (C2). Bernstein's level D is equivalent to Level IV.

Level		**Main function**	**Related to Bernstein's level...**
IV	Mental control	regulation	D
II	Mental representation	representation	C2
II	Sensorimotor representation	representation	C1
I	Sensorimotor control	regulation	A and B

Table 1.2: Levels of the cognitive architecture of complex movements and their relation to Bernstein's levels of movement construction (Schack, 2004).

Overall, there is a strong interplay of the different regulation and representation levels. One might say that Levels I and II are responsible for the functional manipulation of objects and the environment, while Levels III and IV are responsible for functional and distal processing of objects and events.

1.2 Goals as a driving factor for voluntary action control

Theories like the aforementioned ideomotor theory (James, 1890, 1950; Prinz, 1997; Kunde & Weigelt, 2005), TEC (Hommel et al., 2001; Hommel, 2009), and models of the architecture of movement (Bernstein, 1975, 1996; Schack, 2004) emphasize the importance of goals for motor control and the strong link between motor control and cognition.

Additionally, imitation studies have shown that children tend to imitate the goal of observed movements, and ignore the way in which the goal is accomplished (Meltzoff, 1995; Bekkering et al., 2000). Behavioral studies that selectively manipulated grip- and goal-related aspects of observed actions (van Elk et al., 2008), further support the idea that understanding others' actions is organized primarily around action goals.

Further evidence comes from a medical population. Generating actions based on conceptual knowledge about the overall goal of an action is for example selectively impaired in patients with ideational apraxia. The lesions of these patients lead to spatial and temporal errors in executing actions on the basis of a pre-specified goal, although the individual elements may be performed accurately in isolation (Luria, 1980; Karnath, 2012). Another example for impaired cognitive resources for the execution of complex movements are stroke patients. Braun et al. (2007) investigated the mental representation of a complex everyday activity, namely drinking from a cup in patients after stroke. Four out of 16 patients showed normal representation patterns. The results for the other twelve patients showed abnormal mental representation patterns of motor plans after stroke. The more severe the stroke, the more impaired seemed the mental representation to be.

These studies, in addition to the theories mentioned above, support the importance of cognition, namely the ability to anticipate the goal of an action, for motor control during observation of movements and in medical settings. In the following, an overview of the most important studies concerning behavioral experiments on object manipulations and the underlying cognitive aspects of motor control is given.

1.3 Behavioral evidence for anticipatory motor control during object manipulations

There is various behavioral evidence for the goal-directed nature of motor planning. For example, it has been shown that the means to grasp an object is typically selected in a way that allows to accomplish a comfortable posture at the end of the movement, i.e., that more distal goals guide the selection of proximal steps (Rosenbaum et al., 2001; Cohen & Rosenbaum, 2004). The preference of individuals to maximize comfortable hand postures at the end of object transportation tasks, rather than at the beginning has been named the *end-state comfort* effect (ESC; Rosenbaum et al., 1990). The ESC effect and related anticipatory grasp planning has been demonstrated in unimanual and bimanual tasks such as transport of a bar (Hughes et al., 2011, 2012; Seegelke et al., 2011; Fischman et al., 2003; Short & Cauraugh, 1999; Weigelt et al., 2006; Hughes & Franz, 2008), grasp and transport of a knob (Seegelke et al., 2012; Herbort & Butz, 2010), or the overturned glass task (Fischman & Kilborn, 2006; Fischman, Urbin, & Robinson, 2010). The effect has not only been studied in adults (e.g., Cohen & Rosenbaum, 2004; Fischman et al., 2003; Hughes & Franz, 2008; Rosenbaum, van Heugten, & Caldwell, 1996; Rosenbaum, Vaughan, Barnes, & Jorgensen, 1992), but also in children (e.g., Adalbjornsson, Fischman, & Rudisill, 2008; Manoel & Moreira, 2005).

Weigelt and Schack (2010) investigated the developmental pattern of the ESC effect in preschool children. Their results demonstrate a gradual increase of ESC planning from 3 to 5 years of age. Interestingly, exposure to the task increased the percentage of ESC planners in the youngest group (3 years). Stoeckel et al. (2011) examined the cognitive representation for certain grasp postures in children aged 7-, 8-, and 9-years of age. Nine-year olds were more likely to show ESC planning compared to 7- and 8-year olds. Stoeckel et al. (2011) were able to show that the sensitivity towards ESC planning was related to the mental representation of certain grasp postures. Based on the differences between the age groups, they hypothesize that the goal-directed and habitual system play a critical role in anticipatory motor planning. They add, that anticipatory motor planning is, at least partially, mediated by the cognitive representation structures in children's long-term memory. Knudsen et al. (2012) investigated the ESC effect in 3- to 8-year old children in two object manipulation tasks, a bar-transport task and an overturned-glass task. They confirmed the gradual increase of ESC planning for both tasks. The children were better at manipulating the glass compared to the bar. Knudsen et al. (2012) explained this with the familiarity of the task. Acquiring knowledge about action goal effects and their mental representations plays a significant role for the development of anticipatory action planning. This demonstrates the importance of the mental representation of the action goal effects for motor planning and execution as described by ideomotor theory.

Weigelt et al. (2009) combined the ESC and serial position effects in one study. Participants opened a series of 11 drawers, each containing an inverted cup. The cup was turned over to reveal a written letter. The cup was returned to the drawer in its original position, the drawer was closed, and the letters were recalled. Participants performed this ESC task of opening drawers of different heights while doing a serial or free recall memory task. Serial recall requires participants to recall information in the same order it was presented. Free recall allows participants to recall the information in any order. ESC was measured by whether the dominant hand was used and if participants used a "palms up" or "palms down" grip to open the drawer, which should vary according to drawer height. The ESC effect remained intact. The recency effect disappeared for serial and free recall. The disappearance of the recency effect lends support to the hypothesis that motor planning requires cognitive resources, in particular short-term memory. Consistent with these findings, subsequent studies showed that re-planning an intended action reduced letter recall performance, and that the planning stage of a grasping movement, but not execution, shared common cognitive resources with verbal working memory (Spiegel et al., 2012; 2013).

Several studies have shown anticipatory motor control processes using biomechanical factors. For example, when holding but before handling objects, the grip force rises prior to lifting, moving the object, or resisting to an anticipated external load (Johansson & Westling, 1984, 1988; Flanagan & Wing, 1993, 1995, 1997). Studies on prehensile movements have demonstrated that various kinetic and kinematic parameters are pre-adjusted according to target properties before handling the target (Biguer et al., 1982; Jakobson & Goodale, 1991; Carnahan & Mc Fadyen, 1996; Gentilucci et al., 1996). Ansuini et al. (2008) found that finger shaping, prior to object contact, changes with changing action goals, demonstrating that anticipation reflects not only the object, but what one intends to do with it (the action task). Anticipatory postural adjustments have also been measured before self-initiated or externally-triggered postural perturbations, by measuring accelerations of the trunk and the lower limb and modulations of ground reaction forces (Bouisset & Zattara, 1987; Wing et al., 1997; Jacobs & Horak, 2007).

A further example for anticipative motor behavior that demonstrates cognitive processes is a sequential effect called *hysteresis* (Rosenbaum & Jorgensen, 1992; Short & Cauraugh, 1997; Weigelt et al., 2009; Weiss & Wark, 2009; Schütz et al., 2011). In a study of Rosenbaum and Jorgensen (1992), participants had to place the end of a dowel against targets of different heights. The targets had to be reached in ascending or descending order. In ascending order, participants switched from an overhand grip (for the low targets) to an underhand grip (for the high targets) at higher locations than when they had to use the descending order - switching from underhand to overhand.

Our grasp choices are not only influenced by the goal of the action but by prior grasp choices as well. These prior choices can happen directly before the grasp, as in hysteresis, or can have established an effect over a longer period of time, as is the case for *habitual effects*.

The involvement of habitual effects for the selection of grasping movements has been suggested by various studies (Masson et al., 2011; Tucker & Ellis, 1998; Creem & Proffitt, 2001; Herbort & Butz, 2011), some of which will be summarized in the following paragraphs.

Tucker and Ellis (1998) used a stimulus-response paradigm with images of everyday objects as stimuli. They investigated wrist rotation responses to the shown objects, which required either clockwise or counterclockwise wrist rotations when they would be grasped. When the response was congruent with wrist rotation that reflected a functional grasp of the object, reaction times were lower as compared to when the response was incongruent with the wrist rotation reflecting a non-functional grasp. The results suggest that the perception of an object automatically potentiates components of an action that are habitually linked to the object. Masson et al. (2011) used pictures of handled objects like beer mugs to prime reaching for and grasping a bar. The stimuli showed the object either in an upright orientation or in a rotated (90°) orientation. The pictures primed the subsequent grasp, but only when the grasp fitted the object's proper function. This result suggests again that objects evoke actions that are habitually linked to them. This idea had already been addressed by Gibson (1979). Gibson (1979) developed a view of perception and action that focused on information that is available in the environment and, in the course, he defined the term *affordances*. "The affordances of the environment are what it offers the animal, what it provides or furnishes, either for good or ill" (Gibson, 1979; p. 127). Affordances are "equally a fact of the environment and a fact of behavior" (Gibson, 1979; p.129).

Herbort and Butz (2011) suggested an interaction of a habitual system, which associates stimuli with responses that were rewarding in the past, and a goal-directed system for grasp selection for everyday objects. In their Experiment 1, a cup had to be transported to another position. Trials either required a rotation of the cup during the transport phase or no rotation. Grasp selection depended on the goal of the movement sequence (rotation or transport). Participants used a thumb-up grasp more often for the transport than for the rotation task. This result is in accordance with the ESC effect, as participants seemed to take the goal of the rotation movement into account when grasping the cup. When doing the rotation task, participants were more likely to grasp the cup with a thumb down posture for trials on which the cup was presented inverted (180°) than when it was upright. The authors suggested that this was due to a habitual factor, as an upright cup is usually grasped with the thumb up. In their Experiment 3, six different vertically oriented objects had to be moved or rotated. According to the authors three of the objects afforded a thumb-up grasped if presented upright, but no specific grasp if presented in an inverted manner. The other three objects were usually not oriented vertically before they would be grasped and were not associated with a habitual grip for an upright orientation. Herbort and Butz (2011) reported that grasp selection was influenced by object orientation only when different habitual grasps were associated with different object orientations. This finding demonstrated the interplay of a goal-related and a habitual system for grasp selection. When no habitual grip was associated with the object grips that ensured a comfortable end posture were selected most of the time, suggesting that the goal of the movement was the driving factor for grasp selection. The habitual system came into play depending on object type and orientation, thus, when a habitual grip was associated with a specific orientation of the object (Herbort & Butz, 2011).

The aforementioned studies stress the importance of mental representations of action goal effects, which has been demonstrated for different kind of grasping movements. Prior action choices, on both a short-term and a long-term scale, influence action planning. The planning of actions towards action goals requires cognitive resources (Spiegel et al., 2012; 2013). Thus, we can assume that cognitive and motor processes are overlapping (for a more detailed account of behavioral research on motor control see, e.g., Rosenbaum, 2010). However, neither the temporal dynamics nor the neural basis of these processes have been investigated in detail, although this would advance our understanding of the link between motor control and cognition. Neurophysiological data about goal-related and habitual grasping is scarce. Especially the temporal processes of grasp planning and control are of interest to investigate the interactions of a goal-directed and a habitual system. Therefore, we shortly introduce different neurophysiological methods and research results in the next section, to expose the next reasonable steps in this research stream and which method should be used for it.

1.4 Neurophysiology of grasping

Several methods are used in the field of cognitive neurophysiology. The most common ones for human subjects are the analyses of naturally occurring lesions, hemodynamic measures (PET and fMRI), and electromagnetic measures (EEG and MEG). Each method has its advantages and disadvantages. The different methods can complement each other.

Analyzing medical cases with lesions after stroke or other brain damage was the only method to learn something about the cognitive functions in the human brain for a long time (Oeser, 2002) and lesion studies can still show which brain regions are indispensable for a specific function. The rise of neuroimaging technology made it possible to investigate the representation of cognitive functions in healthy subjects.

Positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) are both hemodynamic measures, which measure neural activity indirectly detecting metabolic changes (Huettel, Song, & McCarthy, 2004). These metabolic changes lead to an increase in the regional cerebral blood flow (rCBF). RCBF and neural activity are supposed to be coupled in the way that when a population of neurons in a specific region gets active, blood flow to that region increases as well (Logothetis et al., 2001). As subjects are exposed to a certain amount of radiation during PET experiments, each subject can only be tested on a limited number of conditions (Luck, 2005). This limitation doesn't hold for fMRI. Both, PET and fMRI, have a good spatial but a rather poor temporal resolution, and the costs per scan are still relatively high (Luck, 2005).

Electroencephalography (EEG) and magnetencephalography (MEG) are electromagnetic measures (Rugg & Coles, 1995; Regan, 1989). The EEG measures the summed electrical activity of the brain by recording voltage fluctuations (in microvolt) at the head surface, while the MEG records magnetic fields produced by the electrical activity of the brain. The recorded signals can be precisely timed in milliseconds providing information about when brain sources are activated, for how long, and in which order. Certain conditions are required in order to record brain signals at the scalp. A sizeable population of neurons needs to be synchronously active and needs to have a certain geometric configuration to be measured using EEG or MEG. Potentials from the neocortex are particularly suitable for recording. The spatial resolution of electromagnetic measures is relatively poor compared to hemodynamic measures (Luck, 2005) and they determine processes that occur below the cortex less sensitively. While EEG can be considered an inexpensive method, MEG is more expensive. In the following paragraphs research results related to action control obtained using the methods described above are summarized. First, more general research results concerning the neurophysiology of grasping are given, which were obtained from medical cases (section 1.4.1) and imaging studies (section 1.4.2). Then, in section 1.4.3, the focus is more specific on goal-directed manual actions.

1.4.1 Results from medical cases

A large part of our knowledge about the contribution of different brain areas to grasping and action control is derived from lesion studies and studies using imaging techniques. Medical cases with lesions in a specific brain area can demonstrate the importance of this brain area for grasping and action control. For example, generating actions based on conceptual knowledge about the overall goal of an action is selectively impaired in patients with ideational apraxia. "Ideational apraxia would arise when the motor programming area is destroyed by damage to the supramarginal gyrus" (Koski et al., 2002). The lesions of these patients lead to spatial and temporal errors in executing actions on the basis of a pre-specified goal, although the individual elements may be performed accurately in isolation (Luria, 1980). Another example are lesions of the primary motor cortex or corticospinal fibres, which disrupt grasping (Denny-Brown, 1950; Lassek, 1954; Lang & Schieber, 2004). Typically, synergistic movements of all fingers (power grip) remain intact, while independent finger movement in grasping is lost. A further example comes from the work of Binkofski et al. (1998). According to their lesion studies, the area responsible for grasping is the anterior intraparietal sulcus (AIP), contralateral to the impaired hand. AIP lesions led to deficits in grasping, while reaching remained relatively intact. Our final example here is optic ataxia. Optic ataxia is a disorder of visuomotor transformation, which is usually caused by posterior parietal lesions (Castiello, 2005). When reaching for an object, patients with optic ataxia show abnormally large finger grip apertures and no correlation between maximum grip aperture and object size, which is present in healthy people (Jeannerod, 1986). Patients with optic ataxia demonstrate deficits in visually guided grasping (Glover, 2003; Rossetti, 2003). We can learn from these medical cases that different parietal and frontal areas seem to play an important role for specific functions during reaching and grasping. The exact interplay of different brain areas required for motor control remains unclear though.

1.4.2 Results from imaging studies

Imaging studies that investigated the location of grasp-specific brain activity often used fMRI or PET. Activity in primary motor cortex (M1) has been reported for reach-to-grasp tasks (e.g., Grafton et al., 1996; Culham et al., 2003; Begliomini et al., 2007b). It has further been shown that multiple cortical areas beyond the primary motor cortex (M1) are involved in movement control (for a review see Filimon, 2010). These areas include the premotor cortex (Picard & Strick, 2001; Chouinard & Paus, 2006) and the posterior parietal cortex (PPC; Fogassi & Luppino, 2005; Culham et al., 2006). Even simple movements, like finger flexion with closed eyes, activates frontal and parietal areas in addition to primary sensorimotor areas (e.g. Filimon, 2008). Research by Thoenissen et al. (2002) suggests that frontal areas might be closer to movement execution than parietal areas. In their fMRI study, parietal regions responded during a delayed finger-flexing task regardless of the probability of later executing the movement, while precentral areas responded only when the cue predicted a go trial.

PET and fMRI studies have shown activation of a grasp-specific region within the AIP (Grafton et al., 1996; Binkofski et al., 1998; Culham et al., 2003; Frey et al., 2005; Begliomini et al., 2007b). For participants performing a grasp with the right hand, the focus of activation was located within the left hemisphere at the junction of the AIP with the postcentral sulcus (Castiello & Begliomini, 2008). FMRI activity in AIP increases when grasp precision increases (Begliomini et al., 2007b). This might be due to increased processing of grasp-relevant object features or to increased on-line control necessary for higher precision movements. Begliomini et al. (2007b) observed activity for precision grips but not for whole hand (power) grips in AIP, suggesting that this area is tuned to type of grasp, with a larger number of precision grips, rather than whole hand grips, being represented there. TMS studies further confirmed the importance of the AIP for reach-to-grasp actions (Glover et al., 2005; Tunik et al., 2005; Rice et al., 2006).

Ehrsson et al. (2000; 2001) used fMRI to compare brain activity for precision and power grips in relation to force production. They report higher activity in the contralateral primary sensorimotor cortex for power grips as compared to precision grips. Activity in the ventral PMC, rostral cingulate motor area and at several locations in the PPC and the PFC was stronger for precision than for power grips. While the precision grip task involved extensive activation in both hemispheres, power grip was associated predominantly with contralateral activity. It seems that primary motor cortex as well as premotor and parietal areas are important for control of fingertip forces during precision grip. Other fMRI studies have shown that the ventral premotor cortex (PMv) adapts to repeated exposure of a particular grasping axis, but not to a particular object (Kroliczak et al., 2008). It seems that PMv is more closely linked to the motor demands of an object than to an object per se.

"In humans, the contribution of the PMd [dorsal premotor cortex] to hand movements, the time course of its involvement, and its hemispheric dominance is essentially unknown" (Castiello & Begliomini, 2008, p. 164). However, Begliomini et al. (2007a) report bilateral PMd activity reflecting the control of visually guided hand-grasping actions. According to these authors, PMd might be of special importance for monitoring the configuration of the fingers during grasp planning and execution. Similarities between activity in M1 and PMd modulated by the congruence between grasp type and stimulus size (Begliomini et al., 2007a;

2007b), might suggest grasping control of the PMd through direct connections with M1 (Castiello & Begliomini, 2008).

In 2010, Filimon reviewed the involvement of parietal and frontal areas in reaching, grasping, and pointing. Premotor activity seemed to precede posterior parietal activity in some instances, depending on the task, parieto-frontal circuit, and effector used. Cortical representations for movements seemed to be highly distributed and overlapping. While she concluded that the roles of premotor and parietal areas for motor control remain unclear, "the available evidence supports a cortical organization along gradients of sensory (visual to somatosensory) and effector (eye to hand) preferences" (Filimon, 2010, p. 388). While the aforementioned studies further suggest parietal and frontal areas to be of crucial importance for reaching, grasping, and pointing, their precise neural contribution is not agreed upon.

1.4.3 Neural mechanisms for goal-directed manual actions

Just like behavioral studies, that demonstrate cognitive processes underlying voluntary motor control, neurophysiological findings suggest that voluntary actions are planned and executed in relation to the action goal. In a recent review Waszak et al. (2012) described that the medial frontal cortex seems to play a crucial role in linking actions to their predicted effects. Based on the reviewed data, the authors claim that the brain also seems to pre-activate the representation of the predicted action effect during action selection (Waszak et al., 2012). The following summary of relevant research results is structured by research method used, beginning with results from fMRI studies in section 1.4.3.1 and followed by results from ERP studies in section 1.4.3.2.

1.4.3.1 fMRI: parieto-frontal circuits

In an fMRI study, van Elk et al. (2012) investigated the planning processes of object-directed actions using a motor imagery task. Participants had to imagine how to execute actions with familiar and unfamiliar objects based on goal- or grip-related information. They observed slower action planning and increased activation in parietal areas for unfamiliar objects compared to familiar objects and explain this with the involvement of parietal areas in motor imagery, which might take more effort for unfamiliar actions. For familiar objects, they observed increased activation in anterior prefrontal cortex and suggest that there is a stronger goal-representation for actions with familiar objects compared to unfamiliar ones. Van Elk et al. (2012) suggest that semantic knowledge of actions is activated for actions planned in a goal-related fashion.

In another fMRI study, Zimmermann et al. (2011) investigated the influence of one's body posture on planning of goal-directed actions in a grasp selection task. Their data revealed that the intraparietal sulcus (IPS) and extrastriate body area (EBA) showed different responses based on the congruency between initial body posture and goal posture. They suggest that IPS maintains an internal state of one's body posture, as it was sensitive to congruency between body posture and movement plan. EBA seems to contain a representation of the goal posture, as it was sensitive to goal posture congruency.

A further fMRI study examined the spatial organization of movement preparation and the neural correlates of action planning (Majdandzic et al., 2007). Participants had to insert an object into one of two slots. The object consisted of one large and one small cube. The two slots were matching the objects in size. Participants were instructed on which slots to fill (the final goal) or on which part of the object to grasp (the immediate goal). Thus, they executed the same movement sequence but with an emphasis on a different part. Although the same movements were executed, planning processes were different (Majdandzic et al., 2007). Majdandzic et al. (2007) report differential activity in occipito-parietal and occipito-temporal cortex for the immediate goal, and differential preparatory activity along the superior frontal gyrus and in left inferior parietal cortex for the final goal. Different parieto-frontal circuits seem to be responsible for planning of the same action depending on which factors are emphasized. FMRI studies support the idea that a network of parietal and frontal areas is underlying goal-directed actions like grasping.

1.4.3.2 ERPs for goal-directed manual actions

There is neurophysiological evidence for different control mechanisms underlying goal-directed actions, which depend on the goal-posture. Most existing studies in this field focused on button presses, mental simulation, and action preparation intervals, but few studies investigated the planning and execution of overt complex actions by means of ERPs. For a long time, ERPs have rarely been used to investigate the cerebral activity of overtly executed movements due to fear of movement artifacts distorting the data. When EEG was used to study overt actions, analyses mostly focused on frequency bands. Golf putts (Babiloni et al., 2008; Reinecke et al., 2011) have been studied this way, for example. Studies using ERPs for grasping have mainly focused on mental simulation and preparation processes of the action (e.g, Bozzacchi et al., 2012a; 2012b). Only few studies investigated the overt execution of grasping movements (e.g., van Schie & Bekkering, 2007), although this enables the investigation of the temporal progress of cerebral activity and, thus, of the underlying cognitive processes. Important ERP components that take place before action execution include the P3 and LRP (see also below sections 1.5.1 and 1.5.2). While the underlying cognitive processes of the P3 are still not conclusively understood, it is thought to reflect processes involved in stimulus evaluation and categorization and is elicited in the process of decision making (Luck, 2005). The LRP is thought to reflect the preparation of motor activity on a certain side of the body.

Waszak et al. (2005) explored differences between self-regulated and instructed actions using EEG. Their participants either pressed one of two keys to produce the next stimulus or performed a choice response by pressing one of two keys in response to a stimulus. The behavioral results revealed a temporal attraction effect. That is, the execution of the action was shifted towards the anticipated action effect for self-regulated actions, while it was shifted towards the stimulus for instructed actions. This finding is in line with the aforementioned ideomotor framework. Waszak et al. (2005) also observed ERP differences in action preparation for the two tasks. P3 amplitudes were larger for the instructed action compared to the self-regulated action, for which the P3 complex was almost absent. Waszak et al. (2005) suggest this difference to reflect the formation of the link between stimulus processing and response. Within the same time window, they observed a stimulus-locked frontal lateralized readiness potential, which was only present for the instructed action. They interpret both components to reflect stimulus-driven processes. They also report a negativity for self-regulated actions compared to instructed actions during the preparatory phase of the action for response-locked ERPs over fronto-central scalp sites. Their results suggest that different cortical structures mediate the preparation and possibly execution of self-regulated and instructed actions.

Keller et al. (2006) extend the work of Waszak et al. (2005) by using more abstract stimuli and a larger inter-stimulus interval to rule out that stimulus-related processes contribute to the effects. Based on their results, they suggest that action-effect binding plays a role in planning self-regulated actions.

Fleming et al. (2009) used a different approach to investigate the ERPs of self-reglated and instructed action selection. Participants had to prepare a left or right key press, based on a stimulus showing the direction or based on a stimulus leaving participants a free choice which action to prepare. Following a short delay, a second stimulus instructed participants to either execute the prepared action or change the response to the other hand. The P300 was larger for instructed actions compared to free choice actions. For instructed actions, the change cue evoked a larger P300 than the no change cue. A trend towards the opposite pattern was found for the free choice actions. Fleming et al. (2009) showed differences in neural processes related to the updating of an action plan. They suggest that freely chosen actions may be more flexible and modifiable than instructed plans, which produce a rapid specific response.

Bozzacchi et al. (2012b) investigated the influence of the effect of an action on action preparation. Participants executed a virtual grasp, a key press, or a real grasp. The virtual grasp condition consisted of a key press that started a video clip of a hand reaching for and grasping a cup, the key press in the key press condition had no further consequence, and during the real grasp condition participants had to reach for and grasp a cup. Results showed similar motor preparation for virtual grasps and real grasps which seemed to differ from the key press condition. The authors observed a posterior parietal negativity for virtual and real grasps followed by activity over motor and pre-motor areas. They suggest that it was the final effect of the action and not the actions kinematics that influenced early preparation processes of the action. This is a connection of effect and action planning as predicted by ideomotor theory.

Kirsch and Hennighausen (2010) report distance specific ERPs accompanying goal-related hand movements. Their participants performed linear hand movements of different lengths from a start location to target locations. The amplitude of a negative component over sensorimotor areas preceding movement onset increased, with an increase of the distance from start to target location. During action execution, differences were observed at central and frontocentral electrodes. The authors refer to this component as N4 and suggest that it may be associated with an executive control mechanism. However, they also mention that this suggestion is in contrast to previous results which suggest that the N4 reflects primarily sensory feedback functions (e.g., Brunia, 1987). Furthermore, the N4 is often seen to reflect semantic processing (e.g., Kutas & Hillyard, 1980; Kutas & Federmeier, 2011).

A related ERP study concerning the neural mechanism for immediate and final action goals was done by van Schie and Bekkering (2007). They instructed a precision grasp and transport task which dictated either the grasp participants had to use (immediate goal) or the end position of the transport (final goal). Although participants executed the same overt movement in both conditions, van Schie and Bekkering observed different ERPs for immediate and final action goals. The immediate goal was accompanied by a parieto-occipital slow wave, while the final goal was accompanied by a slow wave over left frontal regions. The authors suggested that the enhanced activation found in posterior parts for the immediate goal indicate this area's involvement in the prehension of the object, while the enhanced activation found in anterior parts for the final goal might indicate frontal involvement in the planning and control of sequential behavior. This research shows that different neural mechanisms control the action depending on whether the emphasis is on the immediate or final goal of an action sequence, demonstrating the importance of goal-relatedness for action control on the neurophysiological level.

1.4.4 Summary

Evidence from medical cases and imaging studies suggest important roles for parietal and frontal areas in reaching, grasping, and pointing, while the exact contribution of premotor and parietal areas for motor control remain unclear. Voluntary actions seem to be planned and executed in relation to the representation of the predicted action effect. Different parieto-frontal circuits seem to be underlying goal-directed actions, depending on the goal-posture. ERP studies also indicate that the final action effect influences early preparation processes of an action, showing a connection between effect and action planning as predicted by ideomotor theory. Furthermore, this action effect binding seems to be more important for self-regulated than for instructed actions. Different cortical structures might mediate the preparation and possibly execution of self-regulated and instructed actions.

The existing neurophysiological data about goal-related and habitual grasping is still scarce. Information on the timing of processes and on the overt execution of movements are lacking. Most results derive from fMRI studies, which provide a high spatial resolution but a rather poor temporal resolution. Thus, temporal processes of grasp planning and control require other methods to be investigated accurately. Therefore, our aim is to contribute to the deeper understanding of grasp planning and control by investigating the cerebral activity underlying grasping movements with electromagnetic measures (EEG or MEG), which are known for their high temporal resolution.

The EEG allows for more experimental flexibility as it permits more movements by participants, while the MEG is stationary with the subject. Being interested in the investigation of overt movements we opt for EEG as the primary method.

As EEG recordings are susceptible to movement artifacts, most EEG studies focus on mental simulation of movements, preparation processes, or button presses in response to specific stimuli. Thus, results mainly demonstrate anticipation and evaluation processes. Recording during the execution of overt movements is still rare, but first studies show that it is possible to investigate the execution phase of manual action using EEG (e.g. Kirsch & Hennighausen, 2010; Van Schie & Bekkering, 2007). Lately, it has also been demonstrated that reliable ERPs can be analyzed during overt and non delayed speech where the movements originate in very close proximity to the brain (e.g., Koester & Schiller, 2008; Ganushchak et al., 2011; Costa et al., 2009).

When sensorimotor processing is studied using EEG, this is typically done by exploring the modulation of ERPs or the frequency-specific changes of the ongoing brain activity. Frequency analyses are usually analysed for longer lasting states, while ERPs are used to investigate short event-related changes. Analyses in the frequency domain represent which EEG frequencies occur during a given time window. While ERP analyses yield a high temporal resolution (in milliseconds), this is not automatically true for frequency analyses due to methodological constraints. Combined methods like event-related synchronization (ERS), event-related desynchronization (ERD) (Pfurtscheller & Lopes da Silva, 2005; Neuper et al., 2006) or Wavelets (Sauer, 2011) make use of time and frequency information but, therefore, loose accuracy in one of these domains. So we decided to focus our analyses on ERPs rather than frequencies.

A short introduction to ERP analyses and ERP components of potential interest (sections 1.5.1 for movement-related potentials and 1.5.2 for cognitive ERP components) follows to further introduce the method used for the experiments described in the following chapters (more detailed descriptions can be found elsewhere, e.g,. Coles & Rugg, 1995; Luck, 2005).

1.5 Measuring event-related potentials (ERPs)

Event-related potentials (ERPs), which are measured by means of EEG, are electrical brain potentials associated with specific sensory, perceptual, cognitive, or motor events (Luck, 2005). The event-related activity occurs in anticipation of or following a specific stimulus or event. Repetitions of the same stimulus will result in approximately similar responses by the brain. Time periods around these events are divided into equal epochs time-locked to the event. As the ERP is very small (microvolts) compared to the EEG waveform (up to about hundred microvolts), it is necessary to discriminate the signal (the ERP) from the background noise (the spontaneous EEG). The most common way of achieving an improved signal-to-noise-ratio is averaging. Averaging involves recording several EEG epochs, which are time-locked to the event. The values for each time-point of the epoch are then averaged. The spontaneous EEG, which has no temporal relation to the time-locking event, should vary randomly across epochs and will average to zero. The waveform after averaging should therefore represent specific brain activity for processing the time-locking event. After averaging, it is possible to evaluate the time-locked event-related potentials. For descriptive analyses the averaged epochs of the subjects are averaged again. The result is called grand-average. The grand-average can be understood as the electrocortical response of an average brain to a specific event.

Particular event-related potential curves can be observed before and after an event. The event, in this case, is the presentation of a stimulus or the response of a subject. Before a stimulus occurs processes such as expectancy or priming can be found, and after the stimulus there are perceptual and evaluative processes. Before a reaction, processes of action preparation are common; after the reaction, processes like the evaluation of a correct or incorrect response can be observed. If response related processes are examined, the response should also define the time window for the examination. This kind of ERP is called response-locked ERP. When the data is averaged to a stimulus presentation, the ERP is referred to as stimulus-locked ERP.

The ERP can be described as a voltage by time by location function. These voltage fluctuations (changes in the electric field) can be understood as a reflection of ongoing psychological processes. The voltage fluctuations have a waveform that consists of positive and negative deflections, which are related to different underlying components. There is a number of ways how to define and name ERP components. Most components are referred to by the letters N or P, which indicate the polarity of the component (positive or negative), and a number indicating the components latency in milliseconds (e.g., 200 or 300) or the ordinal position in the waveform (e.g., 1 or 2). For example, a positive deflection usually peaking 300 milliseconds after the stimulus is called P300. An ERP component can also be defined in terms of the information processing operation it is correlated with. That means, a component is defined in regard to the cognitive function the brain is thought to be performing (e.g., the error-related negativity (ERN), which is observed after errors are committed). Components are referred to as slow waves, if they last for several hundred milliseconds, sometimes even seconds (Rockstroh, Elbert, et al., 1989). Slow waves are usually associated with complex processes/ways of information processing and behavioral control, e.g., the Bereitschaftspotential or the CNV (see below, section 1.5.1). Luck (2005) gives the following definition of the term ERP component: "Scalp-recorded neural activity that is generated in a given neuroanatomical module when a specific computational operation is performed" (p. 59).

1.5.1 Movement-related ERP components of potential interest

Below, the most important movement-related ERP components are reviewed briefly. A sport or movement related example for the use of each component is given.

The Bereitschaftspotential (BP) or readiness potential (RP) was first described by Kornhuber and Deecke (1965). They described the development of a negative potential beginning some 800 ms before the initiation of a voluntary movement. The readiness potential tends to be maximal at electrodes over motor areas of the cortex and is usually described as a reflection of processes related to movement preparation and execution. Some components of the potentials are larger at electrodes contralateral to the responding limb. This lateralized portion of the readiness potential is called the lateralized readiness potential (LRP). Mann et al. (2011) used the BP to investigate the visuomotor mechanisms of expert motor performance. They recorded the BP while expert and non-expert golfers executed putts. Experts showed greater cortical activation in right-central regions compared with non-experts. The authors suggest that the experts allocate more resources to visual-spatial processing and fewer to conscious processing of the movement, linking the visual-spatial area of the cortex to movement preparation and performance.

The contingent-negative variation (CNV) was first described by Walter, Cooper, Aldridge, McCallum, and Winter (1964) as a negative wave between a warning stimulus and a target stimulus. It tends to be largest over central and frontal areas. The CNV is usually regarded as a reflection of motor and non-motor preparation processes. These processes might be related to expectancy, mental priming, association, or attention (for a review see Rohrbaugh & Gaillard, 1983). Frömer et al. (2012) used the CNV to investigate the aiming phase of throwing. Their participants performed simple button releases, unaimed throws, and aimed throws of two levels of difficulty in a virtual reality environment. CNV amplitude was larger for throwing conditions compared to button release and increased with task difficulty in the aimed throwing condition. The authors interpret the CNV amplitude to reflect the increasing motor programming demands for more difficult goal-directed actions.

The error-related negativity (ERN) was first described by Falkenstein et al. (1990), but was independently named by Gehring et al. (1993). The ERN is a negative component at frontal and central electrodes that occurs when participants make and realize an error in sensorimotor and similar kinds of tasks (Fabiani, Gratton, Federmeier, 2007). The ERN might reflect processes that either monitor responses or conflicts between intended and actual responses. Maidhof et al. (2009) investigated performance errors and action monitoring in a motor control task. In their study pianists played scales and patterns. ERPs for correct and incorrect performance were compared. Differences occurred already 100 milliseconds prior to the onset of a note, leading to the authors' conclusion that skilled pianists can detect movement errors prior to their execution. This finding might be generalized to skilled movement execution in general. The authors suggested that this mechanism relies on predictive control processes that compare the predicted outcome of an action with the action goal, which can be seen as neurophysiological support for action control by effect anticipation.

1.5.2 Cognitive ERP components (memory and language) of potential interest

The P300 (alternatively called P3, or P3b) was first described by Sutton, Braren, Zubin, and John (1965) over posterior parietal scalp locations. The P3 is typically elicited by task relevant oddball stimuli. It is one of the most often investigated ERP components, but it's underlying cognitive processes are still not conclusively understood. It seems to reflect processes involved in context updating, stimulus evaluation or categorization (Donchin & Coles, 1988). Examples for sports related research investigating the P300 include the work of Jin et al. (2011) and Taliep et al. (2008). Jin et al. (2011) compared the neural responses from professional badminton players and non-player controls when they watched video clips of badminton games and predicted a ball's landing position. The P300 amplitude was larger and the latency tended to be shorter for the players than for the controls. The authors interpreted the effect to reflect primed access and/or directing of attention to game-related memory representations in the players facilitating their online judgment of related actions. Taliep et al. (2008) investigated P300 differences in skilled and less-skilled cricket batsmen when they watched video footage of different deliveries from a bowler. The P300 latency was shorter for the skilled batsmen compared to the less-skilled batsmen. The authors suggest that skilled cricket batsmen have a superior perceptual decision-making ability compared with less-skilled cricket batsmen.

The N400 was first described by Kutas and Hillyard (1980). It is a negative going deflection, usually largest over central and parietal electrodes. The N400 is elicited by semantic deviations. It can be elicited by linguistic and also meaningful or potentially meaningful nonlinguistic stimuli, for example pictures, faces, environmental sounds, or smells (for a review see Kutas & Federmeier, 2011). Van Elk et al. (2008) investigated the use of semantic knowledge for action. Their participants prepared meaningful or meaningless actions with objects and had to make a semantic categorization response before executing the action. The N400 was larger for words incongruent to the action as compared to congruent words. No effects were found for meaningless actions. The authors suggest that preparation of meaningful actions with an object is accompanied by the activation of semantic information representing the usual action goal associated with the object.

It is not necessary to investigate a special component when doing research on ERPs. At a fundamental level, it is possible to investigate whether two experimental conditions yield different ERP responses. Such a comparison is not based on components but on the evaluation of the waveforms from the different conditions. Analyses can reveal significant effects between conditions within a specified time window. Assuming that brain activity measured by ERPs reflects psychological processes, a difference between conditions would indicate different psychological processes in those conditions (Fabiani, Gratton, & Federmeier, 2007).

1.6 The purpose of this thesis

This thesis aims at a better understanding of the neurophysiological correlates and cognitive components of motor and action control. For this purpose, we conducted three experiments: an object transport task, a bar transport task involving a 90° rotation of the bar, and a handle rotation task covering 180° rotations, emphasizing different movement aspects in each experiment. Using EEG, we investigated movement planning and execution processes for overt goal-related power grips.

ERP research on overt grasping has been done rarely because of the EEG's sensitivity to movement artifacts. As mentioned before in this chapter, some studies have already shown that ERPs are suitable for the investigation of overt movements. Thus, it can be assumed that ERPs are a suitable tool for the investigation of grasping movements. Therefore, an overall aim of our three experiments is to further establish ERPs as a research tool for the investigation of the cognitive processes underlying the overt execution of (manual) actions. Here, our focus is on the goal-relatedness of these actions.

1.6.1 From precision to power grips

To date, ERP research on overt grasping movements was limited to preparation intervals and precision grips (van Schie & Bekkering, 2007). Precision grips were investigated in a grasp and transportation task, in which visual cues emphasized either the grip (the initial goal) or the target location (the final goal). ERPs differed between initial and final goal-cued conditions, suggesting different means of operation dependent on goal-relatedness which is further discussed in chapter 2. Therefore, in experiment 1 (CHAPTER 2), we investigated the cerebral activity and its temporal organization during power grips executed with an emphasis on either the initial or final parts of movement sequences. If we observe the same neural activity pattern for power grips, as has been reported for precision grips, this result would suggest that power and precision grips are controlled by similar neural mechanisms. This result would also extend the notion that goal-directedness is an important mechanism underlying the planning and control of voluntary action to power grips (on the neurophysiological level).

1.6.2 Power grips and their goal effect

Voluntary actions are associated with different decision processes, including the decision whether to act, what action to perform, and when to perform it (Haggard, 2008). The what-decision is of special importance for goal-directed manual actions and action anticipation. Most neurophysiological studies, which tackled the what-decision of manual actions, focused on clinical populations or non-human-primates (Haggard, 2008). Studies using ERPs mainly focused on components that occur before action execution and simple movements like key presses (e.g. Shibasaki & Hallett, 2006). Research on overt complex actions in this area is lacking. To our knowledge, no study has yet investigated ERPs underlying the what-decision of the planning and execution of overt manual action. Therefore, the aim of CHAPTER 3 is to differentiate between cerebral activity for self-regulated and instructed actions during the overt execution of a goal related action. We adopt a bar-transport task, that is known to involve anticipative behavior (Rosenbaum et al., 1990). To manipulate the what-decisions included in the task, we instruct participants concerning grasp and target-location. Both are either free choice or specified by instruction. Thus, enabling us to investigate difference of neural mechanisms between self-regulated compared to instructed actions concerning the grasp and the goal. If we observe differential neural activity between free goal and specified goal conditions, this would support ideomotor theory as action preparation and execution processes would differ dependent on the action effect. If we observe different neural activity between free grasp and specified grasp conditions, this would suggest that action planning is primarily driven by stimulus features as cerebral activity would be influenced in temporal relation to the grasping action. If we observe no difference between specified- and free-grip conditions, this would suggest that the movement sequence was primarily driven by its goal effect as the initial grip would not exert a strong influence on the planning and execution processes.

1.6.3 Goal-directed actions and habituation

The question why people seem to prefer comfortable end state has not been answered yet. Two main explanations that have been suggested are better control or more precision at the end of the movement, or when this is needed (Rosenbaum et al., 2012) and a habitual system favoring movements that were rewarding in the past (Herbort & Butz, 2011). Although cognitive aspects demonstrated by the end-state comfort effect are frequently highlighted, neurophysiological studies for the overt execution of goal-related grasps are hard to find. Therefore, the aim of CHAPTER 4 is to investigate the neural mechanisms underlying the overt execution of goal-related actions with a focus on habitual vs non-habitual grasps. We created a handle rotation task, in which participants had to use thumb-toward (habitual) or thumb-away grips (non habitual) to rotate a handle to a given target position. If neural activity differs between habitual and non-habitual conditions time-locked to rotation start, this would indicate that different neurophysiological processing is needed to plan and execute a grasp in a habitual mode compared to a non-habitual mode. If neural activity differs between habitual and non-habitual conditions time-locked to movement end, this would suggest that different neurophysiological processing is needed to execute an action towards a goal in a habitual mode compared to a non-habitual mode.

1.7 Structure of the thesis

The present CHAPTER 1 gives a general introduction to the neurophysiology and cognitive components underlying motor and action control. The theoretical background, research methods, and related research results are introduced leading up to the purpose of this thesis. CHAPTER 2 describes a study about the neural mechanisms underlying the overt execution of goal-related power grips (see also section 1.6.1). CHAPTER 3 focuses on the what-decision in manual action. Therefore, ERPs for free choice vs specified overt goal-related grasping are investigated (section 1.6.2). The study described in CHAPTER 4 focuses on the investigation of habitual vs non-habitual manual actions (section 1.6.3). A general discussion follows in CHAPTER 5, in which the results from chapters 2, 3, and 4 are discussed in relation to the concepts and models introduced in the present chapter 1, before the whole thesis is summarized in CHAPTER 6. The final CHAPTER 7 serves as an appendix providing supplementary material about analyses and their results from the experiments described in the other chapters.

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2 EVENT-RELATED BRAIN POTENTIALS FOR GOAL-RELATED POWER GRIPS

Abstract

Recent research has shown that neurophysiological activation during action planning depends on the orientation to initial or final action goals for precision grips. However, the neural signature for a distinct class of grasping, power grips, is still unknown. The aim of the present study was to differentiate between cerebral activity, by means of event-related potentials (ERPs), and its temporal organization during power grips executed with an emphasis on either the initial or final parts of movement sequences. In a grasp and transportation task, visual cues emphasized either the grip (the immediate goal) or the target location (the final goal). ERPs differed between immediate and final goal-cued conditions, suggesting different means of operation dependent on goal-relatedness. Differences in mean amplitude occurred earlier for power grips than for recently reported precision grips time-locked to grasping over parieto-occipital areas. Time-locked to final object placement, differences occurred within a similar time window for power and precision grips over frontal areas. These results suggest that a parieto-frontal network of activation is of crucial importance for grasp planning and execution. Our results indicate that power grip preparation and execution for goal-related actions are controlled by similar neural mechanisms as have been observed during precision grips, but with a distinct temporal pattern.

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2.1 Introduction

The ability to control the movements of our hands is of utmost importance to our daily life. Controlling the hands enables us to perform a wide range of actions, like grasping objects of various shapes, manipulating items, or using tools, all of which involve action transformations. In the middle of the last century, Napier (1956) emphasized that the anatomical and biomechanical features of the human hand make it ideal for tool use; grasping can be performed with high precision, but also with strong force. Furthermore, our hands even give us the ability to communicate using gestures, sign language, or writing messages. Because of their clear importance for human action and interaction, manual movements and manual intelligence have become an important topic in cognitive robotics in recent years. Such complex manual movements require anticipatory control, which seems to be based on cognitive networks in long-term memory (Schack & Ritter, 2009). Only very few electroencephalographic (EEG) studies have investigated overt complex movements. Up to now, most event-related potential (ERP) studies have either focused on simple movements like button presses or on the preparation phase of a movement. Therefore, we decided to use a grasping task to study the neural mechanisms underlying overt complex human movement control using EEG.

Grasping is a complex and cognitively organized activity. Therefore, it is used in motor control research to investigate the cognitive architecture of goal-oriented action (Schack & Ritter, 2009). More than a century ago, Woodworth (1899) suggested that goal-directed actions consist of two phases. The first movement phase depends mostly on planning processes that take place before the action. The second movement phase involves discrete feedback-based action control (Elliott et al., 2001; Rosenbaum et al., 1990). The anticipatory character of motor planning processes have been demonstrated in a study by Rosenbaum et al. (1990), which showed that people chose different initial grips when reaching for the same rod depending on which end they planned to place on a disc on the table. Through this change in initial posture, participants in the study of Rosenbaum and colleagues avoided finishing their movements with awkward end postures (i.e., holding the rod with their thumb pointing down), even if this meant initially grasping the rod with an uncomfortable grip (i.e., an underhand grip). The authors concluded that participants anticipated their future hand postures, as the participants showed a preference for final comfort over initial comfort. This tendency to avoid awkward postures at the final position of a movement was termed the *end-state comfort effect* (Rosenbaum et al., 1990).

Interestingly, such planning processes during a reach and grasp task can be observed on a finer scale than the decision between overhand and underhand grasp. Schütz et al. (2011) tested participants in a sequential (predictable) and a randomized (unpredictable) perceptual-motor task, which offered a continuous range of posture solutions for each movement trial. Participants were asked to open a column of drawers in a sequential or randomized order, grasping each drawer on a protruding cylindrical knob. The end-state comfort effect was reproduced under both predictable and unpredictable conditions.

Looking in more detail into the modular organization of grasping, we will find further indicators for anticipation. Before we grasp an object, we reach for it. During this reach phase the fingers preshape in anticipation of the forthcoming grasp. The preshaping of the fingers is not only matched to the object that is grasped, but also to the task that has to be performed with the object (Ansuini et al., 2008). These kinematic effects suggest that anticipation is not only a sensorimotor function, but also a cognitive function reflecting the action goal (Ansuini et al., 2008). In a bar transport task, for example, that replicated the end-state comfort effect, Hughes et al. (2012b) observed that the formation of the grasp posture started at the beginning of the action. This finding implies that participants had selected a grasp prior to the movement which would satisfy end-state comfort. Moreover, when the action goal was changed shortly after movement onset, participants modified their reach-to-grasp movements to ensure a comfortable posture at the end of the movement, demonstrating the influence of action goals for movement planning and execution.

Different planning processes can, additionally, be observed in the kinematic parameters of power and precision grips (Castiello et al., 1992). Participants in the study of Castiello et al. (1992) had to grasp a small or large dowel and use either a precision grip or a whole hand power grip to do so. On 20 % of the trials the object size was unexpectedly changed during the reach phase. The results show shorter movement time and shorter deceleration time for the power grip compared to the precision grip. Maximum grip aperture occurred earlier for the precision grip than for the power grip and, according to Castiello et al. (1992), indicates the temporal coordination of grasp and transport components. They suggest that this temporal difference indicates an earlier anticipation of an object's characteristics in the case of higher precision demands. For trials in which the grip had to be altered during the action, they found changes during the deceleration phase of the reaching movement and, of course, during grasping. Faster movement and deceleration times for power grips indicate that planning processes for these movements must be faster or happen earlier in comparison to the planning processes for precision grips.

There is also neurophysiological evidence for a cognitive function of planning processes toward the action goal, in the form of activation of the motor system during action anticipation (Jeannerod, 2001). Further neurophysiological studies are likely to discover different variables that influence the spatial and, using EEG, particularly the temporal organization of movement planning and execution.

Following the results of behavioral studies, Majdandzic et al. (2007) used fMRI to examine the spatial neuroanatomical organization of movement preparation and the neural correlates of action planning. Their participants inserted an object into one of two slots. The object consisted of a large and a small cube. The two slots matched the objects in size. Participants were given a cue which determined the final goal (which slots to fill) or the immediate goal (which part of the object to grasp). Thus, participants always executed the same movement, but with an emphasis on either of two different parts of the movement sequence. The researchers observed differential preparatory activity along the superior frontal gyrus and in left inferior parietal cortex during the final goal trials, and differential activity in parieto-occipital and occipito-temporal cortex during the immediate goal trials. Their results also show different parieto-frontal circuits responsible for planning of the same action depending on which factors are emphasized. In addition to the previously mentioned study, Castiello and Begliomini (2008) report fMRI results that indicate a specific area to be tuned to the type of grasp, namely the anterior intra parietal sulcus. Castiello and Begliomini (2008) further suggest that a larger number of precision grip configurations, rather than whole hand grip configurations, might be represented here. Taken together, the aforementioned studies demonstrate the importance of goals for motor control. They suggest that the goals of an action are more crucial for motor planning than the trajectory of the movement itself.

In accordance with the above-mentioned fMRI studies, Filimon (2010) found the intra parietal sulcus (IPS) to play an important role for the control of grasping within the distributed parieto-frontal network. Within this network premotor activity seems to precede posterior parietal activity in some instances, depending on the task, parieto-frontal circuit, and effector used. However, the individual contributions of premotor and parietal areas remain unclear. In 2012, Bozzacchi et al. (2012a) used EEG to investigate temporal aspects of action planning, and they reported some controversial findings. They based their study on the assumption of a parieto-frontal network and recorded pre-movement event-related potentials, more specifically the Bereitschaftspotential (BP). The BP can be observed prior to voluntary movement and is considered to be a manifestation of the preparation for action (Kornhuber & Deecke, 1965). One main interest of Bozzacchi et al.'s study was the temporal organization of motor preparation for grasping. Participants performed three different actions: reaching for a teacup, grasping a teacup, and attempting to grasp a teacup while their fingers were constrained by a band, making grasping impossible. Bozzacchi et al. (2012a) observed activity over parietal areas well before action onset for the goal-oriented action of grasping an object, but not for reaching or impossible grasping. They found that activity for grasping preparation started earlier and was more widespread and complex than was previously described in the literature, as reviewed by Shibasaki and Hallett (2006). Regarding the temporal relation of parietal and frontal activity, Bozzacchi et al. (2012a) reported that the earliest parietal activity was followed by frontal activity. They conclude that action preparation is affected in an early phase by the meaning of an action as well as by the type of action to be performed.

In a different EEG experiment, Bozzacchi et al. (2012b) observed similar motor preparation processes for real and virtual grasps (the virtual grasp being a key press, which started a video showing a grasping action) over posterior parietal areas. From this study they conclude that the final action effect, and not the movement kinematics, influenced the early preparation phase. The results provide further support for the suggestion that parietal areas are of crucial importance for grasp planning and that they provide information for grasp preparation. The temporal organization of the neurophysiological correlates underlying grasping and its preparation remains controversial (Filimon, 2010) . As far as we know, only few ERP studies have focused on the temporal organization of overt dynamic grasping movements.

Gratton et al. (1988) examined the mechanisms of pre- and poststimulus response activation in a choice reaction time paradigm that required an overt movement, namely squeezing a zero-displacement dynamometer. Motor potentials following stimulus presentation suggested that partial analyses of stimulus information could activate responses. Gratton et al. (1988) further observed that, at the time of the EMG response, the level of response activation was constant for trials with different response latencies. This study exemplifies that it is possible to investigate the temporal organization of response selection using overt grasping movements.

Van Schie and Bekkering (2007) tried to "clarify the individual contributions of the different parts of the motor system that have been implied to underlie goal representations in action control" (p. 184). They instructed a grasp and transport task which dictated either the grasp participants had to use (immediate goal) or the end position of the transport (final goal). Although participants executed the same overt movement in both conditions, Van Schie and Bekkering observed different ERPs for immediate and final action goals. The immediate goal was accompanied by a parieto-occipital slow wave, while the final goal was accompanied by a slow wave over left frontal regions. The authors suggested that the enhanced activation found in posterior parts for the immediate goal indicates this area's involvement in the prehension of the object. This interpretation is supported by findings of Van Elk et al. (2012), who observed enhanced parietal activation for the observation of grip errors and suggested that it reflects a representation of hand-object interaction. The enhanced activation Van Schie and Bekkering found in anterior parts for the final goal might indicate frontal involvement in the planning and control of sequential behavior (Van Schie & Bekkering, 2007).

In sum, a parieto-frontal network underlying grasping has been shown in several studies. While premotor activity seems to precede posterior parietal activity in some instances (Filimon, 2010), Bozzacchi et al. (2012a) report in their experiment that the earliest parietal activity was followed by frontal activity. Thus, the temporal organization of the neural mechanisms underlying grasping and its preparation remains unclear. The importance of goals for action planning has been shown in behavioral and neurophysiological research. Being able to achieve the goal of an action or performing the same action with an emphasis on either an initial or a final goal all show differences in their respective neurophysiological recordings. These effects suggest different planning processes depending on the specific goals of the action.

Most of these studies addressed neurophysiological activations in precision grasps. In manual action research, the differentiation between power and precision grasps has become increasingly important in the last 20 years for human motor control and cognitive robotics (Schack & Ritter, 2009). Power grasps differ in kinematics and cognitive organization from precision grasps. To our knowledge, no previous study has investigated the temporal organization of the brain processes involved in goal-related actions executed with a power grip. Therefore, the aim of the present study is to differentiate cerebral activity and its temporal organization underlying power grips executed with an emphasis on different parts of the action.

In the present study, participants executed a grasp and transportation task with a specified or unspecified power grip. The specified grip condition focused participants' attention on the initial goal of grasping, while the unspecified grip condition focused their attention toward the final goal of the transport movement. In this regard, our study is similar to the study of Van Schie and Bekkering (2007). Our specified grip condition is comparable to Van Schie and Bekkering's immediate goal-cued condition, as the participant is given instructions on how to grasp before grasping the cylinder and placing it at the target position. The unspecified grip condition is comparable to their final goal-cued condition, as the participant is given the final location and orientation of the cylinder but no further instruction on how to grasp it. We will use the terms *immediate* and *final goal* hereafter to accentuate the importance of goal-relatedness in our task.

Our hypotheses for the behavioral data are based on the results of Van Schie and Bekkering (2007). Reaction times reflect planning processes before the movement onset (Botwinick & Thompson, 1966; Elliott et al., 2010) and we expect final goal-cued trials to require shorter planning processes compared to immediate goal-cued trials due to the greater congruence with everyday action demands (Rosenbaum &, Jorgensen, 1992; Van Schie & Bekkering, 2007). During reach time, both movement phases of the multiple-process model of limb control (Elliott et al., 2010), which builds on the two-component model of Woodworth (1899), overlap. The first phase, which requires planning processes taking place before the action and contains an early corrective component, might be extended for the immediate goal-cued condition compared to the final goal-cued condition due to higher planning demands. As transport times are based on feedback-based control processes and the same movement has to be executed in both conditions, we expect no transport time differences between conditions. We predict that reaction times will be faster for the final-cued condition than for the immediate-cued condition. Reach times might be faster for the final-cued condition in comparison to the immediate-cued condition. We expect no difference for transport times between both cueing conditions.

Given reports of activity in parieto-occipital regions for grasping, and in left frontal regions for reaching the goal of a transport movement (Van Schie & Bekkering, 2007), we focus specifically on these regions. If it is the case that precision and power grips are processed similarly, we expect to find similar neural mechanisms as those reported by Van Schie and Bekkering (2007), which might vary as described below. More specifically, we expect a cueing effect over the parieto-occipital area time-locked to grasping, which is the immediate goal. The activity over parieto-occipital areas for the immediate-cued condition is expected to be more negative overall than the activity for the final-cued condition. Exact time windows for the effects might differ, as the temporal organization of power grips might occur faster in comparison to precision grips. The duration of the deceleration phase of grasping increases with precision requirements (Marteniuk et al., 1987; Castiello et al., 1992). Further, we expect a cueing effect over frontal areas time-locked to movement end, which is the final goal. The activity over frontal areas for the immediate-cued condition is expected to be more positive overall than the activity for the final-cued condition. Van Schie and Bekkering (2007) report a significant effect over left and non-significant effect over right anterior prefrontal regions. It has been shown in the past that right-handed participants show larger contralateral activity regardless of the hand used, while left-handed participants show larger contralateral activity only for responses with the left hand (Kutas & Donchin, 1974). To avoid laterality effects due to differences in handedness, we exclude left-handed participants in this study and counter balanced the side of the executing hand within subjects. Consequently, we expect bilateral ERP effects.

The design of our study allows us to compare cerebral activity for similar movements, that were planned in a different way. The action was planned either with a relative emphasis on selecting a grip (the immediate goal) or with a relative emphasis on selecting a target state (the final goal). Based on the results of Van Schie and Bekkering (2007), we predict that the neural processes for action execution, measured by ERPs, will differ between immediate goal-cued and final goal-cued trials. We predict more negative activity for immediate goal-cued trials than for final goal-cued trials over parietal electrodes in the time window from -300 ms to 0 ms time-locked to the immediate goal. As power grips might be processed faster or earlier than precision grips, the predicted negativity might occur earlier as well. Furthermore, we predict more positive activity for immediate goal-cued trials than for final goal-cued trials over frontal electrodes in the time window from -1100 to 0 ms time-locked to the final goal.

2.2 Materials and Methods

2.2.1 Participants

Eighteen healthy volunteers (mean age 24.39 years; SD 4.06; 13 females) with no known neurological impairments and normal or corrected-to-normal vision participated in the study. All eighteen participants were right-handed, which was evaluated with the use of the Edinburgh Handedness Inventory (mean handedness score: 98,2) (Oldfield, 1971). All participants were compensated with course credit or money. The experimental procedure and written consent form for this study were approved by the ethics committee at Bielefeld University, and adhered to the ethical standards of the sixth revision of the Declaration of Helsinki. All participants gave their informed written consent to participate in the study.

2.2.2 Design and setup

Participants executed a grasp and transport task under two different conditions. In one condition the action was cued with an emphasis on the immediate goal, and in the other condition the same action was cued with an emphasis on the final goal.

Participants were required to grasp an object with a power grip and transport it to a specified goal location. The object was a PVC cylinder with a blue stripe at one end and a yellow stripe at the other end (each about 1 cm in width). The cylinder was positioned on one of three different start/target locations which were aligned next to each other; one on the left, one in the center, and one on the right (see Figure 2.1). In the center position, the blue mark was always on the bottom side and the yellow mark was always on top.

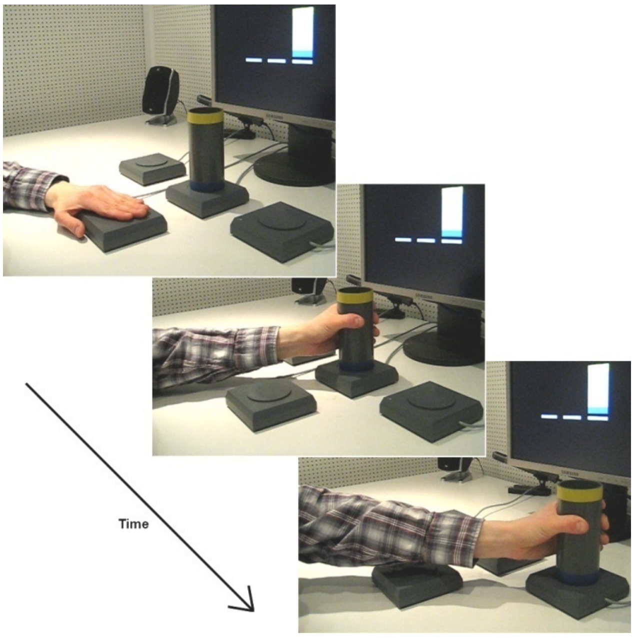

Figure 2.1: Illustration of the experimental setup. The lateral target locations were aligned shoulder width apart. Both of them could be reached comfortably with an extended arm. The center location and start button were placed directly in the middle in front of the participant. The experiment started with the cylinder on the central location. (TOP LEFT) The participant presses the start button, while the angled arm is resting on the table. A picture stimulus appears on the video monitor. (CENTER) The participant grasps the cylinder. (BOTTOM RIGHT) The participant places down the cylinder on the target location.

In each trial, a picture stimulus was presented showing the cylinder in its final location and orientation, which was indicated by the colored marks. The first trial always moved from the center position to either the left or right positions. The next trial was from the lateral location back to the center, bringing the cylinder back to its standard starting position. Only trials from the center to one of the lateral locations entered the analyses.

The cylinder either had to be transported in an upright orientation or it had to be rotated as indicated by the colored marks. At the starting position, the blue mark was at the bottom and the yellow mark was on top. Thus, when the picture stimulus showed the blue mark at the bottom and the yellow mark on top at the final location, the cylinder had to be transported in an upright fashion. Conversely, when the picture stimulus showed the yellow mark at the bottom and the blue mark on top at the final location, the cylinder had to be rotated during transportation. Only trials with an upright orientation of the cylinder during transportation entered the analyses. The other trials served as filler trials, so that participants had to execute different actions and plan their grip anew on every single trial.

Participants performed the task in separated blocks under varying conditions, that is, with different kinds of cues emphasizing different aspects of the action. The first block consisted of picture stimuli showing both colored marks on every trial. Participants grasped the cylinder with a power grip. It was their free decision to grasp with the base of their thumb facing toward the blue or the yellow mark and bring the cylinder to its final location. This cue condition emphasized the final goal. The second block consisted of picture stimuli showing only one of the colored marks. Participants had to grasp the cylinder with the base of their thumb toward the presented mark and bring the cylinder to its final location. This cue condition emphasized the immediate goal. Only trials with the base of the thumb facing upwards in the immediate goal condition entered the analyses. We excluded the trials with the thumb facing down to ensure comparability of the executed movements, because we expected participants to very rarely use this rather uncomfortable grip in the final goal condition. Thus, participants performed the same movement in both blocks, but they were either able to choose the grip themselves or it was pre-specified. The emphasis was either on the immediate goal or on the final goal.

2.2.3 Procedure

Following electrode preparation, participants were seated comfortably in front of a table in an electrically shielded cabin. Participants received written instruction on the upcoming task. They were given information on how to grasp the cylinder and were instructed to maintain stable posture and not to blink during trials. All questions they had concerning the instructions were answered.

The setup was calibrated to each participant's size to prevent expansive movements. The lateral locations were aligned shoulder width apart in front of the participants, such that they could reach both of them comfortably with an extended arm. The center location was positioned equidistant to the two lateral locations. The start button was positioned in front of the central location, such that it could be reached with the hand comfortably while the angled arm was resting on the table. Participants were instructed to relax and not to tense up during the action. Picture stimuli were presented on a video monitor located behind the start/target locations. Before the experiment started, participants performed short blocks of test trials to get acquainted to the task. These test blocks were also used to observe the EEG for obvious artifacts and were repeated until participants executed the task correctly in a relaxed state.

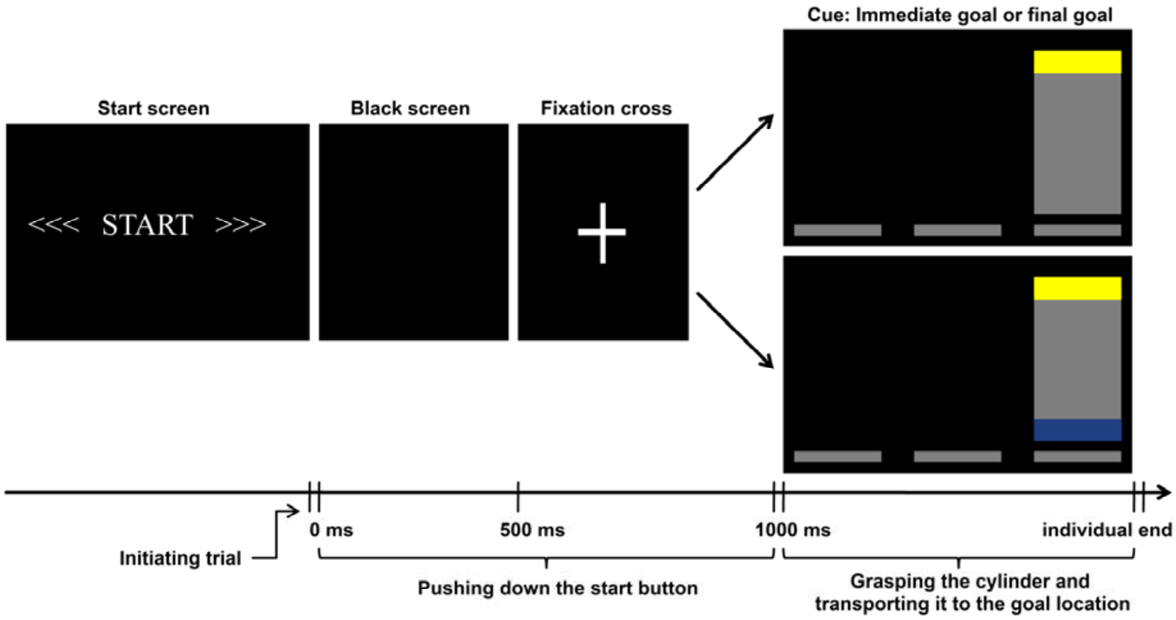

Figure 2.2: Stimulus sequence for one trial. Time is shown in milliseconds. At the beginning of each trial, the start screen required participants to push the start button. This was followed by a black screen, a fixation cross, and a cue. The cue showed participants to which goal location they had to move the cylinder (only transport to the right is shown). The cue could either emphasize the immediate goal (TOP), or the final goal (BOTTOM), or be a filler trial (not shown). In the immediate goal-cued condition participants had to grasp the cylinder with the base of their thumb towards the color mark shown and transport it to the goal location. In the final goal-cued condition participants had to transport the cylinder to the goal location, the grip was not specified.

Each trial started when participants pressed the start button. First, a black screen was shown for 500 ms, followed by a fixation cross for 500 ms. Next, a picture stimulus was shown indicating the final orientation and location of the object. The stimulus remained on the screen until the end of the trial. Participants then transported the cylinder to the target position (see Figure 2.2). The timing of all button actions (start, lift off, placing) were registered. Participants repeated each action 40 times (20 with their left hand, 20 with their right hand) for each cueing condition. The stimulus presentation was controlled by Presentation® software (version: 14.1, www.neuro-bs.com).

2.2.4 Behavioral and electroencephalographic recordings

Behavioral recordings included the time points of lifting the hand off the start button, lifting the cylinder, and placing the cylinder down again. Micro switches were used to detect the exact moment they occurred. These events were recorded on the PC which was presenting the stimuli, as well as on the PC which was recording the EEG. Participants' manual behavior was recorded with a video camera for later offline analysis.

EEG was recorded by a 64 channel amplifier (ANT). A WaveGuard EEG cap (ANT) with sixty-four Ag/AgCl electrodes was used. The electrodes of the cap were arranged according to the international 10-10 system (based on the 10-20 system) (Oostenveld & Praamstra, 2001). In order to detect ocular artifacts, EOG was recorded using four electrodes placed above and below the right eye and lateral to both eyes. During recording the data were average-referenced. The EEG was band-pass filtered (DC-138 Hz) and digitized at 512 Hz. The impedance of all electrodes was less than 5 kΩ.

2.2.5 Data analysis

Video recordings were studied offline for performance errors. A trial was rated as containing an error when the participant used the wrong grip, placed the cylinder on the wrong target, changed the grip during the approach or execution phase of the movement, or dropped the cylinder. Trials with performance errors were excluded from the analyses.

Behavioral analyses for reaction times (time from stimulus presentation to lifting of the hand), reach times (time from lifting the hand to lifting the object), and transport time (time from lifting the object to movement end) were each done separately. Averaged reaction, reach, and transport times were each subjected to a paired t-test to determine the influence of the cue-type (immediate goal-cued, final goal-cued).

Electrophysiological data were band-pass filtered offline from 0.1 to 30 Hz and re-referenced to the average mastoid electrodes. Response-locked analysis to grasping included the time interval from -1500-1000 ms. That means, epochs started 1500 ms before lifting the cylinder from the start position and ended 1000 ms after lifting. Response-locked analysis to movement end included the time interval from -2100-100 ms. That means, epochs started 2100 ms before placing the cylinder down at the target position and ended 100 ms after placing it down. Baseline correction was performed on the first 100 ms of each interval. Ocular artifacts were corrected using the correction procedure of Gratton et al. (1983). Artifact detection was done using a peak-to-peak moving window approach. Epochs containing peak-to-peak amplitudes above the threshold of ±50 µV within a 200 ms window were rejected. This window was moved over the whole epoch in 50 ms steps. Time epochs were visually double-checked for artifacts that would have been missed by the detection algorithm. 20 % of the trials time-locked to grasping in the immediate goal-cued condition and 23 % in the final goal-cued condition were rejected due to artifacts. 15 % of the trials time-locked to movement end in the immediate goal-cued and 17 % in the final goal-cued condition were rejected due to artifacts.

The influence of overt movements on EEG recordings is not fully understood yet. However, ERPs have been analyzed successfully and repeatedly in recent studies (Koester & Schiller, 2008; Ganushchak et al., 2011; Kirsch et al., 2010) which suggests that reliable ERPs can be obtained during overt movements. Importantly, the design of the present study compares conditions in which comparable movements are generated. This means that if there were artifacts still present in the data, these would be the same for all conditions and the reported differences between conditions are highly unlikely to be due to muscle artifacts. Furthermore, the (arm) movements required in our experimental task were comparable to the movements in Van Schie and Bekkering's study which also supports the expectation of reliable ERP effects for our grasp and transport task.

Mean amplitude analysis of the electrophysiological data included the factors *Cue-type* (immediate goal-cued, final goal-cued), *Front-Back* (anterior, central, posterior) and *Left-Right* (left, middle, right). The ERP was averaged separately for every participant and experimental condition. For the assessment of effects of scalp distribution, we differentiated between nine regions of interest (anterior-left (AL): AF7, F7, F5, F3; anterior-middle (AM): F1, Fz, F2; anterior-right (AR): AF8, F8, F6, F4; central-left (CL): C5, C3, CP5, CP3; central-middle (CM): FCz, Cz, CPz; central-right (CR): C6, C4, CP6, CP4; posterior-left (PL): PO7, PO5, PO3, O1; posterior-middle (PM): Pz, POz, Oz; posterior-right (PR): PO8, PO6, PO4, O2). The Greenhouse-Geisser correction was applied when evaluating effects with more than one degree of freedom (reporting corrected p-values and original degrees of freedom). Note that the EEG data were averaged for the left and right hand responses to avoid handedness effects. Hence, further observed lateral activity should not be evoked by handedness.

We analyzed mean amplitudes of the -300-0 ms time window time-locked to grasping and mean amplitudes of the -1100-0 ms time window time-locked to movement end. In line with the assumption that power grip preparation is faster than precision grip preparation, we also explored the -900 to -500 ms time window time-locked to grasping based on visual inspection.

2.3 Results

Participants executed the task correctly in 96 % of trials in the immediate goal-cued condition, and 97% in the final goal-cued condition - the remaining 4% and 3% of trials, respectively, were rejected. We performed a t-test on the arcsine transformed proportions of correct trials. It revealed no significant difference between the immediate goal-cued and final goal-cued conditions, $t(17) = -0.3$, $p = 0.77$.

In the immediate goal-cued condition, 100 % of the correct trials were executed holding the cylinder with the thumb up. In the final goal-cued condition, 99.6 % of the correct trials were executed holding the cylinder with the thumb up.

2.3.1 Behavior

We conducted three paired-samples t-tests to compare each of the reaction times, reach times, and transport times in the immediate goal-cued and final goal-cued conditions.

Reaction times were faster for final goal-cued trials (422 ms, SD = 148 ms) compared to immediate goal-cued trials (551 ms, SD = 203 ms, $t(17) = 4.21$, $p < 0.05$)(see Figure 2.3). According to the multiple-process model of limb control (Elliott et al., 2010), the reaction time can be seen as planning processes happening before movement onset. Thus, the immediate goal-cued condition seems to demand more time to plan the desired action.

Reach times were faster for final goal-cued trials (643 ms, SD = 157 ms) compared to immediate goal-cued trials (767 ms, SD = 198, $t(17) = 4.44$, $p < 0.05$). Reach time includes both phases of goal-directed aiming as suggested by Elliott et al. (2010). That is, an initial impulse phase containing a corrective component followed by a current control phase. A temporal extension of this phase might point to a longer initial impulse phase, suggesting a more complicated motor plan to be executed; similarly, it could point to a longer current control phase, suggesting online control processes to be more demanding. As the same object has to be grasped and transported in both cueing conditions in our experiment, the online control phase should be of similar difficulty in both conditions. Therefore, this reach time difference suggests that the motor planning processes and possible early corrections of the movement for the immediate goal-cued condition are more complicated than for the final goal-cued condition.

Transport times were faster for final goal-cued trials (602 ms, SD = 150 ms) compared to immediate goal-cued trials (658 ms, SD = 184 ms, t(17) = 2.35, p < 0.05). The second phase of the multiple-process model of limb control (Elliott et al., 2010) describes the online control of the movement. This suggests that the transport time might demand more control processes in the immediate goal-cued condition.

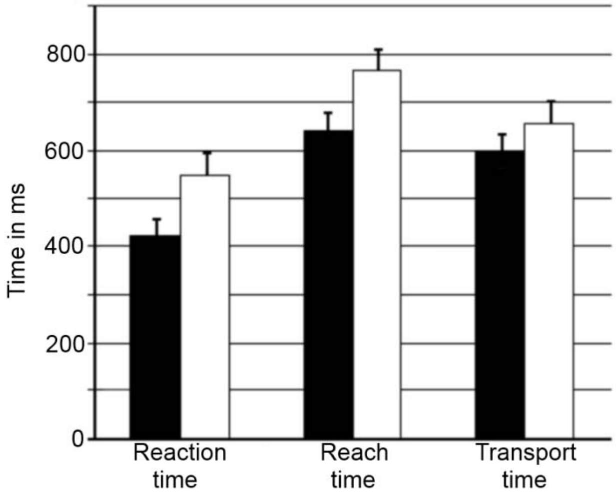

Figure 2.3: Timing of behavior. Average reaction time, reach time, and transportation time for the final goal-cued condition (black) and the immediate goal-cued condition (grey). The error bars represent standard errors.

In sum, the duration of the whole action sequence was significantly shorter for final goal-cued trials (1667 ms, SD = 329 ms) compared to immediate goal cued trials (1976 ms, SD = 404 ms, t(17) = 4.79, p < 0.05).

2.3.2 Electrophysiology

We conducted an ANOVA time-locked to grasping, which is the moment of lifting the cylinder off of the start position, with the factors Cue-type (immediate goal-cued, final goal-cued), Front-Back (anterior, central, posterior), and Left-Right (left, middle, right). We applied the Greenhouse-Geisser correction when evaluating effects with more than one degree of freedom (reporting corrected p-values and original degrees of freedom).

The ANOVA for -300-0 ms revealed a significant 3-way interaction for Cue-type, Front-Back, and Left-Right, $F(4, 68) = 4.51$, $p < 0.05$. The 3-way interaction means that the ERP amplitude differences between the immediate and the final goal condition is different in magnitude for the various combinations of the factors Front-Back and Left-Right. The significant interaction permits the separate comparisons of the immediate and the final goal conditions in the various regions-of-interest (ROI). We performed a t-test for every ROI to determine if there was a significant difference based on Cue-type and in which ROI this difference was present. A significant positivity for the immediate goal-cued condition compared to the final goal-cued condition was present in the AR-ROI, $t(17) = 2.71$, $p < 0.05$. The scalp distribution of the effect in this time window is unexpected and needs to be confirmed by further research. No significant effects were found for the remaining ROIs.

In additional analyses, in line with the assumption that power grip preparation is faster than precision grip preparation, the ANOVA for -900 to -500 ms revealed a significant 3-way interaction for Cue-type, Front-Back, and Left-Right, $F(4, 68) = 3.08$, $p < 0.05$. Following the 3-way interaction, we performed a t-test for every ROI to determine if there was a significant difference based on Cue-type and in which ROI this difference was present. A significant negativity for the immediate goal-cued condition compared to the final goal-cued condition was present in the PM-ROI, $t(17) = -2.14$, $p < 0.05$. The negativity was not significant for the PR-ROI, $t(17) = -1.97$, $p = 0.065$. A positivity for the immediate goal-cued condition compared to the final goal-cued condition was not significant in the AR-ROI, $t(17) = 1.91$, $p = 0.074$. No significant effects were found for the remaining ROIs.

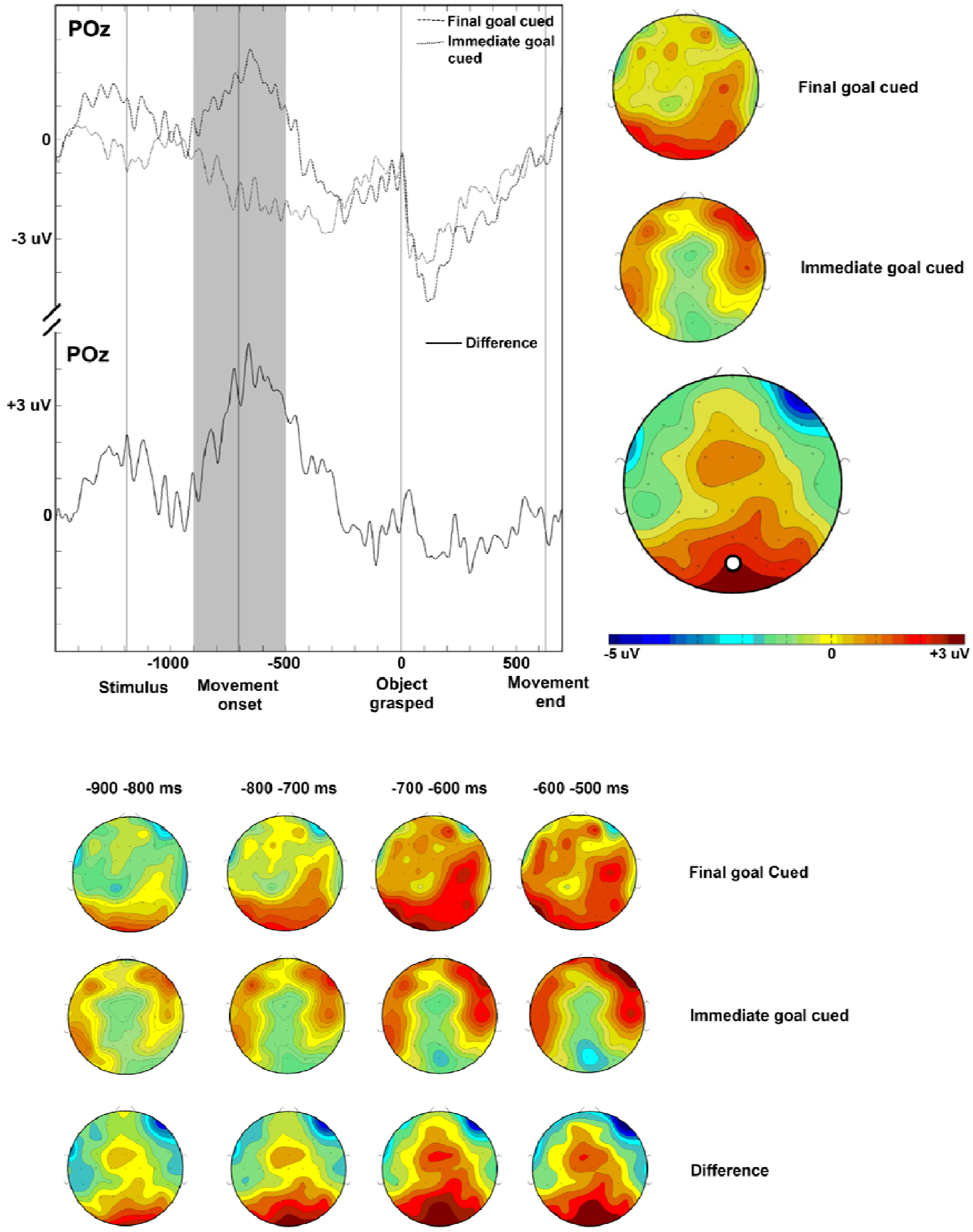

Figure 2.4: Slow wave brain potentials time-locked to grasping of the object. Time is shown in milliseconds. (TOP LEFT) Event-related slow wave potentials recorded at the medial parieto-occipital electrode POz, time-locked to grasping the object, for the final goal cueing condition (dashed), the immediate goal cueing condition (dotted), and the difference between the two cueing conditions (solid). The labels 'Stimulus', 'Movement onset', and 'Movement end' mark the *average* time points of these events. (TOP RIGHT) Topography of slow waves recorded in the -900 ms to -500 ms time interval before grasping (indicated by the grey selection), in the final goal cueing condition, the immediate goal cueing condition, and the difference between the two cueing conditions. The location of electrode POz on the scalp is illustrated by a white marker. (BOTTOM) Topography of slow waves recorded in the -900 to -500 ms time interval before grasping displayed in consecutive 100 ms intervals, in the final goal-cued condition, the immediate goal-cued condition, and the difference between the two cueing conditions.

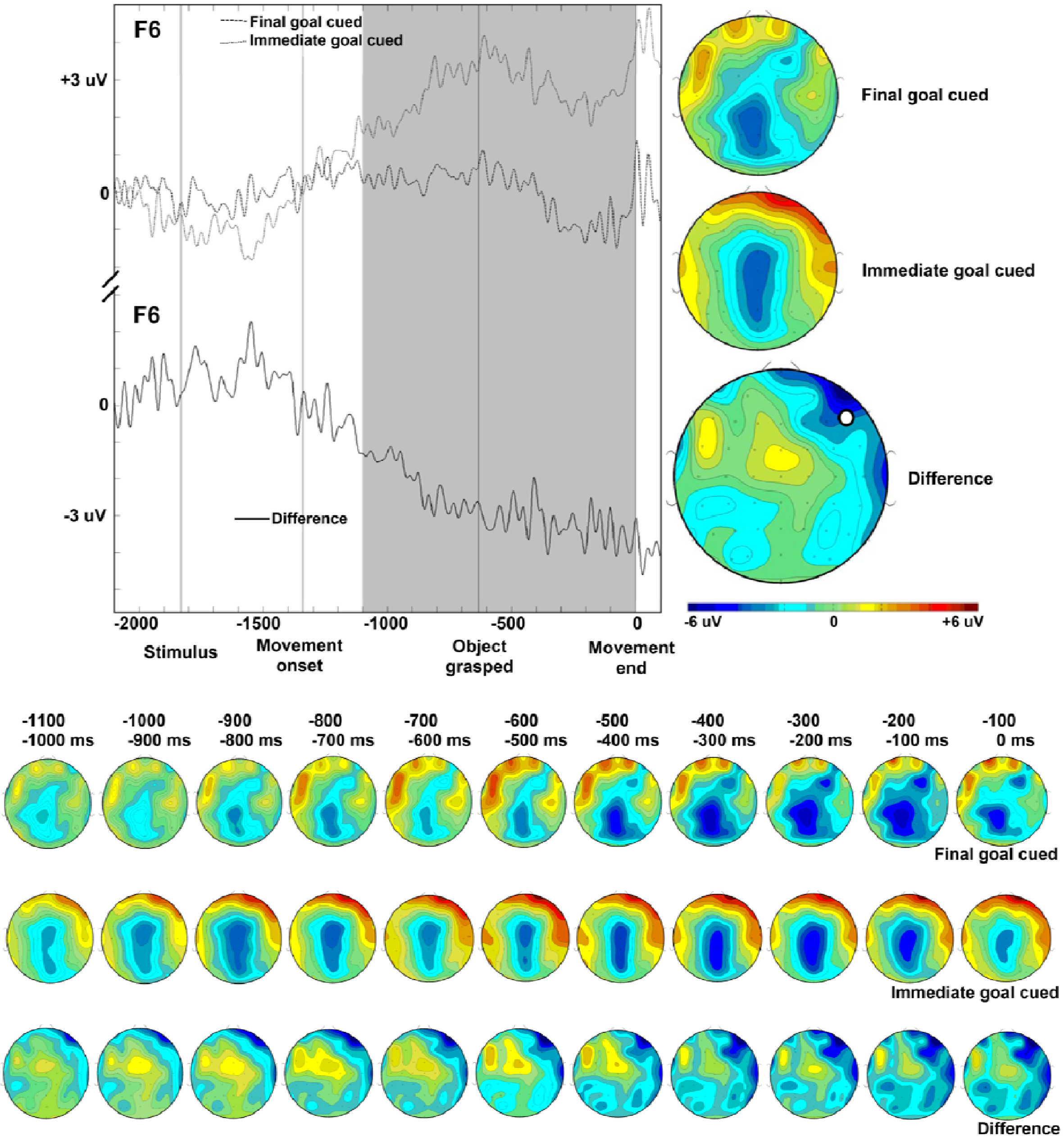

Figure 2.5: Slow wave brain potentials time-locked to movement end. Time is shown in milliseconds. (TOP LEFT) Event-related slow wave potentials recorded at the right lateral frontal electrode F6, time-locked to movement end, for the final goal-cued condition (dashed), the immediate goal-cued condition (dotted), and the difference between the two cueing conditions (solid). The labels 'Stimulus', 'Movement onset', and 'Object grasped' mark the *average* time points of these events. (TOP RIGHT) Topography of slow waves recorded in the -1100 ms to 0 ms time interval before movement end (indicated by the grey selection), in the final goal cueing condition, the immediate goal cueing condition, and the difference between the two cueing conditions. The location of electrode F6 on the scalp is illustrated by a white marker. (BOTTOM) Topography of slow waves recorded in the -1100 to 0 ms time interval before movement end displayed in consecutive 100 ms intervals, in the final goal-cued condition, the immediate goal-cued condition, and the difference between the two cueing conditions.

We conducted an equivalent ANOVA time-locked to movement end, which is the moment of placing the cylinder down at the target position, with the factors Cue-type (immediate goal-cued, final goal-cued), Front-Back (anterior, central, posterior), and Left-Right (left, middle, right).

The ANOVA for -1100-0 ms revealed a significant 3-way interaction for Cue-type, Front-Back, and Left-Right, $F(4, 68) = 4.3$, $p < 0.05$. Following the 3-way interaction, we performed a t-test for every ROI to determine if there was a significant difference based on Cue-type and in which ROI this difference was present. A significant positivity for the immediate goal-cued condition compared to the final goal-cued condition was present in the AR-ROI, $t(17) = 2.24$, $p < 0.05$. No significant effects were found for the remaining ROIs.

The average duration for the whole action sequence differed between 1667 ms for the final goal-cued condition and 1976 ms for the immediate goal-cued condition. This variability might be associated with the results of the electrophysiological data, because for some trials, especially in the immediate goal-cued condition, the baseline was post stimulus onset, while for most trials it was pre stimulus onset as a consequence of the variable movement times. To rule out an influence of the variability of the time epochs on the observed effects, we conducted further analyses excluding all trials, which included a post-stimulus baseline. The data of participants with less than 10 trials were excluded from further analyses. Data from 15 participants entered analyses response locked to grasping and to movement end. As we narrow down the data based on a temporal factor, the temporal occurrence of the effects might change. To accommodate to these changes and to provide a more detailed account of the temporal domain, we analyzed the data in 100 ms step windows. To correct for false positives we combined these time windows into one, only if three or more consecutive windows revealed significant 3-way interactions for Cue-type, Front-Back, and Left-Right, as well as for according t-tests (Lange et al., 1999).

In detail, we performed comparable ANOVAs with the factors Cue-type (immediate goal-cued, final goal-cued), Front-Back (anterior, central, posterior), and Left-Right (left, middle, right) for every single 100 ms time window of both epochs (time-locked to grasping and time-locked to movement end). For time windows that revealed a significant 3-way interaction for Cue-type, Front-Back, and Left-Right, we performed t-tests for every ROI. The results of these ANOVAs and t-tests can be found in section 7.1 *Supplementary material related to chapter 2*. Only when three or more consecutive intervals reached the significance level ($p < 0.05$), these intervals were combined, that is we averaged the amplitudes, to one time window. As a result, we analyzed in addition the time window from -600 to -200 ms time-locked to grasping and from -700 to -200 ms time-locked to movement end. Thus, the following statistics contain time windows, which consist of series of consecutive 100 ms steps that were found significant.

Time-locked to grasping, the ANOVA for -600 to -200 ms revealed a significant 3-way interaction for Cue-type, Front-Back, and Left-Right, $F(4,56) = 3.48$, $p < 0.05$. Following the 3-way interaction, we performed a t-test for every ROI to determine if there was a significant difference based on Cue-type and in which ROI this difference was present. A significant negativity for the immediate goal-cued condition compared to the final goal-cued condition was present in the PL-ROIs, $t(14) = -2.7$, $p < 0.05$, the PM-ROIs, $t(14) = -2.86$, $p < 0.05$, and the PR-ROIs, $t(14) = -2.41$, $p < 0.05$. No significant effects were found for the remaining ROIs.

Time-locked to movement end, the ANOVA for -700 to -200 ms revealed a significant 3-way interaction for Cue-type, Front-Back, and Left-Right, $F(4,56) = 5.09$, $p < 0.05$. Following the 3-way interaction, we performed a t-test for every ROI to determine if there was a significant difference based on Cue-type and in which ROI this difference was present. A significant positivity for the immediate goal-cued condition compared to the final goal-cued condition was present in the AR-ROI, $t(14) = 2.36$, $p < 0.05$. No significant effects were found for the remaining ROIs.

In sum, the analyses based on the predicted time windows time locked to grasping revealed a right frontal positivity for the immediate goal-cued condition compared to the final goal-cued condition from -300 to 0 ms. They also revealed a parieto-occipital negativity for the immediate goal-cued condition compared to the final goal-cued condition from -900 to -500 ms. The same analyses time-locked to movement end resulted in a right frontal positivity for the immediate goal-cued condition compared to the final goal-cued condition from -1100 to 0 ms. The temporally more fine grained analyses time-locked to grasping revealed a parietal negativity for the immediate goal-cued condition compared to the final goal-cued condition from -600 to -200 ms. Time-locked to movement end, we found a right frontal positivity for the immediate goal-cued condition compared to the final goal-cued condition from -700 to -200 ms.

2.4 Discussion

This study explored the neurophysiological basis of power grips. More specifically, we studied the functional impact of different goals on the planning and execution of grasping. The aim of the present study was to differentiate cerebral activity for the same action executed with an emphasis on initial vs. final parts of the movement sequence. In a grasp and transportation task, the relative emphasis was either on the grip (the immediate goal) or on the target location (the final goal). As predicted, the neural processes for action execution (measured by ERPs) differed between immediate goal-cued and final goal-cued trials. Time-locked to grasping, we found differential activity between immediate goal-cued and final goal-cued conditions in parieto-occipital regions considerably preceding grasping execution (see Figure 2.4). We also observed right frontal activity within a time window between -1100 ms and final object placement time-locked to movement end (see Figure 2.5). These results indicate that power grip preparation and execution for goal-related actions are controlled by similar neural mechanisms as precision grips, but with a distinct temporal pattern.

Participants executed the task correctly in 96 % of trials in the immediate goal-cued condition and in 97 % of trials in the final goal-cued condition - equally successfully in both cueing conditions. This indicates that task difficulty did not differ between cueing conditions and, hence, that task difficulty is highly unlikely to be related to any effects found between cueing conditions.

As expected, reaction times were faster for the final goal-cued condition. This result is in line with the findings of Van Schie and Bekkering (2007), who hypothesized that choosing a movement on the basis of a final goal is a preferred mode of operation. The effect fits also with the position of Rosenbaum & Jorgensen (1992), who argued that the goals of an action are more critical for action planning than initial hand postures. According to these authors, people prefer to plan actions based on the final goal and not on the immediate goal, like the initial grasp in our experiment.

Reach times, which describe the timeframe from movement onset to grasping, were faster for the final goal-cued condition as well. This might still be attributed to a preferred mode of operation, as it may be unfamiliar for the participants to pick up an object with a prespecified grip in comparison to goal-related grasping. There might be temporal overlap of movement planning with the reach period. It is also possible that planning of the grip during the reach phase affected reach time. If the ‘unfamiliar’ immediate goal-cued condition took more planning effort during reaching, this could have slowed them down. The 'unfamiliar' planning might take more effort because participants do not have everyday experience with prespecified grips. Rather, we choose grips in our everyday life based on what we want to do with the object (Marteniuk et al., 1987).

Another explanation could be that participants were focused on the possibility of making an error in the immediate goal-cued condition. Although the error rate was at a similar level for both cueing conditions, instructions in the immediate goal-cued condition may have focused participants' attention on the grip and potentially increased their awareness of potential errors in comparison to the final goal-cued condition. In the final goal-cued condition there was no incorrect grip according to the instructions, as it was the participants' choice which grip to use. In contrast, in the immediate goal-cued condition, the possibility of choosing the wrong grip and consequently making an error existed. With the present data, we cannot decide between these alternative interpretations.

Surprisingly, transport times for the final goal-cued condition were faster than for the immediate goal-cued condition. We did not expect a time difference here because the grip has already been executed and the transport movement is exactly the same. That is, the control phase should not be influenced by processes of grip planning. Again, the difference might be a case of increased awareness of potential errors and participants trying not to make mistakes in the immediate goal-cued condition, and constantly 'double checking' their actions. In contrast to our results, Van Schie and Bekkering (2007), who did not find a difference for transport times, used a more complicated setup and a more complicated movement had to be executed. A precision grip had to be used to transport an object over a bridge. It is possible that the simpler movement in our experiment caused the effect to spill over from the early movement phase into the next one. This remains speculation until further research has been conducted. Repeating the bar transport task of our experiment with an extension of the movement over a bridge might help to find an explanation.

Consistent with the hypothesis that the neural processes for action execution will differ between immediate and final goal-cued trials, we observed differential activity between the immediate and final goal-cued conditions over parieto-occipital regions for grasping. The differential activity in our study occurred earlier than the activity reported by Van Schie and Bekkering (2007), who observed differences between -300 and 0 ms time-locked to grasping. This temporal dissimilarity might be due to the difference in grip type used. It is possible that power grip preparation occurs earlier than precision grip preparation, or does not take as long because power grip preparation is easier. The results of both our analyses show a significant negativity for the immediate goal-cued condition compared to the final goal-cued condition. Temporally, the negativity occurs later in our temporally more fine-grained analyses (-600 to -200 ms), than for the predicted time window (-900 to -500 ms), but it still occurs earlier (300 ms difference in the onset) than the negativity described by Van Schie and Bekkering (2007) (-300 to 0 ms). For a long action sequence, like the one we studied, with a temporal variability for execution times among subjects, the neural preparation processes for action execution will vary as well. We narrowed down the data, excluding potentially equivocal trials, for the more fine-grained analyses based on a temporal factor. Thus, the fine-grained analyses might give a more accurate result concerning the timing of the effect. Overall, we see the results of both analyses as a confirmation for the hypothesis that power grip preparation occurs earlier than precision grip preparation, although the exact timing of the process may show some variability. Fewer parameters have to be adjusted for a power grip in comparison to a precision grip. It has already been shown in fMRI experiments that there is increased activity in the anterior intraparietal area (AIP) for increasing precision of the grasp (Begliomini et al., 2007), suggesting differences in movement planning between power and precision grasps. This increased neural activity may reflect more effortful planning of precision vs. power grips.

In addition to parietal activity, we observed differential frontal activity between -300 and 0 ms time-locked to grasping, which was not present in the temporally more fine-grained analyses. Van Schie and Bekkering (2007) reported frontal activity as well, but only time-locked to movement end. Although it is difficult to compare results time-locked to diverse events per se, it seems that we found a frontal effect in a relatively earlier time window. This variation might also be due to differences between power and precision grips. As the duration of the deceleration phase of grasping increases with precision requirements (Marteniuk et al., 1987; Castiello et al., 1992), we can expect the deceleration phase of the whole hand grasp in our experiment to be shorter than the deceleration phase of the precision grip in the experiment of Van Schie and Bekkering (2007). The earlier neurophysiological activity in our study may reflect this different temporal organization of the action.

Frontal activity might follow parietal activity during this grasp and transport task. As the parietal activity occurred earlier in our study, the frontal activity might have started earlier as well. We observed differential frontal activity between immediate and final goal-cued conditions within a time window between -1100 ms and final object placement (i.e., 0 ms) time-locked to movement end. This is in line with the findings of Van Schie and Bekkering (2007). Such an effect can be seen (cf. Fig. 6 in Van Schie & Bekkering, 2007, p. 189) although they did not report consecutive significant *p*-values for the whole time interval. They reported an anterior left positivity -1100 to -500 ms and -300 to 200 ms for precision grips. Varying from the results of Van Schie and Bekkering (2007), who reported significant effects only for differential left frontal activity, we observed differential right frontal activity. The results of both our analyses show this significant positivity for the immediate goal-cued condition compared to the final goal-cued condition. Temporally, the positivity in our more fine-grained analyses, from -700 to -200 ms, lies inside the time interval of the first analyses and in the middle of the time range reported by Van Schie and Bekkering (2007). The exact total duration may differ between the groups of participants. Importantly, the positivity occurs within the wider time window reported by Van Schie and Bekkering (2007) which suggests that the functional significance is comparable.

The right frontal activity cannot be explained with the participants' handedness, as we collapsed data for the left and right hand, i.e., handedness was balanced across participants. An additional visual inspection of each hand's data suggests that handedness did not influence the present ERP effects. Unfortunately, Van Schie and Bekkering (2007) did not explicitly mention whether or not they collapsed data for the left and right hand. Thus, a direct comparison would remain vague.

In sum, we found that ERPs differ between immediate and final goal-cued conditions, suggesting different neural ways of operation dependent on goal-relatedness. The basic pattern of our results was replicated in two analyses. That is, we found an anterior positivity time locked to movement end for the immediate goal-cued compared to the final goal cued-condition and a posterior negativity time locked to grasping for the immediate goal-cued compared to the final goal cued-condition. The posterior negativity appears to occur earlier for power grips than for precision grips, although the exact timing for such a long process varies among participants and needs further confirmation in future research.

Our study confirms the suggestion that parietal areas are of crucial importance in the planning and execution of grasping movements. In accordance with Bozzacchi et al. (2012a), we observed that parietal activity was followed by frontal activity. They concluded that action preparation is affected by the meaning of an action, precisely by the possibility of executing a desired action. Our results suggest that parietal ERP effects are not exclusively found for the possibility of executing a desired action, but also when planning a power grip with the emphasis directed on different components of the action. Furthermore, we establish these findings for the execution of a power grip, while Bozzacchi et al. (2012a) focused on the preparation phase of the action. We suggest that action preparation and execution are affected by the goal-relatedness of the action. Our interpretation is also in accordance with Van Schie and Bekkering (2007) and confirms the suggestion that immediate and final action goals are supported by different parts of the fronto-parietal network. Again, we establish these findings for the execution of a power grip, while Van Schie and Bekkering (2007) focused on precision grips. Precision and power grip preparation and execution seem to be controlled by similar neural mechanisms, but with diverging temporal relations.

Our results for immediate goal-cued and final goal-cued conditions might be seen in parallel to the results of Castiello et al. (1992) for precision and power grips. Castiello et al. (1992) observed longer movement times for precision grips as compared to power grips, but a relatively earlier time point for maximum grip aperture in precision grips. They argued that this reflects the temporal coordination of grasp and transport components and that this temporal difference might be due to an earlier anticipation of an object's characteristics in case of higher precision demands. In our case, we observed longer movement times for the immediate goal-cued condition as compared to the final goal-cued condition. We also found a negativity for the immediate goal-cued condition as compared to the final goal-cued condition time-locked to grasping. Van Schie and Bekkering (2007) found a comparable effect for precision grips in a later time window. It seems possible that this difference is due to an earlier anticipation (Castiello et al., 1992) of the grasp characteristics in the immediate goal-cued condition compared to the final goal-cued condition, as the cue emphasized the grasping action. We suggest that planning processes can be influenced by manipulating the emphasis on one part of a movement sequence, just like planning processes can be influenced by object characteristics like the size of an object (Ansuini et al., 2008; Castiello et al., 1992).

If we split an action into two phases, as in the two-component model by Woodworth (1899) or the multiple-process model of limb control (Elliott et al., 2010), we can see that the two cueing conditions we used in our experiment affected both phases of the action. Both the initial ballistic phase, mainly controlled by planning processes, and the online feedback-controlled phase were affected by the goal cueing condition, as can be seen in the effects for reaction, reach, and transport times, and in the neurophysiological data. The immediate goal-cued condition in comparison to the final goal-cued condition seems to cause more effort for motor planning in both phases of the action. This suggests that executing actions on the basis of the final goal is faster and requires less effort and is thereby the dominant way of planning grasping actions.

We suggest that several components influence grasp planning processes, and the final goal is one of the most influential. Uithol et al. (2012) describe dynamic models of hierarchies in motor control. In these models, "elements higher on the hierarchy are represented longer or are more stable than lower ones. As such, they are able to influence an action for a longer time interval, thereby accounting for our capacity to structure behavior around a goal" (Uithol et al., 2012, p. 1083). The effects we found for different goal cueing conditions might be explained within this hierarchy. While the final goal cueing condition might have served as a stable component for the whole action, the immediate goal cueing condition might have been more influential for the first part of the action, until the immediate goal (grasping the cylinder) had been reached.

It might be interesting for future research to investigate the lateralized readiness potential (LRP), which reflects response preparation, in a similar experiment. The present experiment was not designed to maximize hemispheric differences in the electrical signal of motor activity. Therefore, we neither expected, nor reported an effect on the LRP for this experiment. For the present study, we focused on the neural mechanisms underlying grasp planning and execution in relation to the work of Van Schie and Bekkering (2007). In a future study immediate goal-cued and final goal-cued conditions could each be assigned to one hand and within one block, with the assignment of conditions to hands counterbalanced across blocks. A precue could also be used to instruct the hand for the next trial (Mordkoff et al., 1996; Miller & Low, 2001; Danek & Mordkoff, 2011) to randomly mix left and right hand responses within a block. This would enable an investigation of the LRP and, thus, response preparation processes, extending our understanding of the neurophysiological correlates of manual action. In addition, our work also suggests that the combination of ERP recordings with other established experimental grasping designs (Lindemann et al., 2006; Spiegel et al., 2012; Hughes et al., 2012a) can provide valuable insights into the cognitive control of uni- and bi-manual actions.

In conclusion, our results suggest that a parieto-frontal network is of crucial importance for grasp planning and execution. According to our data, parietal activity is followed by frontal activity. To our knowledge, this is the first study to differentiate cerebral activity and its temporal organization underlying power grips executed with an emphasis on different parts of the action. Power grip preparation and execution for goal-related actions seem to be controlled by similar neural mechanisms as precision grips, but with a distinct temporal pattern. Grasp and transport actions seem to be preferably processed in a goal-related manner.

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3 THE WHAT-DECISION IN MANUAL ACTION: ERPs FOR FREE CHOICE VS SPECIFIED OVERT GOAL-RELATED GRASPING

Abstract

This study explored the neurophysiological mechanisms underlying the *what*-decision of planning and execution of an overt goal-related manual action. We aimed to differentiate cerebral activity, by means of event-related potentials (ERPs), between predominantly self-regulated and instructed actions. In a bar-transport task, participants were given free or specified choices about the initial grip and/or final goal. The ERPs for action execution differed between free- and specified-goal conditions, but not between free-and specified-grasp conditions. We found differential activity for the goal specification in mid-frontal, mid-central, and mid-parietal regions from -1100 to -700 ms and -500 to 0 ms time-locked to grasping and in anterior right regions from -1900 to -1400 ms time-locked to movement end. There was no differential activity for grasp specifications. These results indicated that neural activity differed between free and specified actions, but only for goal conditions, suggesting different ways of operation dependent on goal-relatedness. To our knowledge, this was the first study to differentiate cerebral activity and its temporal organization underlying the what-decision involved in overt goal-related actions. Our results support the ideomotor theory by showing that neural processes underlying action preparation and execution depend on the anticipated action goal.

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3.1 Introduction

Human actions are characterized as either more intention-based or stimulus-based. While stimulus-based actions are associated with automatic pre-specified processes, intention-based actions are associated with self-regulated free-choice processes. These processes include decisions about whether to act, what action to perform, and when to perform it (Haggard, 2008). It is difficult to study entirely intention-based actions under controlled experimental conditions due to their voluntary nature (Haggard, 2008). In most cases stimuli and intentions interactively lead to a response (Goschke, 2003) or to its suppression (Haggard, 2008). One mechanism underlying the planning and control of voluntary action is goal-directedness. Goal-directedness is critical for making the what-decision. A framework of action planning that incorporates this idea is called ideomotor theory. It suggests that actions are represented by their perceivable effects (Prinz, 1987). Thus, self-regulated actions depend on the anticipation of action effects (Prinz, 1987).

The anticipatory character of motor planning processes regarding the what-decision of voluntary action has been demonstrated, for example, in a bar-transport task. Previous research using this methodology showed that people have a preference for final comfortable postures over initial comfortable postures. This tendency was termed the end-state comfort effect (Rosenbaum et al., 1990). Here, we focus on the neurophysiological mechanisms underlying the planning and control of the what-decision for specific goal-related manual actions.

Most previous neurophysiological studies, that have tackled what-decisions of manual actions, focused on clinical populations or non-human primates (for a review see Haggard, 2008). Studies that investigated intention- and stimulus-based actions using ERPs have mainly focused on components that occur before action execution and used simple movements like key presses (e.g. Shibasaki & Hallett, 2006). Research on overt complex actions in this area is to our knowledge lacking.

These studies suggested that different cortical structures mediate the preparation and potentially the execution of intention- and stimulus-based key presses (Waszak et al., 2005). Also, freely chosen actions seem to be more flexible and modifiable than specified choices. Specified choices have also been shown to produce rapid specific responses (Fleming et al., 2009). Furthermore, the anticipated final sensory effect of the action, and not the upcoming action kinematics, may influence the what-decision in the early preparation processes of an action (Bozzacchi et al., 2012b).

Van Schie and Bekkering (2007) instructed participants to grasp an object with a precision grip and transport it to a new location. In the grasp-and-transport-task, participants were cued by either the grasp type (immediate goal) or by the ending location (final goal). They found enhanced activation in posterior parts of the brain, around the parieto-occipital sulcus, for the immediate goal. They argued that this indicated this area's involvement in the prehension of the object. They also found enhanced activation in anterior prefrontal cortex for the final goal. They suggested that this indicated frontal involvement in the planning and control of sequential behavior. Westerholz et al. (2013) found similar effects with a distinct temporal pattern for goal-related power grips.

The aforementioned studies underlined the importance of action goals for motor control and built a solid base for research on self-regulated actions. However, to our knowledge, no study has yet investigated ERPs underlying the what-decision in the planning and execution of overt manual action. The goal of our study was to investigate whether differences exist between cerebral activity related to free-choice versus specified actions during the overt execution of a goal-related action. If distinct ERP components for these potentially distinct neurocognitive processes exist, then it would extend the current knowledge about action planning and execution.

In the present study, participants executed a bar-transport task, which has been shown to involve anticipatory behavior (Rosenbaum et al., 1990) and was suitable to investigate intention based goal-directed actions. The grasp participants used to pick up the bar and the target-position of the bar were either free choice or specified by instruction.

Self-regulation mainly guides actions for free choice of grasp or target-position, while instructions mainly guide actions for specified grasp or target-position. Our experiment did not feature purely intention-based and stimulus-based conditions, as we only manipulated the what-decision of voluntary action. For trials where the participants' decision was instructed the what-decision was unnecessary, because grasp and goal were specified. In contrast, for trials where the participants' decision was self-regulated the what-decision was free for the participants to decide on their own. To avoid confusion, we will use the terms free and specified from now on. The present study investigated differences in neural mechanisms related to free compared to specified actions concerning the grasp and the target-position. For that reason, we focused our analysis on the differences between both the specified- versus free-goal conditions, and the specified- versus free-grip conditions.

Previous studies have found similar, non-overlapping time windows, within the time range from -900 to 0 ms (time-locked to grasping) and -1100 to 200 ms (time-locked to movement end) for the present grasp-and-transport-task were of special importance for action planning and execution (van Schie & Bekkering, 2007; Westerholz et al., 2013). We expected effects to arise within the same two time windows.

We predicted that participants would show the end-state-comfort effect and reach a final posture with the thumb facing upwards, unless instructed otherwise. This would mean, that if the goal was specified they would grasp the bar in a way that allowed them to end in a comfortable final posture and if the grasp was specified they would execute a movement that allowed them to end in a final comfortable posture. Furthermore, we predicted reaction, reach, and transport times to be faster for the free goal compared to the specified goal conditions because of the greater congruence with everyday actions (Rosenbaum et al., 1990; van Schie & Bekkering, 2007) and previous findings (Westerholz et al., 2013).

A similar effect might be found for reaction, reach, and transport times between the specified- and free-grip conditions. As people usually do not have to use prespecified grasps in their everyday lives, free grips were expected to result in faster responses and movement times compared to specified grips. However, we expected the action goal to be the major influence for the planning and execution of the movement sequence, not the initial grip. Thus, specification of the grasp could have a weaker or no influence on the timing of the behavior.

Based on previous results (Waszak et al., 2005; Westerholz et al., 2013), time-locked to grasping, we predicted a negativity for the specified- versus free-goal condition over frontal-central scalp sites and a negativity for the specified- versus free-goal condition over parieto occipital cortex. Further, we predicted a positivity for the specified- versus free-goal condition over right frontal areas time-locked to the movement's end.

We further compared ERPs between specified- and free-grip conditions. These conditions might influence cerebral activity, especially in temporal relation to the grasping action, if action planning is driven by stimulus features. If the movement sequence was driven primarily by its goal effect, then the initial grip might not exert a strong influence on the planning and execution processes. In this case, no ERP difference between specified- and free-grip conditions should be present.

3.2 Materials and methods

Twenty four volunteers (mean age=24.08 years; SD=5.96; 12 females) with no known neurological impairments and normal or corrected-to-normal vision participated. Twenty one participants were right-handed and three were left-handed (EHI mean handedness score 74.1) (Oldfield, 1971). Participants were compensated for their time with course credit or money.

Participants were required to grasp a bar with a power grip and transport it to a target-position (Fig. 3.1 A). The bar was a wooden stick, painted black on one end and white on the other. The bar lay on a cradle at the start of each trial, where participants could grasp it either with an overhand or an underhand grip. Two target-locations were aligned lateral to the cradle. The bar had to be brought to one of these locations, with either the white or the black end facing upwards.

Participants executed the task under four conditions. Instructions included specified or free-choice grip postures and specified or free-choice target-positions of the bar. Either both the grip and the target-position, one of them, or none were specified.

In each trial, a picture stimulus was presented indicating the grip posture and target-location. First, the bar had to be moved from the cradle to a target-location. Only these trials entered the analyses. Afterwards, it had to be moved back to the cradle. The black-white-orientation of the bar for its resting position was always specified and counterbalanced across trials.

The bar had to be rotated 90° on every trial, as it was lying in a horizontal orientation but had a vertical orientation on the target-location. The picture stimuli consisted of six squares (two rows of three squares), showing the grip posture and target-location (see Fig. 3.1 B). The grip posture was encoded by the colors green and orange. The target-location was represented by a black and a white lateral square representing both ends of the bar. Stimuli for all conditions were shown in randomized order.

The setup was calibrated to each participant’s size. Target-locations were each placed in front of the participants' shoulders, such that they could reach both of them comfortably with an extended arm. The cradle was positioned equidistant to the two target-locations. The start button was positioned in front of the cradle. Picture stimuli were presented on a video monitor located behind the cradle. Before the experiment started, participants performed test trials.

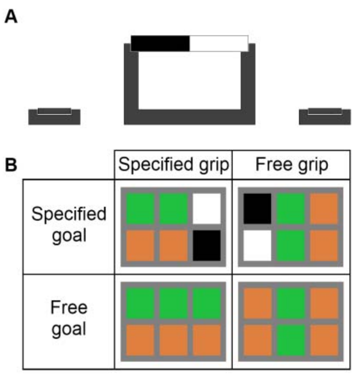

Figure 3.1: Setup and stimuli. (A) Task setup showing the bar that had to be grasped with an overhand or underhand grip. Then it had to be brought to either the left or right goal location with the white or black end up or down. (B) Possible stimuli showing grasp and goal. Green and orange represent the grasp. Green on the top row requires an overhand grip. Green on the bottom row requires an underhand grip. Green in the middle column is a free choice. Black and white represent both ends of the bar and, thus, the final location (left or right) and orientation of the bar (black end up or down).

Each trial started when participants pressed the start button (Fig. 3.2). First, a black screen was shown for 500 ms, followed by a fixation cross for a randomized duration between 500 and 1500 ms. Next, a picture stimulus was shown indicating movement instructions. The stimulus remained on the screen until participants had hold the bar on the target position for 1.5 s. We considered the moment of arriving at the target-location as the movement end of the bar-transport task, as the goal of the action had been reached and there was no more movement. The next picture stimulus showed participants how to replace the bar on the cradle. The timing of all actions (start, lift off, placing) were registered. The experiment consisted of eight blocks of 32 trials each with a 20 s break after each block. Participants used one hand for the first four blocks and the other hand for blocks five to eight; counterbalanced across participants. The stimulus presentation was controlled by Presentation® software (version: 14.1, www.neuro-bs.com).

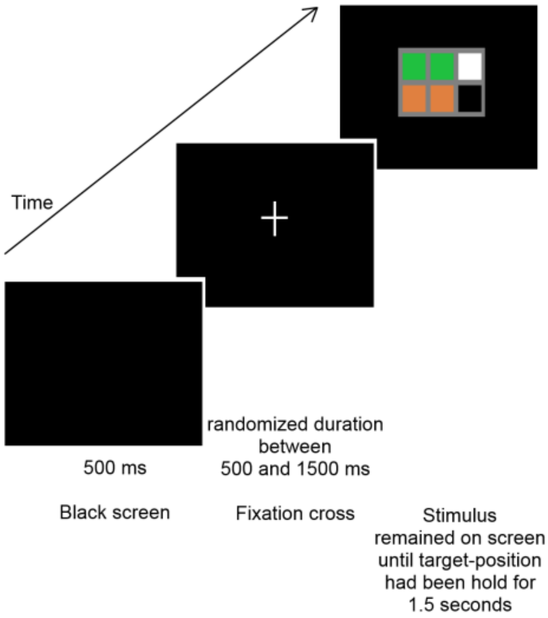

Figure 3.2: Time course of the task events. Black screen followed by fixation cross and then a stimulus.

Behavioral recordings included the time points of lifting the hand off the start button, lifting the bar off the cradle, and placing the bar down at the target-location. Micro switches were used to detect the exact moment they occurred. Participants' performance was recorded with a video camera for later offline analysis. Whenever participants reached the final posture with their thumb facing upwards, this was considered as a comfortable end-state.

EEG was recorded by a 64 channel amplifier (ANT). A WaveGuard EEG cap (ANT) with 64 Ag/AgCl-electrodes was used. The electrodes of the cap were arranged according to the international 10-10 system (based on the 10-20 system) (cf. Oostenveld & Praamstra, 2001). EOG was recorded to detect ocular artifacts. During recording the data were average-referenced. The EEG was band-pass filtered (DC-138 Hz) and digitized at 512 Hz. The impedance of all electrodes was less than 5 kΩ. Trials with performance errors were excluded from the analyses.

Electrophysiological data were band-pass filtered offline from 0.1 to 30 Hz and re-referenced to the average mastoid electrodes. Response-locked analysis to grasping included the time interval from -1800 to 1100 ms. Response-locked analysis to movement end included the time interval from -2700 to 200 ms. Baseline correction was performed from -1800 to -1600 ms time-locked to grasping and -2700 to -2500 ms time-locked to movement end. The mean voltage over these periods was subtracted from the waveform for each epoch. Ocular artifacts were corrected using the correction procedure of Gratton et al. (1983). Artifact detection was done using a peak-to-peak moving window approach with a threshold of ±50 µV within a 200 ms window, which was moved over the whole epoch in 50 ms steps. 25% of the trials time-locked to grasping in the specified-grip/specified-goal condition, 23% in the free-grip/specified-goal condition, 23% in the specified-grip/free-goal, and 22% in the free-grip/free-goal condition were rejected due to movement artifacts. 25% of the trials time-locked to movement end in the specified-grip/specified-goal condition, 21% in the free-grip/specified-goal condition, 23% in the specified-grip/free-goal, and 23% in the free-grip/free-goal condition were rejected due to movement artifacts. In order to investigate the influence of the determination of the target-location, both specified-goal conditions were averaged together and both free-goal conditions were averaged together. In order to investigate the influence of determination of the grip posture, both specified-grip conditions were averaged together and both free-grip positions were averaged together. The EEG data were averaged for the left and right hand to avoid handedness effects.

For the assessment of effects of scalp distribution, we differentiated between nine regions of interest (anterior-left (AntL): AF7-F7-F5-F3; anterior-middle (AntM): F1-Fz-F2; anterior-right (AntR): AF8-F8-F6-F4; central-left (CentL): C3-C5-CP3-CP5; central-middle (CentM): FCz-Cz-CPz; central-right (CentR): C4-C6-CP4-CP6; posterior-left (PostL): PO7-PO5-PO3-O1; posterior-middle (PostM): Pz-POz-Oz; posterior-right (PostR): PO8-PO6-PO4-O2). The Greenhouse-Geisser correction was applied when evaluating effects with more than one degree of freedom.

3.3 Results

3.3.1 Behavior

Participants executed the task correctly in 88% of trials in the specified-grip/specified-goal condition (48% end-state-comfort), 96% in the free-grip/specified-goal condition (73% end-state-comfort), 98% in the specified-grip/free-goal condition (96% end-state-comfort), and 99% in the free-grip/free-goal condition (97% end-state-comfort). An ANOVA on the arcsine transformed proportions of correct trials revealed a significant difference between cueing conditions, $F(3, 92) = 10.83$, $p < 0.05$, indicating fewer correct trials in the specified-grip/specified-goal condition as compared to the other conditions.

3.3.2 Timing

A two way ANOVA with the factors time (reaction time, reach time, transport time) and conditions (free goal, specified goal) revealed a significant interaction for time and condition, $F(2, 46) = 3.5$, $p < 0.05$. A two way ANOVA with the factors time (reaction time, reach time, transport time) and conditions (free-grip, specified-grip) revealed a significant interaction for time and condition, $F(2, 46) = 9.8$, $p < 0.05$. Following the results of the ANOVA, we conducted three paired-samples t-tests (Holm-Bonferroni corrected) to compare each of the reaction times, reach times, and transport times in the corresponding conditions. Reaction times ($t(23) = 5.56$, $p < 0.001$) were shorter for free- (629 ms, SD = 124) compared to specified-goal trials (767 ms, SD = 234). Reach times ($t(23) = 6.19$, $p < 0.001$) were shorter for free- (577 ms, SD = 134) compared to specified-goal trials (749 ms, SD = 209). Transport times ($t(23) = 7.41$, $p < 0.001$) were shorter for free- (803 ms, SD = 145) compared to specified-goal trials (895 ms, SD = 140).

Reaction times ($t(23) = 0.88$, $p = 0.39$) were not significantly different for specified- (700 ms, SD = 186) compared to free-grip trials (695 ms, SD = 169). Reach times ($t(23) =$

5.03, $p < 0.001$) were shorter for free- (642 ms, SD=163) compared to specified-goal trials (684 ms, SD = 164). Transport times (t(23) = 6.4, $p < 0.001$) were shorter for free- (826 ms, SD = 138) compared to specified-grip trials (873 ms, SD = 142).

3.3.3 Electrophysiology

We performed ANOVAs with the factors Condition (specified-goal, free-goal; and separately specified-grip, free-grip), Front-Back orientation of the ROI (anterior, central, posterior), and Left-Right orientation of the ROI (left, middle, right) for the mean amplitude of every single 100 ms time window of both epochs (from -1800 to 1000 ms time-locked to grasping and from -2700 to 200 ms time-locked to movement end). For time windows that revealed a significant three-way interaction for Condition, Front-Back, and Left-Right, we performed t-tests for every ROI. The results of these ANOVAs and t-tests can be found in section 7.2 *Supplementary material related to chapter 3*. Only when three or more consecutive intervals reached the significance level ($p < 0.05$) (cf. Lange et al., 1999), these intervals were combined. As a result, we analyzed the mean amplitude of the time windows from -1100 to -700 ms and -500 to 0 ms time-locked to grasping/lifting the object and the time window from -1900 ms to -1400 ms time-locked to movement end for specified- and free-goal conditions.

The ANOVA for -1100 to -700 ms revealed a significant three-way interaction for Condition, Front-Back, and Left-Right, F(4, 92) = 5.57, $p < 0.05$. The three-way interaction meant that the ERP amplitude differences between the specified- and free-goal condition was different in magnitude for the various combinations of the factors Front-Back and Left-Right. The significant interaction permitted the separate comparisons of the specified- and free-goal conditions in the various regions-of-interest. We performed a t-test for every ROI to determine if there was a significant difference based on condition. A significant negativity for the specified- compared to the free-goal condition was present in the AntZ-ROI, t(23) = -2.4, $p < 0.05$, and the CentZ-ROI, t(23) = -2.51, $p < 0.05$. No significant effects were found for the remaining ROIs.

The ANOVA for -500 to 0 ms revealed a significant three-way interaction for Condition, Front-Back, and Left-Right, F(4, 92) = 4.78, $p < 0.05$. A significant negativity for the specified- compared to the free-goal condition was present in the AntZ-ROI, t(23) = -2.71, $p < 0.05$, the CentZ-ROI, t(23) = -2.92, $p < 0.05$, and the PostZ-ROI, t(23) = -2.06, $p = 0.05$. No significant effects were found for the remaining ROIs.

The ANOVA for -1900 to -1400 ms revealed a significant three-way interaction for Condition, Front-Back, and Left-Right, F(4, 92) = 3.49, $p < 0.05$. A significant positivity for the specified- compared to the free-goal condition was present in the AntR-ROI, t(23) = 2.69, $p = 0.05$. No significant effects were found for the remaining ROIs.

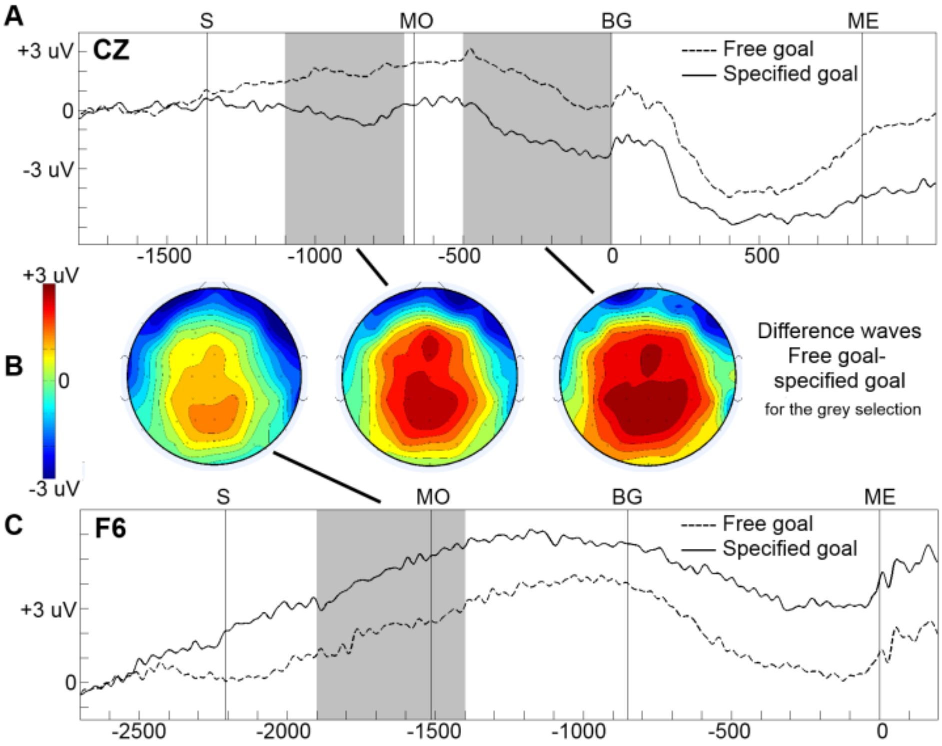

Figure 3.3: Slow wave brain potentials and topographic scalp distributions. (A) Grand averaged ERPs at electrode Cz time-locked to grasping and (C) at electrode F6 time-locked to movement end. Both show the free goal condition (dashed) and the specified goal condition (solid). Time is shown in ms. Average time points for stimulus presentation (S), movement onset (MO), bar grasped (BG), and movement end (ME) are marked. (B) Topography of the difference waves in significant time intervals (indicated by the grey selection in the middle) for the free goal condition minus the specified goal condition.

3.4 Discussion

As predicted, the neural processes for action execution differed for free and specified goals in mid-frontal, mid-central, and mid-parietal regions time-locked to grasping. We further observed differential activity between free- and specified-goal conditions in right frontal regions time-locked to movement end. There was no differential activity between free- and specified-grasp conditions. These results indicated that preparation and execution underlying the what-decision of free and specified actions were controlled by different neural mechanisms which depended on the goal effect of the action. As expected, participants showed a preference to act towards the end-state-comfort effect demonstrating the dominant influence of the goal at the behavioral level (Rosenbaum et al., 1990).

Differences in correct execution indicated that the fully specified condition (specified grip/specified goal) was harder than the other conditions. Thus, the task may have been perceived as easier if it contained a free decision. Another explanation may have been that the fully specified condition required uncomfortable final postures, as most errors happened on such trials.

In line with previous findings (Westerholz et al., 2013), reaction, reach, and transport times were shorter for the free- compared to the specified-goal condition. Shorter reaction times for self-regulated actions may have indicated a frequency effect. Because, in general, people execute everyday actions based on intentions, this could have meant that it required less effort. Self-regulated actions seemed to be more flexible and modifiable than instructed plans (Fleming et al., 2009), making online planning and motor implementation processes apparently easier.

Reaction times did not differ significantly between free- and specified-grip conditions. This is in line with the ideomotor theory claiming that actions are selected with respect to their anticipated sensory effects (Prinz, 1987). As the final sensory effect did not change depending on whether the grip was specified or not, information about the initial goal of the action sequence probably did not influence action selection essentially.

Reach and transport times differed significantly between free- and specified-grip conditions, with free-grip trials being shorter. Assuming that free actions are more modifiable than specified actions (Fleming et al., 2009), online planning toward a desired end posture would be less effortful and faster for free grip.

There was a negativity for the specified- compared to the free-goal condition in the AntZ-, CentZ-, and PostZ-ROIs between -1100 and -700 ms and between -500 and 0 ms time-locked to grasping. This fits with our expectations of a negativity for specified actions compared with free actions. The effects observed over mid-frontal and mid-central areas also fit well with the assumption that the frontomedian cortex plays a crucial role in intentional actions (for a review see Krieghoff et al., 2011). The mesial precentral area might be close to motor execution, reflecting the imminence of an already planned movement (Desmurget &

Sirigu, 2012). The negativity suggests more effortful planning processes for instructed actions as compared to self-regulated actions. Anterior negativity has also been shown for stronger engagement of working memory, when information must be maintained (Kluender & Kutas, 1993). Our results suggest that self-regulated actions show a greater congruency with everyday actions and seem to have an easier-to-access mental representation of these actions.

The negativity for the specified- compared to the free-goal condition over occipital cortex fits also with previous findings (van Schie & Bekkering, 2007). The negativity appears to reflect a more effortful prehension movement. Another explanation might be that "the posterior parietal cortex contains stored movement representations" (Desmurget et al., 2009, p. 813), which contain mental images of movements as well as intentions to produce movements. Movement intentions in parietal areas might be generated in relation to their predicted consequences (Desmurget et al., 2009). Thus, the desired action effect might influence the online planning directly before grasping.

As predicted, we observed a positivity for the specified- compared to the free-goal condition over right frontal areas time-locked to movement end. This positivity occurred from -1900 to -1400 ms, i.e., before the predicted time frame from -1100 to 200 ms. To control for an influence of the stimulus on the effect, we performed stimulus-locked analysis, but found no significant effect (see supplementary material Table A3.5). Thus, the positivity might reflect early movement planning and anticipation processes of the action sequence, as the effect appeared in response-locked analyses but not in stimulus-locked analyses. For a better understanding of this planning phase, we performed a further analysis time-locked to movement-onset, and found a significant positivity for the specified- compared to the free-goal condition in the AntR-ROI from 600 to 1200ms (see supplementary material Table A3.7). This result confirms the location of the effect over right frontal areas, while the temporal occurrence of the effect might hint towards online-planning and control processes. The frontal positivity might also indicate processes concerning the unsuitability of the upcoming action, whether the action can be accomplished in a suitable way or not (Bozzacchi et al., 2012a).

We found no significant difference between the neural processes for action execution in free- and specified-grip trials, neither time-locked to grasping, nor time-locked to movement end. Specifying the action effect thus influences planning processes for the action, whereas specifying the grip has no major influence. The importance of action effects compared to initial grips has also been demonstrated by Van Elk et al. (2008), who manipulated the task instructions in a similar task (focus on goal vs. grip of an action).

Like Waszak et al. (2005), we observed different cortical structures mediating the execution of free and specified actions. These differences might reflect that the ideomotor principle holds for free actions only (Herwig et al., 2007). It further holds for final but not initial action goals. Our results are in line with the findings of Rosenbaum et al. (1990) regarding the anticipatory character of motor planning processes. First, specifying the action goal influenced the planning processes regarding action execution, while specifying the grip did not cause such an effect. Secondly, the differential cerebral activity we observed between specified- and free-goals demonstrated that choices regarding the action goal affected planning and execution processes. Overall, we found the goal of a grasp-and-transport-task to be of crucial importance for the planning and execution of the action, while the initial grasp did not have a major influence on the neurophysiological signature of the current bar-transport task. Thus, the present results support the notion that knowledge about action goal effects and its cognitive representation play a significant role for anticipatory action planning. It remains unclear whether cognitive control functions of grasping are lateralized. Therefore, further research on the role of left versus right handedness in ERP research on manual action is needed.

In this study, we investigated the neurophysiologic mechanisms underlying the what-decision of planning and control of manual action. Our results confirm the fundamental assumption of the ideomotor theory for the planning and execution of actions on a neural level. On this level, the what-decision of voluntary actions seems to be planned and executed based on the mental representation of the actions' goal-relatedness and not on the (initial) movement itself. We have shown that neurophysiological brain processes for the what-decision of manual actions were organized by the action's goal specification ("intention") and less so by the specification of stimulus characteristics (i.e., features for the immediate movement/grasp).

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4 HABITUAL VS NON-HABITUAL MANUAL ACTIONS: AN ERP STUDY ON OVERT MOVEMENT EXECUTION

Abstract

This study explored the neurophysiological mechanisms underlying the planning and execution of an overt goal-related handle rotation task. More specifically, we studied the neural basis of motor actions concerning the influence of the grasp choice. The aim of the present study was to differentiate cerebral activity between grips executed in a habitual and a non-habitual mode, and between specified and free grip choices. To our knowledge, this is the first study to differentiate cerebral activity underlying overt goal-related actions executed with a focus on the habitual mode. In a handle rotation task, participants had to use thumb-toward (habitual) or thumb-away (non-habitual) grips to rotate a handle to a given target position. Reaction and reach times were shorter for the habitual compared to the non-habitual mode indicating that the habitual mode requires less cognitive processing effort than the non-habitual mode. Neural processes for action execution (measured by event-related potentials (ERPs)) differed between habitual and non-habitual conditions. We found differential activity between habitual and non-habitual conditions in left and right frontal areas from -600 to 200 ms time-locked to reaching the target position. No differential neural activity could be traced for the specification of the grip. The results suggested that the frontal negativity reflected increased difficulty in movement precision control in the non-habitual mode compared to the habitual mode during the homing in phase of grasp and rotation actions.

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4.1 Introduction

We seamlessly and effortlessly pick up and manipulate objects in our everyday life. We usually do so with the consequences of our behavior in mind, indicating the cognitive effort underlying motor planning and control. Planning processes before action execution have been shown in a study by Rosenbaum et al. (1990). Participants did not seem to strive for a comfortable grip (overhand) and to avoid an uncomfortable grip (underhand) when grasping a bar. Apparently, participants preferred a comfortable hand posture at the *end* of the movement when placing the bar onto a target position. Rosenbaum et al. (1990) suggested that participants anticipated their future hand postures and called this effect the end-state comfort effect, as the participants showed a preference for final comfort over initial comfort. In the experiment, participants had to take hold of a bar lying on a pair of cradles. There was a target position on both sides of the cradles, one to the left and one to the right. Participants had to grab the bar and bring either the right or left end of the bar to the right or left target position. If the right end of the bar had to be placed on one of the two targets, participants grasped it with an overhand grip. If the left end of the bar had to be placed on one of the two targets, participants grasped it with an underhand grip. Further experiments found sequential effects for motor planning that further emphasize the role of mental representations for motor control (Cohen & Rosenbaum, 2004; Rosenbaum & Jorgensen, 1992; Weigelt et al., 2006; Weigelt et al., 2007).

The question why people seem to prefer comfortable end states has not been answered yet. It might be that ending comfortably provides better control or more precision at the end of the movement, or when this is needed (Rosenbaum et al., 2012). A habitual system would be another explanation for grasp choices (Herbort & Butz, 2011). The habitual system favors movements that were rewarding in the past and, therefore, grasps that people habitually use for object manipulation. Most studies in this area focused on bar-transport tasks with a vertical or horizontal orientation of the bar, while there are only few experiments covering more orientations. Following the work of Rosenbaum et al. (1993) we investigated a more fine-grained version of the bar-transport task. Surprisingly, although cognitive aspects demonstrated by the end-state comfort effect were frequently highlighted, neurophysiological studies for the overt execution of goal-related grasps are hard to find. The aim of this study was to investigate the neural mechanisms underlying the overt execution of goal-related actions with a focus on habitual vs non-habitual grasps.

One possible explanation for the end-state comfort effect is the precision hypotheses. Precision requirements are oftentimes higher at the end of the movement. Ending in a comfortable posture allows for greater precision and faster movements because faster movements are possible at the middle of the range of motion (Rosenbaum et al., 1996; Short & Cauraugh, 1999). A wider range of motion would also lead to greater control at the end of the movement. Further evidence for this hypothesis comes from another study by Rosenbaum, Vaughan, Jorgensen, Barnes and Stewart (1993). They used a handle connected to a disk which was turned clock-like from a starting position to a target position. The handle was constructed in a way that allowed subjects to grasp it at its rotational axis. A pointer at one end of the handle indicated its orientation. Eight numbers around the perimeter were used as possible target positions. The experimenter announced a target number. Then the subjects had to take hold of the handle and turn the disk until it showed in the direction of the target. The disk had low friction and had to be carefully brought to the target position. All required rotations included 180 degrees. Again, subjects showed the end-state comfort effect. That is, the probability of grasping the handle with the thumb towards the pointer was related to the pointer's final position. The minimum of the probability, for participants performing the task with their right hand, was near the 4 o'clock position, which was presumably the most awkward posture. For participants performing the task with their left hand, the minimum probability was near 7 o'clock, again, the presumably most awkward posture. The authors hypothesized that participants ended the task in a comfortable posture because this ensured precise task completion.

In line with the precision hypothesis, Rosenbaum et al. (1996) showed that the end-state comfort effect can be eliminated when the precision requirements at the end of the movement are eliminated. The previous experimental setup (Rosenbaum et al., 1993) was modified so that no more precision was needed to bring the disk in the target position. The disk locked in automatically when it reached the target position. Half of the subjects did not show the end-state comfort effect. Rosenbaum et al. (1996) suggested that the subjects who showed the end-state comfort effect did so only because they overestimated the precision requirements of the task. It seemed that participants' initial grasp choices were influenced by the anticipated precision or control needed at the end of the task. Further findings indicating that movements are not planned towards end-state comfort but rather towards a comfortable posture at the moment, when control is needed, have been reported by Hughes et al. (2012) and Künzell et al. (2013). Hughes et al. (2012) varied the precision demands at the beginning and end of a bar transport task and observed initial state comfort for 50 % of their participants. In the experiment of Künzell et al. (2013), participants had to grasp a bar and move it through obstacles of varying size at the beginning and end of the movement. Künzell et al. (2013) suggested that movements were planned for optimal control during the movement part that demands the highest precision.

In addition to the end-state comfort effect, Rosenbaum et al. (1993) observed a preference for grasping the handle with the thumb towards the pointer. Participants did not perform the same handle rotations, for example the rotation from position 1 to position 5 and the rotation from position 5 to position 1, with the same movements. Instead, they showed a tendency to grasp the handle with the thumb towards rather than away from the pointer. The authors called this effect, which they observed also in another experiment (Rosenbaum et al., 1992), the thumb-towards bias. They suggested that attentional factors explain the effect, as the thumb and index finger are more strongly associated with attention than the little finger.

A contrasting explanation for the thumb-towards bias was proposed by Herbort and Butz (2011). They interpreted the grip position as a habitual bias, as most tools used in everyday life are grasped with the thumb toward the functional end of the tool. Künzell et al. (2013) argued in favor of a habitual mode as long as no specific demands, like precision demands, require a cognitive-motor planning process. The aforementioned studies provided evidence that cognition and action are strongly interwoven. They indicated that people grasp objects depending on what they intend to do with them. Grasp selection seems to be influenced by the action goal and also by a habitual mode.

In line with behavioral studies, neurophysiological findings suggested that voluntary actions were planned and executed with their intended goal in mind. In a recent review Waszak et al. (2012) described that the medial frontal cortex seems to play a crucial role in linking actions to their predicted effects. The brain also seems to pre-activate the representation of the predicted action effect during action selection (Waszak et al., 2012).

In an fMRI study, van Elk et al. (2012), investigated the planning processes of object-directed actions using a motor imagery task. Participants had to imagine how to execute actions with familiar and unfamiliar objects based on goal- or grip-related information. They observed increased activation in parietal areas for unfamiliar objects and explain this with the involvement of parietal areas in motor imagery, which might take more effort for unfamiliar actions. For familiar objects, they observed increased activation in anterior prefrontal cortex and suggested that there is a stronger goal-representation for actions with familiar objects compared to unfamiliar ones.

There is neurophysiological evidence for different control mechanisms underlying goal-directed actions, which depend on the goal-posture. Most existing studies in this field focused on button presses, mental simulation, and action preparation intervals, but few studies investigated the planning and execution of overt complex actions by means of ERPs.

One example for such an ERP study is the work by van Schie and Bekkering (2007), who investigated neural mechanisms underlying immediate and final action goals for precision grips. They used a grasp and transport task and instructed either the grasp participants had to use (immediate goal) or the end position of the transport (final goal). Although participants executed the same overt movement in both conditions, Van Schie and Bekkering observed different ERPs for immediate and final action goals. The immediate goal was accompanied by a parieto-occipital slow wave, while the final goal was accompanied by a slow wave over left frontal regions. The authors suggested that the enhanced activation found in posterior parts for the immediate goal indicate this area's involvement in the prehension of the object, while the enhanced activation found in anterior parts for the final goal might indicate frontal involvement in the planning and control of sequential behavior. This research showed that different neural mechanisms control the action depending on whether the emphasis is on the immediate or final goal of an action sequence.

Westerholz et al. (2013) found a similar effect for the planning and execution of goal-related power grips, but with a distinct temporal pattern. They differentiated cerebral activity for the same action executed with an emphasis on initial vs. final parts of the movement sequence. In a grasp and transportation task, the relative emphasis was either on the grip (the immediate goal) or on the target location (the final goal). ERPs differed between immediate and final goal-cued conditions, suggesting different means of operation dependent on goal-relatedness. Differences occurred from -600 to -200 ms time-locked to movement end over right frontal areas. In accordance with previous findings (Van Schie & Bekkering, 2007; Filimon, 2010; Bozzacchi et al., 2012a), the results suggested that a parieto-frontal network is of crucial importance for grasp planning and execution.

A further experiment by Westerholz et al. (2014) indicated that ERPs differ between self-regulated and instructed conditions in a bar transport task, but only when the action effect is manipulated, suggesting different ways of operation dependent on goal-relatedness.

Bozzacchi et al. (2012a) suggested that action preparation is affected by the meaning of the action and by the awareness of being able to perform it. They performed an EEG study and compared the preparation phases of grasping for cup, impossible grasping of a cup (where the grasp was mechanically hindered) and reaching for a cup. In a related experiment, Bozzacchi et al. (2012b) recorded ERPs for a virtual grasp, a real grasp and a key-press. They suggested once more that action preparation is affected by the meaning of the action and that this is true for virtual actions as well.

The aforementioned studies served as a starting point for the present study. Participants executed a handle rotation task inspired by Rosenbaum et al. (1993). They had to grasp a handle and rotate it to a specified target position. The grip they used to take hold of the handle was either free choice or specified by the instruction. The specified instructions included two different types of grip. The grip was either a thumb-toward grip or a thumb-away grip. In the thumb-toward condition participants had to grasp the handle with the thumb or the base of the thumb toward the end of the handle that had to be rotated to the target position. In the thumb-away condition participants had to grasp the handle with the thumb or the base of the thumb pointed away from the end of the handle that had to be brought to the target position. The thumb-toward condition represented the use of a habitual mode, as in everyday life tools are mostly used with the thumb towards the functional end of the tool (Herbort & Butz, 2011). Thus, the thumb-away condition represented the use of a non-habitual mode. The aim of the present study was twofold. First, we aimed to extend existing knowledge for the execution of free choice and specified choice goal-related rotation tasks to the neurophysiologic field. Second, we aimed to differentiate between different neural control processes for action execution determined by the habitual mode and, thus, provide a more detailed account for pre-specified goal-related actions.

Previous studies (Van Schie & Bekkering, 2007; Westerholz et al., 2013; Westerholz et al., 2014) found different time windows in the time range from -900 to 0 ms time-locked to grasping for a grasp and transport task. This time range is of special importance for action planning and execution, when the same goal related action was executed but planned differently. The same studies found the time range from -1100 to 200 ms time-locked to movement end to be of importance for action planning and execution. As we investigated the planning and execution of a related task, a goal related grasp and rotation task, we hypothesized that neurophysiological processes, underlying grasping, reflect action planning in this time range.

As mentioned above, several studies (Van Schie & Bekkering, 2007; Westerholz et al., 2013) reported goal-related effects on motor control processes time-locked to grasping over parietal-occipital cortex. Based on these results, we predict differential cerebral activity for the habitual condition compared to the non-habitual condition over parietal occipital cortex time-locked to grasping. Those studies further reported goal-related effects time-locked to movement end over left and right frontal regions. Thus, we predict differential cerebral activity for the habitual condition compared to the non-habitual condition over left and right frontal regions time-locked to movement end. We predict no significant difference for the specified grip choice and free grip choice conditions, because the determination of the initial grip of an action sequence should have no major effect on the planning and execution of the whole action sequence.

We predicted that participants would show the end-state comfort effect in the free grip choice condition. Based on the results of Rosenbaum et al. (1993), we expected the end-state comfort planning to be most activated for the biomechanically most difficult postures, especially uncomfortable end postures. That is, for right hand grips the end-state comfort effect would be strongest at a 4 o'clock end position and for left hand grips it would be strongest at an 8 o'clock end position. In addition to the end-state comfort effect, we predicted that participants would act according to the thumb-toward bias (Rosenbaum et al., 1993) in the free grip condition. That means, participants would show a tendency to grasp the handle with the thumb toward the end which has to be rotated to the target position.

We predicted reaction times, reach times, and transport times to be faster for the habitual condition compared to the non-habitual condition. The habitual preference might show up in reaction, reach, and rotation times in the specified grip choice condition, in faster times for the habitual condition compared to the non-habitual condition. Rosenbaum et al. (1992) reported that, in general, participants reacted faster when they grasped a bar with the thumb towards a pointer than when they grasped away from it. The authors further suggested that reaching for the bar started before participants had finalized their handgrip decision, which must then have been completed while the hand was in motion. Other studies (Van Schie & Bekkering, 2007) have already reported faster times for habitual movements. Previous bar-transport experiments (Westerholz et al., 2013; Westerholz et al., 2014) have shown that not only the reaction time, reflecting planning processes before movement onset (Botwinick & Thompson, 1966; Elliott et al., 2010), but reach and transport times which represent online planning, motor implementation processes, and movement execution, were affected as well.

We predicted no significant difference for reaction times between the specified grip choice and free grip choice conditions, whereas we expected reach and rotation times to be faster for the free grip choice condition compared to the specified grip choice condition. Fleming et al. (2009) differentiated free and instructed choices and found similar preparation levels for both conditions, thus we expected no significant differences for reaction times. However, due to habitual reasons we expected that less decision making will be necessary in the free grip choice compared to the specified grip choice condition. These processes might show up after action initiation, when the hand is already in motion (Rosenbaum et al., 1992; Westerholz et al., 2013; Westerholz et al., 2014).

4.2 Materials and methods

4.2.1 Participants

Twenty eight healthy volunteers (mean age 25.43 years; SD 3.6; 18 females) with no known neurological impairments and normal or corrected-to-normal vision participated in the study. All participants were right-handed, which was evaluated with the Edinburgh Handedness Inventory (mean handedness score: 97.5)(Oldfield, 1971). All participants were compensated for their time with course credit or money. All participants provided written informed consent and the experimental procedure was approved by the ethics committee at Bielefeld University, and adhered to the ethical standards of the sixth revision of the Declaration of Helsinki.

4.2.2 Design and setup

Participants executed a grasp and rotation task under three different conditions (Fig. 4.1). Instructions included specified or free-choice grip postures and a specified goal-position, where the rotation had to end. The three conditions were: 1. Specified grip posture with the thumb facing towards the end of the handle which had to be brought to a specified goal-position; 2. specified grip posture with the thumb facing away from the end of the handle which had to be brought to a specified goal-position; 3. free-choice grip posture of whether the thumb was facing towards or away from the end of the handle which had to be brought to a specified goal-position.

Participants were required to reach for a handle which was connected to a disk, grasp it with a power grip, and turn it to a goal position. A white marker was located on the disk, at one end of the handle. When the handle was rotated, it turned the disk and the white marker. Depending on the position of the white marker, it could point to one of eight equally spaced white markers that were located just beyond the perimeter of the disk. The end of the handle that was facing the white marker was marked yellow, while the end of the handle that was facing away from the white marker was marked blue. A start button was located in front of the apparatus with the handle.

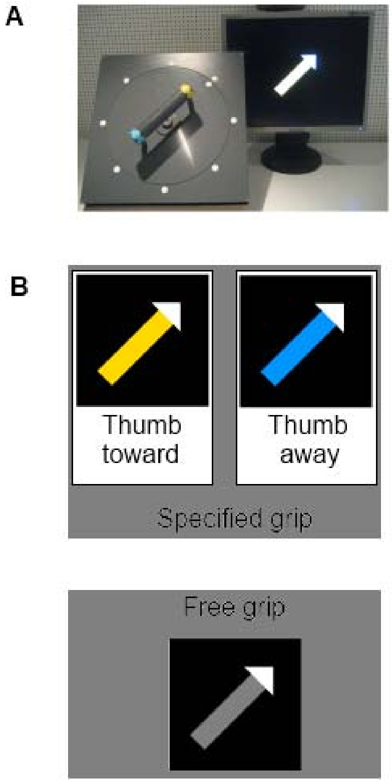

Figure 4.1: Task design. (A) Task setup showing the apparatus with the handle that had to be grasped with the thumb towards or away from the marker. Then it had to be rotated to a position indicated by the stimulus screen. (B) Possible stimuli for all conditions showing the grasp to use and the final orientation of the handle. Blue and yellow represent specified grips. A yellow arrow requires a grip with the thumb towards the yellow mark and thus towards the pointing direction. A blue arrow requires a grip with the thumb towards the blue mark and thus away from the pointing direction. A grey arrow indicates a free grip choice for the participant. The white arrow head points to the final orientation of the handle.

In each trial, a picture stimulus was presented indicating the grip posture and goal location. First, the handle had to be grasped and turned from its initial position to the final goal location. Then, participants had to press the start button shortly. Afterwards, the disk automatically turned to the next start position.

The bar had to be rotated 180 degrees on 80 % of all trials; these were the experimental trials. The remaining 20 % of trials required varying degrees of rotation and were used as filler trials. Every start position of the handle was used for the same number of trials. The order of start positions was randomized. The picture stimuli consisted of arrows, showing the grip posture and goal location. The arrowhead was white and pointed to the goal location. The color of the arrow's shaft, which was either yellow, blue, or grey, indicated the grip posture. Yellow indicated a grip with the base of the thumb facing towards the yellow marked end of the handle and thus towards the white marker. Blue indicated a grip with the base of the thumb facing towards the blue marked end of the handle and thus away from the white marker. Grey indicated a free choice between the two possible grip postures. Stimuli for all conditions were shown in a randomized order.

4.2.3 Procedure

Following electrode preparation, participants were seated comfortably in front of the table with the experimental setup. Participants received written instruction on the upcoming task. They were given information on how to grasp and turn the handle and were instructed to maintain stable posture and not to blink during trials. All questions they had concerning the instructions were answered.

The setup was calibrated to each participants' size to prevent expansive movements. The apparatus was positioned in front of the shoulder of the used arm and hand, such that participants could reach it comfortably with an extended arm. The start button was positioned in front of the apparatus, such that it could be reached with the hand comfortably. Participants were instructed to relax and not to tense up during the action. Picture stimuli were presented on a video monitor, which was located directly in front of the participant and laterally to the apparatus. Before the experiment started, participants performed short blocks of test trials until they performed the task correctly. These test blocks were also used to observe the EEG for obvious artifacts and were repeated until participants executed the task correctly in a relaxed state.

Each trial started when participants pressed the start button. First, a fixation cross for a randomized duration between 500 and 1500 ms was shown. Next, a picture stimulus was shown indicating the grip posture and the goal position of the handle. The stimulus remained on the screen until participants had reached the goal position. Participants were instructed to keep their gaze on the center of the screen throughout the movement. The next picture stimulus instructed participants to shortly press the start button. The disk then automatically turned to the next start position. Afterwards, a picture stimulus instructed the participants to press down the start button again, which started the next trial. The timing of all actions (hand lift, rotation start, rotation end) were registered. The experiment consisted of two blocks of 120 trials each. Participants used one hand for the first block and the other hand for the second block. They received instructions again for the second hand and also performed test trials until they performed the task correctly. Half of the participants performed the task with their right hand first, the other half performed the task with their left hand first. Participants repeated tasks for each of the specified grip conditions 48 times (24 with their left hand, 24 with their right hand) and for the free choice grip condition 96 times (48 with their left hand, 48 with their right hand). The stimulus presentation was controlled by Presentation® software (version: 14.1, www.neuro-bs.com). In a post-experiment questionnaire, participants rated the difficulty of the task for each condition on a scale from 1 (easy) to 6 (difficult).

4.2.4 Behavioral and electroencephalographic recordings

Behavioral recordings included the time points of lifting the hand off the start button, starting to turn the handle, and reaching the goal location. Micro switches were used to detect the exact moment they occurred. These events were recorded on the PC which was presenting the stimuli, as well as on the PC which was recording the EEG. Participants' performance was recorded with a video camera for later offline analysis.

EEG was recorded by a 64 channel amplifier (ANT). A WaveGuard EEG cap (ANT) with sixty-four Ag/AgCl electrodes was used. The electrodes of the cap were arranged according to the international 10-10 system (based on the 10-20 system)(Oostenveld & Praamstra, 2001). In order to detect ocular artifacts, EOG was recorded using four electrodes placed above and below the right eye and lateral to both eyes. During recording the data were average-referenced. The EEG was band-pass filtered (DC-138 Hz) and digitized at 512 Hz. The impedance of all electrodes was less than 5 kΩ.

4.2.5 Data analysis

Video recordings were studied offline for performance errors. A trial was rated as containing an error when the participant used the wrong grip, changed the grip during the execution phase of the movement, or let go of the handle before the required goal position was reached. Trials with performance errors were excluded from the analyses. For correct trials, grasp behavior was documented.

Participants' average reaction, reach, and rotation times were subjected to a repeated measures ANOVA, to determine within-subject effects for grip type (specified grip posture thumb towards, specified grip posture thumb away, free grip posture). Based on the results of the ANOVA relevant conditions were then compared pair-wise by means of t-test.

For the comparison between different specified grip postures, behavioral analyses for reaction times (time from stimulus presentation to lifting of the hand), reach times (time from lifting the hand to rotation onset), and rotation time (time from rotation onset to rotation end) were each done separately. Averaged reaction, reach, and transport times were each subjected to a paired t-test to determine the influence of the condition (specified grip posture thumb towards, specified grip posture thumb away).

For the comparison between specified and free grip postures, behavioral analyses for reaction times, reach times, and rotation time were each done separately. Averaged reaction, reach, and transport times were each subjected to a paired t-test to determine the influence of the condition (specified grip posture, free grip posture).

Electrophysiological data were band-pass filtered offline from 0.1 to 30 Hz and re-referenced to the average mastoid electrodes. Response-locked analysis to grasping included the time interval from -2200-1200 ms. That means, epochs started -2200 ms before turning the handle from the start position and ended 1200 ms after the rotation started. Response-locked analysis to movement end included the time interval from -3200-300 ms. That means, started -3200 ms before reaching the target position and ended 300 ms after reaching it. Baseline correction was performed on the first 100 ms of each interval. Ocular artifacts were corrected using the correction procedure of Gratton et al. (1983). Artifact detection was done using a peak-to-peak moving window approach. Epochs containing peak-to-peak amplitudes above the threshold of ±50 µV within a 200 ms window were rejected. This window was moved over the whole epoch in 50 ms steps. 33 % of the trials time-locked to grasping in the specified grip thumb toward condition, 34 % in the specified grip thumb away condition, and 33 % in the free grip posture condition were rejected due to artifacts. 34 % of the trials time-locked to movement end in the specified grip thumb toward condition, 36 % in the specified grip thumb away condition, and 34 % in the free grip posture condition were rejected due to movement artifacts. For a comparison of thumb towards and thumb away conditions, the ERP was averaged separately for both experimental conditions. On average 30 trials per participant for the thumb toward condition and 29 trials for the thumb away condition entered analyses time-locked to grasping. On average 29 trials per participant for the thumb toward condition and 28 trials for the thumb away condition entered analyses time-locked to movement end. For a comparison of specified and free grip conditions, the data for specified thumb towards and specified thumb away grips were averaged together to form the specified grip condition, which was then compared to the free grip condition. On average 60 trials per participant for the free grip condition and 59 trials for the specified grip condition entered analyses time-locked to grasping. On average 60 trials per participant for the free grip condition and 58 trials for the specified grip condition entered analyses time-locked to movement end.

The EEG data were averaged for the left and right hand to avoid handedness effects. Hence, further observed lateral activity should not be evoked by handedness.

Mean amplitude analysis of the electrophysiological data included the factors *Condition* (thumb towards, thumb away; and separately specified grip, free grip), *Front-Back* (anterior, central, posterior) and *Left-Right* (left, middle, right). For the assessment of effects of scalp distribution, we differentiated between nine regions of interest (ROIs; 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). The Greenhouse-Geisser correction was applied when evaluating effects with more than one degree of freedom.

We analyzed the data in 100 ms step windows. To correct for false positives we combined these time windows into one, if three or more consecutive windows revealed significant 3-way interactions for Condition, Front-Back, and Left-Right, as well as for according t-tests (Lange et al., 1999). In detail, we performed ANOVAs with the factors Condition (thumb towards, thumb away; and separately specified grip, free grip), Front-Back (anterior, central, posterior), and Left-Right (left, middle, right) for every single 100 ms time window of both epochs (time-locked to grasping and time-locked to movement end, incl. Greenhouse-Geisser correction where necessary). For time windows that revealed a significant 3-way interaction for Condition, Front-Back, and Left-Right, we performed t-tests for every ROI (see *Supplementary material related to chapter 4*). Only when three or more consecutive intervals reached the significance level ($p < 0.05$), these intervals were combined, that is we averaged the amplitudes, to one time window. As a result, we analyzed the time window from -600 to 200 ms time-locked to movement end for thumb towards and thumb away conditions. Thus, the following statistics contain time windows, which consist of series of consecutive 100 ms steps that were found significant.

No significant effects were found for thumb towards and thumb away condition time-locked to grasping. No significant effects were found for specified and free grip conditions, neither time-locked to grasping, nor time-locked to movement end.

4.3 Results

4.3.1 Behavior & difficulty rating

Participants executed the task correctly in 96 % of trials in both specified grip conditions. The remaining 4 % of trials were rejected. Participants executed the task correctly in 97 % of trials in the free grip condition. The remaining 3 % of trials were rejected. They grasped towards yellow and thus towards the white marker in 81 % of trials, and towards blue and thus away from the white marker in 16 % of trials. For the probability of grasping with the thumb towards the marker for every final orientation see Table 4.1.

Final orientation	Probability of grasping thumb-toward (Left hand)	Probability of grasping thumb-toward (Right hand)
1	1.00	0.89
2	0.94	0.90
3	0.90	0.80
4	0.83	0.52
5	0.72	0.69
6	0.55	0.85
7	0.83	0.88
8	0.95	0.96

Table 4.1: Grasp behavior. Probability of grasping with the thumb towards the marker in the free grasp condition for every final orientation for the left and right hand.

Participants rated the difficulty of the task in the specified grip thumb toward condition with 2.0, in the specified grip thumb away condition with 3.28, and in the free grip condition with 1.25 on a scale from 1 (easy) to 6 (difficult).

4.3.2 Timing

A two-way ANOVA with the factors time (reaction time, reach time, rotation time) and grip type (specified grip thumb toward, specified grip thumb away, free grips) revealed a significant interaction for time and grip type, $F(4, 108) = 58.8$, $p<0.001$. Following the results of the ANOVA, we conducted three paired-samples t-tests to compare each of the reaction times, reach times, and rotation times in the corresponding conditions (Table 4.2).

Reaction times were faster for specified grip thumb toward trials (651 ms) compared to specified grip thumb away trials (713 ms, $t(27) = -3.87$, $p < 0.001$). Reaction times were not significantly different for free grip trials (657 ms) compared to specified grip trials (682 ms, $t(27) = -1.73$, $p = 0.09$).

Reach times were faster for specified grip thumb towards trials (979 ms) compared to specified grip thumb away trials (1311 ms, t(27) = -11.62, p < 0.001). Reach times were faster for free grip trials (905 ms) compared to specified grip trials (1145 ms, t(27) = -10.3, p < 0.001).

Rotation times were not significantly different for specified grip thumb towards trials (1039 ms) compared to specified grip thumb away trials (1014 ms, t(27) = 0.9, p = 0.37). Rotation times were faster for free grip trials (1002 ms) compared to specified grip trials (1027 ms, t(27) = -2.25, p = 0.03).

Execution of the whole action sequence was faster for specified grip thumb towards trials (2669 ms) compared to specified grip thumb away trials (3039 ms, t(27) = -8.93, p < 0.001). Execution of the whole action sequence was faster for free grip trials (2563 ms) compared to specified grip trials (2853 ms, t(27) = -8.93, p < 0.001).

	Reaction time	**Reach time**	**Rotation time**	**Total execution time**
Habitual grip	651 (221)	979 (206)	1039 (228)	2669 (442)
Non-habitual grip	713 (293)	1311 (286)	1014 (194)	3039 (455)
Free grip	657 (198)	905 (193)	1002 (213)	2563 (395)
Specified grip	682 (256)	1145 (236)	1027 (199)	2853 (434)

Table 4.2: Average reaction, reach, rotation, and total execution time (in ms) and standard deviations (in brackets) for conditions that entered major analyses. For the specified grip condition data from the habitual grip and non-habitual grip condition were averaged together.

4.3.3 Electrophysiology

We conducted an ANOVA time-locked to movement end, which is the moment of reaching the goal position with the handle, with the factors Condition (thumb towards, thumb away), Front-Back (anterior, central, posterior), and Left-Right (left, middle, right).

The ANOVA for -600 to 200 ms revealed a significant 3-way interaction for Condition, Front-Back, and Left-Right, F(4, 108) = 3.84, p = 0.01. The 3-way interaction meant that the ERP amplitude differences between the thumb toward and the thumb away condition was different in magnitude for the various combinations of the factors Front-Back and Left-Right. The significant interaction permitted the separate comparisons of the thumb towards and the thumb away conditions in the various regions-of-interest. We performed a t-test for every ROI to determine if there was a significant difference based on Condition and in which ROI this difference was present. A significant negativity for the thumb away condition compared to the thumb toward condition was present in the AL-ROI, t(27) = 2.29, p = 0.03. A significant negativity for the thumb away condition compared to the thumb toward condition was present in the AR-ROI, t(27) = 2.16, p = 0.04 (see Fig. 4.2). No significant effects were found for the remaining ROIs.

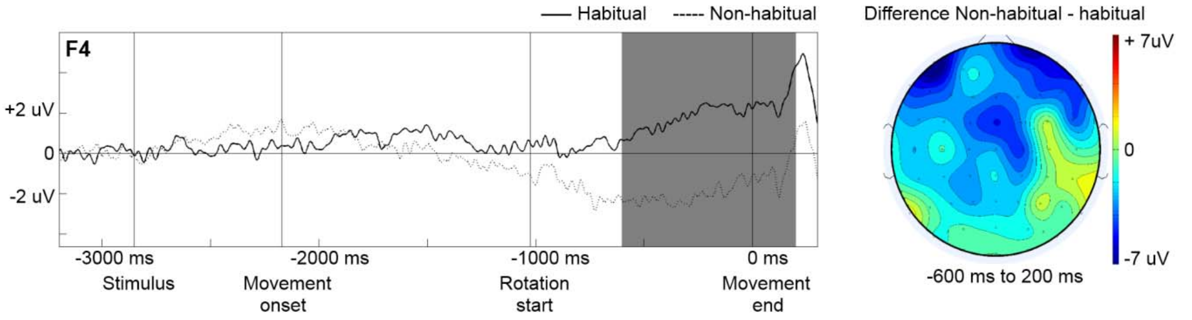

Figure 4.2: Slow wave brain potentials time-locked to movement end at electrode F4. (Left) Grand averaged ERPs recorded at electrode F4, time-locked to movement end, for the habitual (thumb toward) condition (solid) and non-habitual (thumb away) condition (dashed). The labels 'Stimulus,' 'Movement onset,' and 'Rotation start' mark the average time points of these events. (Right) Topography of the difference wave in the -600 to 200 ms time interval around movement end (indicated by the left grey selection) for the non-habitual condition minus the habitual condition.

4.4 Discussion

This study explored the neurophysiological mechanisms underlying the planning and execution of an overt goal-related handle rotation task. More specifically, we studied the neural basis of motor actions concerning the influence of the grasp choice. The aim of the present study was to differentiate cerebral activity between habitual and non-habitual grips, and between specified and free grip choices. In a handle rotation task, participants had to use thumb-toward (habitual) or thumb-away (non-habitual) grips to rotate a handle to a given target position. As predicted, the neural processes for action execution (measured by ERPs) differed between habitual and non-habitual conditions. We found differential activity between habitual and non-habitual conditions in left and right frontal areas from -600 to 200 ms time-locked to reaching the target position. However, no significant difference between both conditions appeared in analyses time-locked to grasping. In addition, we found no differential activity between free grip choice and specified grip choice conditions. The results indicated that the homing in phase of habitual and non-habitual actions were controlled by different neural processes which depend on the control requirements of the action. The results can be seen in line with the theory that anticipatory grasp choices are influenced by the demands of the task (Rosenbaum et al., 2012) and by habitual factors (Herbort & Butz, 2011).

Participants executed the task correctly in 96 % of trials in the habitual condition, 96 % of trials in the non-habitual condition, and, hence, in 96 % of trials in the specified grip condition, and in 97% of trials in the free grip choice condition. While this may have indicated that task difficulty did not differ between cueing conditions, participants rated the difficulty of the task in the non-habitual condition with 3.28, in the habitual condition with 2, and in the free grip choice condition with 1.25 on a scale from 1 (easy) to 6 (difficult). Thus, participants rated the non-habitual condition the most difficult. This confirmed our assumption that a thumb away grip was an uncommon grip, which our participants do not use habitually. However, the rating for the non-habitual condition provided a value near the middle of the scale between easy and difficult indicating that it was still unproblematic to execute the task.

In the free grip choice condition, participants showed a strong tendency to act according to the thumb-toward bias. They took hold of the handle with the thumb towards the pointer more often than away from the pointer for all target positions. The thumb-toward bias was much stronger than reported by Rosenbaum et al. (1993) and, therefore, stronger than we expected. An explanation for this discrepancy could have been the kind of stimuli used to instruct the task. Our stimuli consisted of an arrow with a white head pointing to the target position. This kind of visual stimuli might have drawn participants' attention more to the pointer than did the auditory stimuli used by Rosenbaum et al. (1993). Thus, the stronger thumb-towards bias found here could be explained with attentional factors (Rosenbaum et al., 1992).

Due to the strong thumb-toward bias, the end-state comfort effect was not as pronounced as expected. Participants showed a tendency to act according to the effect. Their tendency to grasp the handle with the thumb-toward the pointer was lowest for target position 6 for left hand movements and target position 4 for right hand movements. This was in line with the results reported by Rosenbaum et al. (1993). They found the lowest probability for thumb-toward grasps for the same target positions and suggested that a thumb-away grasp for these positions would ensure a more comfortable end posture and thus more precision and control for the homing in phase of the movement. In addition to the explanation offered above, the results for the end-state comfort effect could have been influenced by the participants' perceived precision needed near the end of the turning movement. The stimulus presentation on the video monitor changed and the task was registered as complete, when the target position was first reached. That means, it was not necessary to accurately end on the target position to complete the task, but rotating the pointer through the target position would have been sufficient. Participants could have realized this during the experiment and, accordingly, could have ignored the precision demands of ending on target. However, none of the participants reported using such a strategy in the post experimental questionnaire. Offline analyses of the video footage did not support the explanation either, participants seemed to act as accurate as possible.

Reaction times (from stimulus presentation to movement onset) were faster for the habitual condition compared to the non-habitual condition. Thumb-toward grips seemed to be the preferred movement choice for this task, as can be seen in the behavioral data for free choice grips. This might have explained the faster reaction times, as participants would most likely have chosen thumb-towards grips themselves, if the grips would not have been specified. The faster reaction times in the habitual condition further indicated that actions executed in the habitual mode require less cognitive effort. Reaction times did not differ significantly between free grip choice and specified grip choice conditions. This was in line with previous findings from our lab (Westerholz et al., 2014). The final effect of an action sequence seemed to be more important for action planning than initial grips. As the final effect of the action sequence did not change depending on whether the grip was specified or not, planning processes taking place before the action were not influenced essentially.

Reach times (from movement onset to rotation start) were faster for habitual compared to non-habitual grips. The differences could have been explained with more experience for the habitual action, as less decision making has to be done after action initiation compared to the non-habitual grips. Reach times for the free grip choice condition were faster compared to the specified grip choice condition. This result was in line with previous findings (Westerholz et al., 2013; Westerholz et al., 2014). Reach times for the free grip choice condition could have been faster because actions based on self regulation seemed to be more flexible and modifiable than actions based on an instructed plan (Fleming et al., 2009), which made online planning and motor implementation processes more effortless and, thus, faster.

Rotation times (from rotation start to rotation end) did not differ significantly between habitual and non-habitual conditions. This finding came as a surprise, as we expected the homing in phase to be faster for habitual grips. The behavioral results of the free grip choice condition, which show a strong tendency to use thumb-toward grips, suggested that a thumb-toward grip offers participants more control and precision at or near the target position (Rosenbaum et al., 1993). Maybe this advantage in control did not necessarily provide a temporal advantage as well. Rotation times were faster for free grip choices compared to specified grip choices. As participants were able to choose the optimal strategy, end-state comfort and/or thumb-toward, for every target position in the free grip choice condition, they executed their preferred homing in movement all the time, which were probably the fastest movements as well. In the specified grip choice condition, participants had to execute preferred and undesired homing in movements, which could have slowed down their average rotation times.

Consistent with the hypothesis that the neural processes for action execution would differ between habitual and non-habitual conditions, we observed differential frontal activity between both conditions. The differential activity occurred between -600 and 200 ms time-locked to reaching the final rotation goal. In the time window from -600 to 200 ms there was a negativity for the non-habitual trials compared to the habitual trials in the AL- and AR-ROIs. This seemed to fit with the assumption that the homing in phase was more difficult with the thumb held away from the pointer than towards the pointer (Rosenbaum et al., 1993). It also fitted with the assumption that frontal areas were involved in supporting final action goals and played a role in planning and control of sequential actions (Van Schie & Bekkering, 2007).

Note that participants executed the same rotation movements in both conditions. Thus, the movements themselves cannot explain the effect. Participants also finished rotations with the same posture in both conditions. Thus, the final posture cannot explain the effect per se. What differed between conditions was the combination of the movement and final posture. In other words, the difference was whether participants were homing in on the target location with their thumb toward the pointer or with their thumb away from the pointer. The cerebral activity could have represented this difference. The negativity for the non-habitual condition could have been due to more effortful control processes near the target location. Online planning and control processes in the non-habitual condition could have been more effortful because of less experience with thumb-away grips especially in conjunction with the critical part of the movement, as we observed no other effects during the action sequence.

One might wonder, if another explanation for the effect could have been a systematic eye-movement artifact. Participants could have focused their gaze differently during the homing in phase when grasping thumb towards compared to grasping thumb away. Rosenbaum et al. (1993) hypothesized that grasping thumb toward might be perceptually advantageous for such a task. Eye movements could have provided better visibility of the pointer close to the target position. However, as we instructed participants to keep their gaze fixed on the screen throughout the movement and we corrected for ocular artifacts using the procedure by Gratton et al. (1983), it was highly unlikely that eye-movements caused the observed effect.

To our surprise, we observed no significant effect in the time range from -900 to 0 ms time-locked to grasping for the non-habitual condition compared to the habitual condition. Reaction and reach time differences between the non-habitual and the habitual condition suggested planning and control processes to be easier, and thus faster, for the habitual condition. We expected such differences to appear in the neurophysiological data, based on previous findings (Van Schie & Bekkering, 2007; Westerholz et al., 2014). These previous experiments required participants to lift an object and place it down at a target location. In contrast, the present experiment did not involve a transport phase. The handle was connected to a disk and had to be grasped and rotated, its orientation changed but its location did not. Maybe the additional transport phase in previous studies (Van Schie & Bekkering, 2007; Westerholz et al., 2014) caused planning and control processes on a neural level, which do not occur for a rotation movement. Planning and control of the grip might require more precision for an action sequence that involves a transport phase, in order to pick up the object carefully and not to drop it. These suggestions are in line with the functional distinction of transport phase and grasping (Marteniuk et al., 1990).

As expected, we found no significant difference between the neural processes for action execution in free grip choice and specified grip choice trials. This result was in line with previous findings (Westerholz et al., 2014), which showed different cerebral activity between self-regulated and instructed conditions only when the action effect was manipulated. As we did not manipulate the action effect between conditions, no significant difference between the neural processes for both conditions was observed. In accordance with previous suggestions (Rosenbaum et al., 2012), this result may indicate that planning and execution of a movement sequence were not based on initial grips but on the final action effect, which, in this case, was also the moment that required most control. Specifying the action effect thus influenced planning processes for the action, while specifying the grip had no major influence for planning processes of the action, as the desired action effect could be reached regardless of which grip is used. The importance of action effects compared to initial grips has further been demonstrated in a study by Van Elk et al. (2008) whose participants were faster in judging the correctness of an action, when asked to focus on the goal of the action than when instructed to attend to the grip of the action. Our findings further support the idea that achieving optimal required control where it is most needed, is of crucial importance for action planning and execution.

For future research it might be of interest to focus on the investigation of the end-state comfort effect. Participants in our experiment showed a strong tendency toward the thumb-toward bias, while the end-state comfort appeared less often than reported before (Rosenbaum et al., 1993). Participants showed the end-state comfort effect in about 50 % of the trial for the most uncomfortable end-posture. A comparison of these thumb-toward and thumb-away grips in the free grip condition might help us to better understand anticipatory grip planning and execution processes. We did not compare any data for only one end-posture because of the reduced number of trials. A future study might focus on specific end positions to collect data for a comparison of comfortable and uncomfortable free grip choices. Another interesting idea for future studies would be a comparison between habitual specified vs. habitual non-specified grips, and non-habitual specified vs. non-habitual non-specified. This comparison would provide a more detailed account of differences between specified and non-specified grips. It could further demonstrate that the habitual grip type whether specified or not is faster and requires less cognitive effort. Our present dataset did not allow this comparison, as splitting the data did not result in enough trials for each condition to do valid analyses.

In sum, we found that reaction and reach times, as well as ERPs differed between habitual and non-habitual grasping actions, suggesting that actions in the habitual mode require less cognitive processing effort for control demanding parts of an action sequence compared to the non-habitual mode. Differences in neural activity occurred from -600 to 200 ms time-locked to reaching the target location of the rotation task in left and right frontal areas. To our knowledge, this is the first study to differentiate cerebral activity underlying overt goal-related actions executed with a habitual or non-habitual grip. Our results indicated that the planning and execution of goal-related actions were controlled by neural mechanisms which depended on the precision and control requirements of the action in the homing in phase.

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5 GENERAL DISCUSSION

This thesis is concerned with the neurophysiological underpinnings of motor control, more specifically with grasping. Motor control has its application in almost all fields of life, from high-level-sports, physical therapy, playing an instrument, and dancing, over language learning, communication, and handwriting to other everyday actions like cooking and grasping a cup to drink. When making voluntary movements, we usually take the final goal of the action into account. These anticipation processes demonstrate a cognitive component underlying motor control. To advance our understanding of the link between motor control and cognition, we investigated the neural mechanisms and cognitive components of motor and action control. Our focus lies on the neural and cognitive processes underlying the planning and execution of overt manual object manipulations. More specifically, we used EEG to investigate the processes underlying the planning and execution of goal-related grasp-and-transport as well as grasp-and-rotation tasks involving power grips. These tasks are known to elicit the end-state comfort effect (Rosenbaum et al., 2010) and, thus, are suitable to investigate cognitive processes underlying manual action. Here, we studied specific aspects of different movement sequences in three experiments. In our first experiment, we differentiated between initial and final goals of an action, while we focused on instructed and free goals in our second experiment. The third experiment finally investigated the habitual factor involved in the planning and execution of manual goal-related actions.

It has been shown that ERPs differed between initial and final-goal cued conditions in a grasp and transport task for precision grips (van Schie & Bekkering, 2007). This result suggested different means of operation dependent on goal-relatedness. The aim of CHAPTER 2 was to extend these results to power grips in a bar-transport task. Therefore we differentiated between cerebral activity and its temporal organization during power grips executed with an emphasis on either the initial or final parts of a movement sequence. Our results suggest that a parieto-frontal network of activation is of crucial importance for grasp planning and execution. They further indicate that power grip preparation and execution for goal-related actions are controlled by similar neural mechanisms as have been observed during precision grips, but with a distinct temporal pattern. Our results also support the notion that goal-directedness is an important mechanism underlying the planning and control of voluntary action.

Voluntary actions are associated with different decision processes, including the decision whether to act, what action to perform, and when to perform it (Haggard, 2008). The what-decision is of special importance for goal-directed manual actions and action anticipation, but most ERP studies, which tackled the what-decision of manual actions, focused on components that occur before action execution and simple movements like key presses (e.g. Shibasaki & Hallett, 2006). Studies investigating ERPs underlying the what-decision of the planning and execution of overt manual action are hard to find. Therefore, the aim of CHAPTER 3 was to differentiate between cerebral activity for self-regulated and instructed actions during the overt execution of a goal-related action, more specifically a bar-transport task. We found differential activity between free-goal and specified-goal conditions, but not between free-grasp and specified-grasp conditions. Our results support ideomotor theories as action preparation and execution processes differed depending on the action effect. That we observed no difference between free-grasp and specified-grasp conditions might further stress the importance of the final action effect or final action goal for action preparation and execution in relation to initial action goals.

Two main explanations for the end-state comfort effect have been suggested: more control during the critical movement phase (Rosenbaum et al., 2012) and a habitual system favoring movements that were rewarding in the past (Herbort & Butz, 2011). As neurophysiological studies for the overt execution of goal-related grasps are hard to find, the aim of CHAPTER 4 was to investigate the neural mechanisms underlying the overt execution of goal-related actions with a focus on habitual vs non-habitual grasps. In a handle rotation task, participants performed thumb-toward (habitual) and thumb-away grips (non-habitual) to rotate a handle to a given target position. Neural processes for action execution differed between habitual and non-habitual conditions. Our results indicate that the homing in phase of habitual and non-habitual actions are controlled by different neural activity which depend on the control requirements of the action sequence. They further suggest that less effort is needed to execute an action towards a goal in a habitual mode compared to a non-habitual mode.

Taken together, we have shown that the goal-relatedness of an action and habitual factors influence the planning and execution of voluntary action on a behavioral and a neural level. This influence is already present in early phases of a movement sequence and illustrates the relevance of cognitive aspects for action execution. As the effects we report in this thesis last for several hundred milliseconds, we can assume that they are not a mere reflection of motor activation but rather of cognitive processes, like motor planning. That the effects were not observed in stimulus-locked analyses further makes a pure reflection of sensorial processes highly unlikely.

5.1 Neurophysiology of grasping

The (human and non-human primate) brain has at least two distinct cortical motor circuits that contribute to voluntary action (Haggard, 2008). Both circuits converge on the primary motor cortex, which executes motor commands by sending them through the spinal cord towards the effectors. One circuit subserves voluntary action (which comprises the pre-supplementary motor area, the basal ganglia, and the prefrontal cortex), and the other subserves stimulus-driven actions (which comprises the parietal lobe and the lateral part of the premotor cortex; see review by Haggard, 2008). For the present thesis, the cortical areas are of primary interest, as the EEG reflects mainly cortical activity. As mentioned in the introduction, multiple cortical areas beyond the primary motor cortex are involved in movement control (Filimon, 2010), including the premotor cortex and the posterior parietal cortex. Traditionally, the parietal cortex has been considered as a sensorimotor association area, while frontal areas were responsible for voluntary action (Haggard, 2009). However, the exact roles of premotor and parietal areas for motor control seem controversial (Filimon, 2010). While some studies suggest that frontal areas might be closer to movement execution than parietal areas (e.g. Thoenissen et al., 2002), other studies indicate that the posterior parietal areas play a key role in voluntary actions (Desmurget et al., 2009, 2012; Desmurget & Sirigu, 2009). The results of Desmurget et al. (2009) suggest that the presupplementary motor area might be responsible for the preparation of motor commands for voluntary action, while the inferior part of the posterior parietal cortex might generate sensory representations of the predicted consequences of the movement (Haggard, 2009). Different studies showed that different fronto-parietal circuits plan the same grasp and place task, when the relative emphasis is either on the end-state of the movement sequence, or on the selection of the initial grasp (Majdandzic et al., 2007; Van Schie & Bekkering, 2007).

What do the results of the studies described in the previous chapters suggest about the functionality of fronto-parietal networks? In the following, our results concerning the frontal areas are discussed, followed by a discussion of the parietal areas involved in the planning and control of grasping.

First of all, we have to mention again that the EEG reflects mainly cerebral activity and has a limited spatial resolution. Therefore, the following discussion will be based on frontal and parietal regions, but not on specific brain structures.

5.1.1 Frontal regions of interest

Medial frontal brain areas have been associated with the planning of actions in relation to an intended target location (Majdandzic et al., 2007) and the planning of movement sequences (Rowe et al., 2000; Shima & Tanji, 2000; Rushworth et al., 2004). These areas have also been reported to be involved in maintaining a final goal in working memory while processing subgoals (initial goals), as in the Tower of London task (Koechlin et al., 1999; Burgess et al., 2000; Sakai et al., 2002). Stronger activation measured by fMRI (Majdandzic et al., 2007; Rowe et al., 2000; Koechlin et al., 1999) in frontal regions could reflect that participants maintained a stronger goal-representation throughout an action.

Experiment (described in Chapter)	Time window	Time-locking event	ROIs	Effect	Possible functional processing
1 (2)	-700 -200	End	**AR**	Positivity for immediate vs final goal-cued	Planning & control
2 (3)	-1100 -700 -500 0	Grasping	**AZ**, CZ	Negativity for specified vs free goal	Planning
2 (3)	-1900 -1400	End	**AR**	Positivity for specified vs free goal	Planning & anticipation
3 (4)	-600 200	End	**AL, AR**	Negativity for thumb away vs thumb toward	Planning & control

Table 5.1: Major frontal effects. The table shows the number of the experiment and in which chapter this experiment is described, the time window in which the effects occurred, in relation to which time-locking event, in which region of interest, what kind of effect was observed and its possible functional processing.

Chapter 2 reported a positivity for the immediate compared to the final goal-cued condition in frontal regions -700 to -200 ms time-locked to movement end. The effect indicates frontal involvement in the planning and control of sequential behavior (Van Schie & Bekkering, 2007). Van Schie and Bekkering (2007) speculated that "a coordinated monitor-and-control mechanism [...] pulls behavior in the direction of specific action goals" (p.192). Such processes might be more effortful in the immediate goal cued condition because the focus has to be readjusted from the initial to the final goal, this might require enhanced online planning and control processes. The joint activation of an immediate followed by a final goal might cause conflicts or errors in task performance (Van Schie & Bekkering, 2007). By contrast, the whole movement sequence might be based on continuous processes and pulled in the direction of one specific action goal when the movement is planned towards the final goal. This would also fit in with the suggestion that frontal areas are responsible for the preparation of motor commands for voluntary action (Desmurget et al., 2009). This preparation might require less effort when the movement is planned specifically towards the final goal, in comparison to planning towards an initial goal and subsequent readjustments towards the final goal.

In chapter 3, we reported differential activity between specified and free goal conditions in mid-frontal, mid-central, and mid-parietal regions from -1100 to -700 ms and -500 to 0 ms time-locked to grasping and in anterior right regions from -1900 to -1400 ms time-locked to movement end. We observed a negativity for the specified compared to the free goal condition in mid-frontal and mid-central regions from -1100 to -700 ms and -500 to 0 ms time-locked to grasping. These findings are in line with the suggestion that the frontomedian cortex plays a crucial role in intentional actions (reviewed by Krieghoff et al., 2011). The mesial precentral area might reflect the imminence of an already planned movement (Desmurget et al., 2012). The negativities, reported in chapter 3, might suggest more effortful planning processes for instructed actions as compared to self-regulated actions. Self-regulated actions might be more habitual and, thus, seem to have an easier-to-access mental representation of these actions.

We further observed a positivity for the specified compared to the free goal condition over right frontal areas from -1900 to -1400 ms time-locked to movement end. As the effect appeared in response-locked analyses but not in stimulus-based analyses, it is unlikely that the stimulus caused the effect. We suggested in chapter 3 that the positivity might reflect early movement planning and anticipation processes of the action sequence. Analyses time-locked to movement *onset* confirmed the location of the effect over right frontal areas, while the temporal occurrence of the effect (from 600 to 1200 ms) might hint towards online-planning and control processes. This assumption is in line with the suggestion that frontal areas are involved in the planning and control of sequential behavior (Van Schie & Bekkering, 2007), and would also go along with the suggestion that frontal areas are responsible for the preparation of motor commands for voluntary action (Desmurget & Sirigu, 2009).

In chapter 4, we report a negativity for the non-habitual compared to the habitual condition in left and right frontal areas from -600 to 200 ms time-locked to reaching a target position. Here, too, the effect fits with the assumption that frontal areas are involved in the planning and control of sequential behavior (Van Schie & Bekering, 2007) and that frontal areas are responsible for the preparation of motor commands for voluntary action (Desmurget et al., 2009). Together with the according reaction times, the effects suggest that non-habitual actions require more cognitive effort for the control demanding phase of a movement sequence compared to habitual actions. The precision control required for the homing-in phase of the current handle rotation task seems to be more effortful under non-habitual conditions.

One might wonder why we found a frontal positivity in chapters 2 and 3, while we found a negativity in chapter 4. First of all, in every experiment, we saw one condition as more similar to the execution of everyday actions and, thus, as the standard way of processing. Technically this could be called the control condition. The other condition is deviating from this standard. Depending on whether the deviation is more negative or positive than our standard we refer to it as a negativity or a positivity. That we found a negativity for the standard condition in chapters 2 and 3, but a positivity in chapter 4 might be due to different instructions and different task demands (Kutas et al., 1977; Meiran et al., 2014). These different task demands were a transportation phase, which was present in chapters 2 and 3, but not in chapter 4, different angles of rotation (no rotation in chapter 2; 90° in chapter 3; 180° in chapter 4), and higher precision demands at the end of the movement in chapter 4 compared to chapters 2 and 3. In chapters 2 and 3 a grasp-and-transport task was executed that required lifting and placing of an object, while chapter 4 featured a grasp-and-rotation task that required neither lifting nor placing of an object. Thus, grip forces might have been more important in chapters 2 and 3 because of the required transport phase compared to chapter 4. Further, the task in chapter 4 required an extended rotation movement and more final precision control than the tasks executed in chapters 2 and 3. Although a power grip was used in all experiments, the task in chapter 4 required high precision demands for the homing in phase of the rotation movement. This experiment might actually have been one of the first ERP studies on the overt execution of a precision task that required a power grip. This combination of power grip and precision control might offer possibilities for future research and might further clarify the role of frontal activity for motor control.

Frontal effects, reported in chapters 2 and 3, were observed over just one hemisphere but not bilaterally, although participants had to perform the action with both hands to avoid handedness effects. It is possible that left-handed actions require more demanding planning and control processes for right-handers, than actions executed with the right hand (Bozzacchi et al., 2012a, 2012b; Di Russo et al., 2005). As the majority of participants in our present studies were right-handed (18 out of 18 in ch. 2; 21 out of 24 in ch. 3), the aforementioned effects might explain why we observed right frontal activity only. Other studies suggested that movements of the right (dominant) hand only activate contralateral areas, while movements of the left (non-dominant) hand activate bilateral areas (Kawashima et al., 1993; Bai et al., 2005). This bilateral activity for left hand actions would be more intense, than the contralateral activity for right hand actions. Strong ipsilateral activation that has been observed in the left hemisphere during left-hand movements seemed to be related to task complexity (Verstynen et al., 2005). The activation was present for right-handed and, to a lesser degree, left-handed individuals (Verstynen et al., 2005). Grabowska et al. (2012) reported that the preferred hand (either left or right) was controlled mainly by the hemisphere contralateral to that hand and that the non-preferred hand was controlled by both hemispheres. They furthermore reported that participants, who were forced to switch handedness from the left to the right hand during childhood, shared features of left- and right-handers regarding their motor control architectures. Unfortunately, we do not have sufficient information about the proportion of participants, who were forced to switch handedness, in our samples. Furthermore, research on handedness is oftentimes based on the activation of the motor cortices, while it remains unclear whether cognitive control functions of grasping, which we are interested in, are lateralized in terms of functional brain processing.

Flores-Medina et al. (2013) investigated the contribution of each brain hemisphere for different types of complex movements in patients with left or right hemisphere stroke. They differentiated between transitive (tool use) and intransitive (communication gestures) goal-oriented actions. They suggested that the neurocognitive representations of both kinds of complex movements differ. While transitive actions showed a bilateral distribution, intransitive actions showed a preferential left hemisphere representation. They suggested that movements requiring tool use demand higher neurocognitive processing compared to more automatic movements like communication gestures. The bilateral activation reported in chapter 4 might reflect the precision demands required for the task. This might have demanded higher processing costs compared to the experiments in chapters 2 and 3, which resulted in unilateral frontal effects. However, further research is needed on the role of left vs. right handedness in ERP research on manual action. This could possibly be a study including left - right execution as an experimental factor or investigating various handedness groups (dominant left, dominant right and ambidexterous).

5.1.2 Parietal regions of interest

Parietal areas are involved in mental imagery of actions. This process takes more effort for difficult, novel, and unfamiliar actions or manipulation of unfamiliar objects (de Lange et al., 2005, 2006; van Elk et al., 2012). Posterior parietal activity is affected by the goal of the action and by the awareness of being able to perform this goal (Bozzacchi et al., 2012a, 2012b). Parietal activity has been associated with the execution and online monitoring of reaching and grasping (Majdandzic et al., 2007; van Elk et al., 2010; van Schie & Bekkering, 2007). The observation of an incorrect hand-object interaction might also affect parietal activity (van Elk, Bousardt et al., 2012).

Experiment (described in chapter)	**Time window**	**Time-locking event**	**ROIs**	**Effect**	**Possible functional processing**
1 (2)	-600 -200	Grasping	**PL, PM, PR**	Negativity for immediate vs final goal-cued	Anticipated sensory representations of movement effects
2 (3)	-500 0	Grasping	AZ, CZ, **PZ**	Negativity for specified vs free goal	Control or generation of movement intentions

Table 5.2: Major parietal effects. The table shows the number of the experiment and in which chapter this experiment is described, the time window in which the effects occurred, in relation to which time-locking event, in which region of interest, what kind of effect was observed and its possible functional processing.

Chapter 2 suggests that parietal areas are of crucial importance in the planning and execution of grasping movements. An effect between immediate and final goal conditions was observed in parietal regions -600 to -200 ms time-locked to grasping. Following the suggestion of Van Schie and Bekkering (2007) for a comparable effect over parietal areas, the negativity for the immediate goal might indicate this area's involvement in the prehension of the object. A quite similar suggestion is that the effect reflects a representation of hand-object interaction (Van Elk et al., 2012). The effect, observed in chapter 2, might represent a stronger focus on the grasp in the immediate goal cued condition compared to the final goal cued condition shortly before grasping. Another explanation might be derived from the work of Desmurget et al. (2009), which suggests that parietal areas might generate sensory representations of the anticipated movement consequences. This might require enhanced activation for the immediate goal cued condition, as it is harder to anticipate the consequences of the movement based on an initial goal. Planning and execution of a grasp and transport action might be easier based on a final goal due to habituation, as we usually grasp things for a purpose (e.g., a cup to drink from it or place it on a cupboard).

In chapter 3, we reported differential activity between specified and free goal conditions in mid-parietal regions from -1100 to -700 ms and -500 to 0 ms time-locked to grasping. We observed a parietal negativity for the specified compared to the free goal condition in the time interval directly before grasping from -500 to 0 ms. The negativity might reflect a more effortful prehension movement (Van Schie & Bekkering, 2007) for the specified goal condition, but could also be due to the generation of movement intentions in relation to their predicted consequences (Desmurget & Sirigu, 2009). It might be more effortful to generate these intentions based on a specified response, as it has already been suggested that freely chosen actions might be more flexible and modifiable then instructed plans, which produce a rapid specific response (Fleming et al., 2009).

In chapter 4, in contrast to the studies in chapters 2 & 3, we observed no significant effect over parietal areas time-locked to grasping between both conditions. This might be due to the fact that the studies from chapters 2 & 3 required participants to lift an object and transport it to a target location, while the study in chapter 4 did not involve a transport phase. Planning and control of the grip might require more precision when a transport phase follows, as grip forces and placement of the fingers on the object are more important as the possibility of losing grip of the object is much higher, when the object has to be lifted.

In chapter 3 and chapter 4, grip choice (free vs. specified) had no significant effect on the ERP amplitudes. These results are in accordance with previous suggestions (Rosenbaum et al., 2012) that planning and execution of an action sequence are based on the control demanding moment of the action. This moment was the final goal of the action in the reported experiments and not the grasp, which was an initial goal of the movement sequence. Thus, following the suggestion that parietal areas of the brain generate sensory representations of the predicted consequences of a movement (Desmurget & Sirigu, 2009), we would expect no significant effect between free and specified grip conditions, because the predicted consequences of the movement do not change whether the grip is specified or not.

In sum, chapters 2, 3, and 4 confirm the importance of parieto-frontal circuits for grasping. We can further claim that the activity in those circuits in our studies depended on the task. This claim is based on the observation that no differential activity occurred over parietal areas when the movement sequence involved a rotation phase instead of a transport phase after grasping. Chapters 2 and 3 suggest that the goal of an action sequence is involved in planning and execution processes of the action sequence. It seems that this involvement is reflected in the neural activity of parieto-frontal circuits underlying the action. Furthermore, a habitual factor seems to influence cerebral activity in parieto-frontal circuits. As has been shown in chapter 4, actions executed in a habitual mode seem to require less cognitive effort, and might facilitate preparation of motor commands in frontal areas. Overall, according to our studies, it seems likely that frontal areas are responsible for the preparation of motor commands for voluntary action and parietal areas generate sensory representations of the predicted consequences of the movement (Haggard, 2009; Desmurget & Sirigu, 2009).

5.2 A hierarchical view of the motor system & the ideomotor principle

Several studies have suggested a hierarchical view of the motor system, in which lower-level action features (like grasping an object) are determined by higher-level action features (the goal of the movement) (Grafton & Hamilton, 2007; Rosenbaum et al., 2007; Cooper, 2002; van Elk, Bousardt et al., 2012). In accordance with this view, studies have reported more effective planning processes, in terms of faster reaction times (van Schie & Bekering, 2007; van Elk et al., 2012) or lower error rates (van Elk, Bousardt et al., 2012), when action sequences are planned in relation to the final goal of the sequence compared to initial goals. The hierarchical view of the motor system and the ideomotor principle are closely related. The ideomotor principle could be a functional mechanism underlying the effects observed in the present experiments. As mentioned before, no significant effect appeared between free grip choice and specified grip choice trials in chapters 3 and 4. These results suggest that the action sequences in our experiments were planned and executed in relation to the final goal of the action sequence. This supports the ideas of a hierarchical view of the motor system and the ideomotor principle.

Bernstein (1975) already made suggestions which neurophysiological structures matched the levels of his hierarchical model of motor control. He even made an assumption concerning fronto-parietal areas we discussed previously. Bernstein (1975) suggested that frontal areas are mainly responsible for planning and executing movements and, thus, for the generation of a model for the needed future. According to Bernstein, sensory related systems are located in parietal areas, which are mainly responsible for providing a model of the past. We agree that frontal areas are involved in a creation or generation process as we concluded from our studies that frontal areas are responsible for the preparation of motor commands for voluntary action. While Bernstein (1975) describes the parietal areas as the receiving end of an information system, our data suggest that parietal areas generate sensory representations of the predicted consequences of the movement. This is in line with the position that no separate localizations exist for a model of the needed future but that frontal and parietal areas are inter dependent and, apparently, have to work together in a network.

Note that not all neurophysiological structures that Bernstein (1975) assigned to the levels of his model can be investigated with EEG. The nucleus ruber and rubrospinal tract Bernstein assigned to level A of his model are structures lying too far away from the scalp to cause a significant signal for the EEG. Activity of the striatum and thalamus (assigned to level B and C as well) will not be identifiable. The pyramidal and extrapyramidal motor system (assigned to level B and C) largely originate at the cortex and could therefore generate a few signals detectable with EEG there (Trepel, 2012). Thus, neither the neurophysiological activity of level B neither that of level C are suitable for a direct investigation using EEG. Level D is completely cortical and, therefore, appears suitable for EEG analyses, taking into consideration the usual limitations of EEG that a sizeable population of neurons needs to be synchronously active and needs to have a certain geometric configuration (Regan, 1989).

Even though we cannot fully map our findings to Bernstein’s theoretical model, the insights may be of value for future work concerning the model and its underlying neural mechanisms. As we are especially interested on this link between cognition and motor control, we chose to try to integrate our neurophysiological findings into the elaborated model on the cognitive architecture of complex movements (Schack, 2004). This elaborated model stresses cognitive aspects underlying motor control. We attempt to suggest neurophysiological underpinnings of Schack’s (2004) cognitive model. The levels of this model have counterparts in Bernstein's model (see section 1.1, Table 1.2) and their suggested matching neurophysiological structures. As mentioned in the introduction, Schack's (2004) model describes that the cognitive architecture of complex movements is organized over four hierarchical levels. These are a mental and a sensorimotor control level, as well as mental and a sensorimotor representation level. The levels of sensorimotor control and representation are responsible for the functional manipulation of objects and the environment, while the levels of mental control and representation are responsible for functional and distal processing of objects and events. As there is an interplay of the different levels of movement architecture it is not possible to ascribe the effects found in our experiments uniquely to a single level. The effects will be discussed below in relation to the levels that probably were the major factors underlying action organization.

Chapter 2 demonstrated that goal-directedness is important for planning and control of voluntary action. ERPs differed between immediate and final goal-cued conditions time-locked to movement end. On a theoretical level, these effects might reflect different mental representations. The level of mental representations is responsible for the transformation of an anticipated action goal into a movement program suitable to reach that goal (Schack, 2004). Although the same movements were executed in both conditions the transformation process from action goal to movement program needed to be different, as the emphasis was on either the immediate or the final goal of the movement sequence and, thus, the action goals were not the same. This also fits with the suggestion of van Schie and Bekkering (2007) that enhanced activation found in anterior parts for the final goal might indicate frontal involvement in the planning and control of sequential behavior. We also observed different ERPs between immediate and final goal-cued conditions time-locked to grasping. This differential activity occurred from -600 to -200 ms before grasping and might show processes responsible for the transformation of the intended action effects into action goals. These processes might be ascribed to the level of mental control. As the same movements were executed and the same sensory effects were reached in both conditions, no major differences should have occurred on the levels of sensorimotor control and sensorimotor representation.

In chapter 3, we explained that human actions are characterized as either more intention-based or stimulus-based, and that, in most cases, stimuli and intentions interactively lead to a response (Goschke, 2003). We then focused on one aspect of voluntary action and manipulated the what-decision of manual action, as there is little evidence from studies investigating ERPs underlying the what-decision of the planning and execution of overt manual action. This manipulation might have taken place on the levels of mental control and sensorimotor control, as these levels are responsible for the control of intention-based and stimulus-based actions (Schack, 2010). Since our experiment did not feature purely intention-based and stimulus-based conditions, both control levels would have contributed to the execution of the experimental task. In the free target-position conditions the level of motor control might have been more important for motor control as compared to the specified target-position conditions, because the free conditions can be considered more intentional compared to the specified conditions. The level of sensorimotor control might have been more important for movement control in the specified conditions compared to the free conditions, as the specified conditions can be considered more stimulus based than the free conditions. This might have led to the negativity over mid-frontal, -central and -posterior areas for the specified condition compared to the free condition from -1100 to -700 and from -500 to 0 ms time-locked to grasping, and the right-frontal positivity for the specified compared to the free condition from -1900 to -1400 ms time locked to movement end.

In addition, our results from chapter 3 also suggest that differences between free target-position conditions and specified-target position conditions occurred on the levels of mental and sensorimotor representations. This suggestion is based on the finding that the specification of the goal and, thus, of the action effect, but not of the grip influenced planning and control processes on a neural level. These kinds of sensory goal effects and effect-oriented adjustments of the movement are suggested to be integrated on the mental and sensorimotor representation levels (Schack, 2004).

The results reported in chapter 4 concerning the habitual control of movement might have been integrated on the level of mental representations, as effect-related information that change depending on expertise and learning processes are represented here (Schack, 2004). The reported effects also depended on goal-relatedness and, thus, sensory effects of the movement, suggesting processing on the level of sensorimotor representation. Overall, due to the limitations of the EEG and the interplay of the different regulation and representation levels, we can only make first and tentative proposals regarding the neurophysiological bases of the levels of movement organisation. To solve this issue and investigate the contribution of each level of action organization and its underlying neural mechanisms, future research, that directly targets the organization of goal-related grips is necessary.

5.3 Perspectives

Altogether, it has been shown in chapters 2, 3, and 4 that ERPs are suitable for the investigation of overt complex actions like grasp-and-transport and grasp-and-rotation actions. The usage of ERPs does not have to be restricted to movement preparation processes or simple movements like key presses. We can confidently state that ERPs are a valuable research tool for the investigation of the cognitive processes underlying the overt (and non delayed) execution of manual actions. Thus, our studies can be used as a base for future studies on the neurophysiological correlates underlying the overt execution of manual action.

The tasks used in the present experiments, grasping bars, may not be a model for all everyday actions. However, the idea for the experimental settings described in chapters 2, 3, and 4 originated in the observation of a waiter who grasped glasses, which were standing upside-down on a table, with an uncomfortable grip in order to hold them in a comfortable posture when he was pouring water into them (Rosenbaum et al., 2012). Grasping glasses is certainly an everyday action, and the effect has been shown in overturned glass tasks (e.g., Herbort & Butz, 2011; Knudsen et al., 2012; Logan & Fischman, 2011) as well as in bar-transport tasks. Thus, we argue that a bar-transport task is an adaptation of an everyday activity to a laboratory setting and can be generalized to everyday action. For future studies, the overturned glass task or other tasks using everyday objects should be used to get results that are even closer to everyday activities and, thus, might be more applicable for real life.

It might also be of interest to see how our results can be transferred and extended for sports settings. Many sports require grip choices (e.g. climbing, Judo), while others require the anticipation of object manipulations including grip postures (e.g. table tennis). Streuber et al. (2012) investigated the influence of visual information in table tennis. They found that visibility of the ball was of major importance when preparing a response stroke, but that the opponent's body and racket were also important. Future research might go into more detail and investigate the importance of the grip used to hold the racket. Bläsing et al. (2014) reported that expert climbers represent different artificial climbing grips based on their functional features, in contrast to novices who represent the grips based on their shape and color. According to these authors, this finding demonstrated the cognitive organization of climbing skills in experts. The neural processes underling the execution of grasps used in climbing were not investigated in that study. Piras et al. (2014) investigated visual search strategies in Judo during the execution of the first grip and found no connection between main fixation area and the target of their grip. This result suggests that fixations were not target-directed but aimed at anticipating the opponent's movement in order to execute a successful first grip. The grip selection process itself was not investigated. Knowledge about the underlying neural mechanisms and the timing of these, mostly very fast executed, grips could be used in sports training and rehabilitation.

Further knowledge about neural mechanisms underlying grasping and, more general, manual actions could also help in the development of a humanoid robot platform suitable for interaction scenarios with humans. Humans express their will and shape the world by performing motor actions. When people interact with technological systems like robots, they act on the control elements for those systems. To build a robot that is able to anticipate the will and, thus, the motor actions of a human, the cognitive and motor processes involved in action generation and interaction have to be understood (Schack & Ritter, 2009, 2013). One essential part of the action system seems to be action recognition (Jeannerod, 2006), a similar concept similar to the relation between speech production and speech recognition. Action recognition serves important functions. If one can recognize an action, one can interpret the social meaning of it. This also applies to human robot interaction. A service robot that is supposed to anticipate a human's requests has to recognize not only motor actions but their social meaning and the mood of the human. The other way around, it is easier for people to accept and work with a robot if people can recognize and understand the robots actions and intentions. Action recognition furthermore facilitates the learning of that action. Thus, improved action recognition might help robots to learn human like movements and humans to learn from robots, e.g., in a rehabilitation setting.

In the experiments reported above, we compared ERP waveforms from different conditions and found slow shifts in brain potentials, while special ERP components did not occur. This did not come as a surprise, as we focused on the neural mechanisms underlying grasp planning and execution, starting with an experiment in relation to the work of van Schie and Bekkering (2007), who found slow shifts in brain potentials as well. However, as the investigation of well-known ERP components is of interest for potential future studies on manual action and as one might have expected some components to occur in our experiments, we discuss in the next paragraphs how the LRP, P300, N400, and CNV could be investigated in studies following our work.

Experiments focusing on analyses of the lateralized readiness potential (LRP), which is thought to reflect the preparation of motor activity on a certain side of the body, need to be designed to maximize hemispheric differences in the electrical scalp signal of motor activity. To analyse the LRP one needs stimuli which indicate left-hand responses and stimuli which indicate right-hand responses (e.g., Luck, 2005; Kadosh et al., 2007). It does not necessarily have to be the imperative stimulus which indicates the hand in order to record LRPs. This can also be done using techniques like precues as described by Miller and Mordkoff (Mordkoff, Miller, & Roch, 1996; Miller & Low, 2001; Danek & Mordkoff, 2011). In any case, a stimulus must indicate which hand the participant should prepare for the response, so that a period of response preparation occurs. The stimuli used in our experiments contained no information about which hand to use on the next trial. For every block of our experiments participants used only one hand, which was assigned before the block started. For every single trial participants knew in advance which hand to use and prepare for the upcoming response, accordingly, our study designs were not suitable to investigate the LRP.

Future research might investigate the LRP in similar experiments. The conditions of interest could each be assigned to one hand and within one block, with the assignment of conditions to hands counterbalanced across blocks. This approach might be more prone to movement artifacts, as participants cannot leave one arm in a resting position throughout each block of the experiment. Now that we have shown that the investigation of overt manual actions is possible using ERPs, the investigation of the LRP might be a promising approach for future studies, given that participants are instructed and trained to move each arm independently from a relaxed resting posture in a comfortable way.

Another prominent component that has been used to investigate motor preparation processes is the contingent negative variation (CNV). The CNV usually appears between a warning stimulus and a target stimulus. Our experiments contained no warning stimulus, but follow up studies could easily integrate a warning stimulus to further investigate the motor and non-motor preparation processes of the experimental tasks. CNV amplitude seems to increase with more preparatory information given by the warning stimulus (Ulrich et al., 1998) and with task difficulty (Frömer et al., 2012). Thus, for the experimental setup used in chapter 2, one might expect increased CNV amplitude for the immediate goal-cued condition compared to the final goal-cued condition, because in the immediate goal-cued condition grip and target location were given, while in the final goal-cued condition only the target location was given. For the experimental setup in chapter 3, one might expect increased CNV amplitude for the specified conditions compared to the free conditions. For a comparison of habitual and non-habitual actions one might expect increased CNV amplitude for non-habitual actions, because they might require more cognitive processing effort than non-habitual actions, as discussed in chapter 4.

The P300 reflects processes involved in stimulus evaluation or categorization (Luck, 2005). It appeared in none of our experiments. This did not seem surprising, as our stimuli did not present any grasp that could be evaluated or categorized. For movement-related, research stimuli containing or implying a movement might be necessary (as for example in the work of Jin et al., 2011 & Taliep et al., 2008). The stimuli used in the present experiments would have to be changed accordingly to investigate the P300. A hand could be added to the stimuli to imply either the grip that has to be used or the final posture. A stimulus could, for example, show a hand which is grasping a bar to imply the grip or a hand holding a bar in the final posture. An uncommon grip or final posture, and, thus, an improbable (but task-relevant) movement might lead to a P300.

There is an interesting parallel between action and language in that both seem to be organized in a hierarchical system. Actions constitute a specific relation between an actor and an object . A similar statement can be made about verbs in spoken language (Gallistel, 2011). It has been suggested that motor actions and sentences are represented in parallel (Roy et al., 2013). They seem to share common syntactic, i.e., structural representations. Linguistic syntax might have even evolved from a motor origin. First studies using a grasp and transport task have shown that specific motor anomalies occur in parallel to linguistic deficits (Roy et al., 2013).

The semantic knowledge for action has been investigated with the N400 (van Elk et al., 2008). The preparation of meaningful actions with an object seems to be accompanied by the activation of semantic information representing the usual action goal associated with the object (van Elk et al., 2008). Thus, further studies in this domain, investigating differences between habitual and non-habitual actions or comfortable and non-comfortable end-postures of an action sequence, might help to understand the interplay of the motor and the linguistic system, and to improve rehabilitation treatments in this area.

5.4 References

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6 SUMMARY

This thesis aims at a better understanding of the neurophysiological underpinnings of motor control, more specifically of grasping. The process of controlled interaction with the world is vital for our existence. It is a basic need for action and communication. The control of body movements is of crucial importance for everyday tasks and has its application in almost all fields of life, like high-level-sports, physical therapy, playing an instrument, typing, or grasping a cup to drink. When making voluntary movements of this kind, we usually take the final goal of the action into account. That we anticipate the movement outcome demonstrates a cognitive component underlying motor control. In this thesis, we investigated the neural mechanisms and cognitive components of motor and action control, to advance our understanding of the link between motor control and cognition. We focus on the neural and cognitive processes underlying the planning and execution of overt manual object manipulations. More specifically, we used the electroencephalogramme (EEG) to investigate the processes underlying the planning and execution of goal-related grasp-and-transport as well as grasp-and-rotation tasks involving power grips. These tasks are known to elicit the end-state comfort effect and, thus, are suitable to investigate cognitive processes underlying manual action. Here, we studied specific aspects of different movement sequences in three experiments. In our first experiment, we differentiated between initial and final goals of an action, while we focused on instructed and free goals in our second experiment. The third experiment finally investigated the habitual factor involved in the planning and execution of manual goal-related actions.

ERP research on overt grasping has been done rarely because of the EEG's sensitivity to movement artifacts. Some studies have already shown that ERPs are suitable for the investigation of overt movements. Thus, we assumed that ERPs are a suitable tool for the investigation of grasping movements. The results of our studies confirmed this assumption. Besides the further establishment of ERPs as a research tool for the investigation of the cognitive processes underlying the overt execution of (manual) actions, our main findings confirm the existence of a parieto-frontal network on a cerebral level for the planning and control of manual actions, extend existing knowledge to power grips, and create first assumptions for power grips used under precision demands.

ERP research on overt grasping movements was limited to preparation intervals and precision grips. Precision grips were investigated in a grasp and transportation task. Visual cues emphasized either the initial goal (the grip) or the final goal (the target location). ERPs differed between initial and final goal-cued conditions, suggesting different means of operation dependent on goal-relatedness. The aim of CHAPTER 2 was to extend these results to power grips in a bar-transport task. Therefore we differentiated between cerebral activity and its temporal organization during power grips executed with an emphasis on either the initial or final parts of a movement sequence. Our results suggest that a parieto-frontal network of activation is of crucial importance for grasp planning and execution. They further indicate that power grip preparation and execution for goal-related actions are controlled by similar neural mechanisms as have been observed during precision grips, but with a distinct temporal pattern. Our results also support the notion that goal-directedness is an important mechanism underlying the planning and control of voluntary action, as ERPs differed between immediate and final goal-cued conditions.

Voluntary actions are associated with different decision processes, including the decision whether to act, what action to perform, and when to perform it. The what-decision is of special importance for goal-directed manual actions and action anticipation. Most neurophysiological studies, which tackled the what-decision of manual actions, focused on clinical populations or non-human-primates. Studies using ERPs mainly focused on components that occur before action execution and simple movements like key presses. Research on overt complex actions in this area was lacking. To our knowledge, no study had yet investigated ERPs underlying the what-decision of the planning and execution of overt manual action. Therefore, the aim of CHAPTER 3 was to differentiate between cerebral activity for self-regulated and instructed actions during the overt execution of a goal related action. We adopted a bar-transport task, that is known to involve anticipative behavior. To manipulate the what-decisions included in the task, we instructed participants concerning grasp and target-location. Both were either free choice or specified by instruction. Thus, enabling us to investigate differences of neural mechanisms between self-regulated compared to instructed actions concerning the grasp and the goal. We found differential activity between free-goal and specified-goal conditions, but not between free-grasp and specified-grasp conditions. Our results support ideomotor theories as action preparation and execution processes differed depending on the action effect. That we observed no difference between free-grasp and specified grasp conditions might further stress the importance of the final action effect or final action goal for action preparation and execution in relation to initial action goals.

The question why people seem to prefer a comfortable end state has not been answered yet. Two main explanations that have been suggested are better control or more precision at the end of the movement, or when this is needed and a habitual system favoring movements that were rewarding in the past. Although habitual factors influencing the end-state comfort effect are frequently highlighted, neurophysiological studies for the overt execution of goal-related grasps are hard to find. Therefore, the aim of CHAPTER 4 is to investigate the neural mechanisms underlying the overt execution of goal-related actions with a focus on habitual vs non-habitual grasps. We created a handle rotation task, in which participants had to use thumb-toward (habitual) or thumb-away power grips (non habitual) to rotate a handle precisely to a given target position. Neural processes for action execution differed between habitual and non-habitual conditions. Our results indicate that the homing in phase of habitual and non-habitual actions are controlled by different neural activity which depend on the control requirements of the action sequence. They further suggest that less effort is needed to execute an action towards a goal in a habitual mode compared to a non-habitual mode.

As the effects we report in this thesis last for several hundred milliseconds, we can assume that they are not a mere reflection of motor activation but rather of cognitive processes, like motor planning. That the effects were not observed in stimulus-locked analyses further makes a pure reflection of sensorial processes highly unlikely. Taken together, we have shown that the goal-relatedness of an action and habitual factors influence the planning and execution of voluntary action on a behavioral and especially on the neural level. This influence is already present in early phases of a movement sequence and illustrates the relevance of cognitive aspects for action execution. In CHAPTER 5, we further discuss these results in relation to different brain areas and a hierarchical view of the motor system, before showing perspectives for future research.

7 APPENDIX

7.1 Supplementary material related to chapter 2

Time window	-1400 -1300	-1300 -1200	-1200 -1100	-1100 -1000	-1000 -900	-900 -800	-800 -700	-700 -600
F(4,56)	1.3	2.01	3.12	3.18	**4.53**	2.28	1.44	1.99
t(14)								
Time window	-600 -500	-500 -400	-400 -300	-300 -200	-200 -100	-100 0	0 100	100 200
F(4,56)	**3.74**	**3.3**	**3.26**	**3.48**	**3.72**	**4.63**	**4.16**	**3.84**
t(14)	-2.66 PL -2.71 PM -2.32 PR	-2.72 PL -2.66 PM -2.29 PR	-2.73 CM -2.6 PL -2.7 PM -2.37 PR	-2.51 CM -2.27 PL -2.61 PM -2.23 PR				
Time window	200 300	300 400	400 500	500 600	600 700	700 800	800 900	900 1000
F(4,56)	2.81	2.91	2.3	1.96	2.33	2.12	1.73	1.5
t(14)								

Table A2.1: 100 ms-time-step-analyses time-locked to grasping. F-Values for the 3-way interactions of the ANOVAs with the factors Cue-type, Front-Back, and Left-Right; significant values in bold face ($p < 0.05$). ROIs and t-values are reported only for significant effects of Cue-type (immediate goal-cued vs. final goal-cued; $p < 0.05$) as follow-up analyses for significant 3-way interactions.

Time window	-2000 -1900	-1900 -1800	-1800 -1700	-1700 -1600	-1600 -1500	-1500 -1400	-1400 -1300	-1300 -1200	-1200 -1100	-1100 -1000	... ...
F(4,56)	0.31	0.82	1.21	2.64	**3.07**	2.16	2.48	2.8	**3.29**	2.7	
t(14)											
Time window	-1000 -900	-900 -800	-800 -700	-700 -600	-600 -500	-500 -400	-400 -300	-300 -200	-200 -100	-100 0	0 100
F(4,56)	3.21	**3.66**	**4.04**	**4.88**	**6.29**	**5.57**	**4.45**	**3.84**	**3.43**	**3.18**	**3.41**
t(14)				2.26 AR	2.47 AR	2.26 AR	2.44 AR	2.28 AR			2.2 AR

Table A2.2: 100 ms-time-step-analyses time-locked to movement end. F-Values for the 3-way interactions of the ANOVAs with the factors Cue-type, Front-Back, and Left-Right; significant values in bold face ($p < 0.05$). ROIs and t-values are reported only for significant effects of Cue-type (immediate goal-cued vs. final goal-cued; $p < 0.05$) as follow-up analyses for significant 3-way interactions.

7.2 Supplementary material related to chapter 3

Time window	-1600 -1500	-1500 -1400	-1400 -1300	-1300 -1200	-1200 -1100	-1100 -1000	-1000 -900	-900 -800	-800 -700
F(4,92)	1.63	1.47	2.57	**4.08**	**4.38**	**5.78**	**6.67**	**5.61**	**3.76**
t(23)				2.29 AntR		2.39 AntR -2.16 CentZ	-2-28 AntZ 2.09 AntR -2.62 CentZ	-2.42 AntZ -2.50 CentZ	-2.37 AntZ -2.34 CentZ
Time window	-700 -600	-600 -500	-500 -400	-400 -300	-300 -200	-200 -100	-100 0	0 100	100 200
F(4,92)	2.81	**3.58**	**4.45**	**4.74**	**4.93**	**4.79**	**3.92**	**3.53**	**3.46**
t(23)			-2.77 AntZ -2.40 CentZ	-3.21 AntZ -2.94 CentZ	-2.84 AntZ -3.12 CentZ -2.14 PostZ	-2.71 CentZ -2.32 PostL -2.53 PostZ	-2.58 CentZ -2.30 PostZ		
Time window	200 300	300 400	400 500	500 600	600 700	700 800	800 900	900 1000	1000 1100
F(4,92)	3.09	2.90	2.48	2.16	2.33	2.22	2.41	2.26	2.43
t(23)									

Table A3.1: 100 ms-time-step-analyses time-locked to grasping. F-Values for the 3-way interactions of the ANOVAs with the factors Condition, Front-Back, and Left-Right; significant values in bold face ($p < 0.05$). ROIs and t-values are reported only for significant effects of Condition (specified goal vs. free goal; $p < 0.05$) as follow-up analyses for significant 3-way interactions.

Time window	-1600 -1500	-1500 -1400	-1400 -1300	-1300 -1200	-1200 -1100	-1100 -1000	-1000 -900	-900 -800	-800 -700
F(4,92)	0.48	0.31	0.25	0.23	0.40	0.40	0.18	0.50	0.39
t(23)									
Time window	-700 -600	-600 -500	-500 -400	-400 -300	-300 -200	-200 -100	-100 0	0 100	100 200
F(4,92)	0.83	0.83	0.68	0.71	0.53	0.57	0.53	0.53	0.61
t(23)									
Time window	200 300	300 400	400 500	500 600	600 700	700 800	800 900	900 1000	1000 1100
F(4,92)	0.75	0.70	0.67	0.89	0.84	0.91	0.98	1.26	1.19
t(23)									

Table A3.2: 100 ms-time-step-analyses time-locked to grasping. F-Values for the 3-way interactions of the ANOVAs with the factors Condition, Front-Back, and Left-Right; significant values in bold face ($p < 0.05$). ROIs and t-values are reported only for significant effects of Condition (specified grip vs. free grip; $p < 0.05$) as follow-up analyses for significant 3-way interactions.

Time window	-2500 -2400	-2400 -2300	-2300 -2200	-2200 -2100	-2100 -2000	-2000 -1900	-1900 -1800	-1800 -1700	-1700 -1600
F(4,92)	0.49	1.37	1.53	2.27	1.78	2.75	**3.44**	**3.20**	**3.42**
t(23)							2.24 AntL 2.64 AntR	2.33 AntR	2.47 AntR

Time window	-1600 -1500	-1500 -1400	-1400 -1300	-1300 -1200	-1200 -1100	-1100 -1000	-1000 -900	-900 -800	-800 -700
F(4,92)	**3.67**	**3.26**	2.34	2.38	2.37	1.88	0.18	1.44	2.01
t(23)	2.90 AntR	2.80 AntR							

Time window	-700 -600	-600 -500	-500 -400	-400 -300	-300 -200	-200 -100	-100 0	0 100	100 200
F(4,92)	2.82	3.20	2.03	2.00	1.34	0.82	1.00	1.08	1.26
t(23)									

Table A3.3: 100 ms-time-step-analyses time-locked to movement end. F-Values for the 3-way interactions of the ANOVAs with the factors Condition, Front-Back, and Left-Right; significant values in bold face ($p < 0.05$). ROIs and t-values are reported only for significant effects of Condition (specified goal vs. free goal; $p < 0.05$) as follow-up analyses for significant 3-way interactions.

Time window	-2500 -2400	-2400 -2300	-2300 -2200	-2200 -2100	-2100 -2000	-2000 -1900	-1900 -1800	-1800 -1700	-1700 -1600
F(4,92)	**3.58**	2.55	1.29	2.04	1.58	0.88	1.22	0.55	1.41
t(23)									
Time window	-1600 -1500	-1500 -1400	-1400 -1300	-1300 -1200	-1200 -1100	-1100 -1000	-1000 -900	-900 -800	-800 -700
F(4,92)	1.76	1.46	1.53	1.62	1.44	1.07	1.05	1.38	1.74
t(23)									
Time window	-700 -600	-600 -500	-500 -400	-400 -300	-300 -200	-200 -100	-100 0	0 100	100 200
F(4,92)	1.55	1.25	1.47	1.32	1.24	1.09	1.23	0.96	1.11
t(23)									

Table A3.4: 100 ms-time-step-analyses time-locked to movement end. F-Values for the 3-way interactions of the ANOVAs with the factors Condition, Front-Back, and Left-Right; significant values in bold face ($p < 0.05$). ROIs and t-values are reported only for significant effects of Condition (specified grip vs. free grip; $p < 0.05$) as follow-up analyses for significant 3-way interactions.

Time window	0 100	100 200	200 300	300 400	400 500	500 600	600 700	700 800	800 900
F(4,92)	0.67	1.14	0.57	0.95	1.86	2.53	1.44	1.35	1.33
t(23)									
Time window	900 1000	1000 1100	1100 1200	1200 1300	1300 1400	1400 1500	1500 1600	1600 1700	1700 1800
F(4,92)	1.11	1.31	1.65	1.71	1.34	0.77	0.36	0.45	0.67
t(23)									
Time window	1800 1900	1900 2000	2000 2100	2100 2200	2200 2300	2300 2400	2400 2500	2500 2600	2600 2700
F(4,92)	0.96	0.95	1.23	1.62	1.71	1.82	2.32	3.03	2.87
t(23)									

Table A3.5: 100 ms-time-step-analyses time-locked to stimulus presentation. F-Values for the 3-way interactions of the ANOVAs with the factors Condition, Front-Back, and Left-Right; significant values in bold face ($p < 0.05$). ROIs and t-values are reported only for significant effects of Condition (specified goal vs. free goal; $p < 0.05$) as follow-up analyses for significant 3-way interactions.

Time window	0 100	100 200	200 300	300 400	400 500	500 600	600 700	700 800	800 900
F(4,92)	0.86	0.89	1.07	0.49	0.68	0.41	0.45	0.99	1.33
t(23)									
Time window	900 1000	1000 1100	1100 1200	1200 1300	1300 1400	1400 1500	1500 1600	1600 1700	1700 1800
F(4,92)	1.39	0.24	0.21	0.33	0.53	0.84	0.72	0.61	0.58
t(23)									
Time window	1800 1900	1900 2000	2000 2100	2100 2200	2200 2300	2300 2400	2400 2500	2500 2600	2600 2700
F(4,92)	0.79	0.66	0.57	0.70	0.84	0.82	0.89	0.85	0.80
t(23)									

Table A3.6: 100 ms-time-step-analyses time-locked to stimulus presentation. F-Values for the 3-way interactions of the ANOVAs with the factors Condition, Front-Back, and Left-Right; significant values in bold face ($p < 0.05$). ROIs and t-values are reported only for significant effects of Condition (specified grip vs. free grip; $p < 0.05$) as follow-up analyses for significant 3-way interactions.

Time window	-800 -700	-700 -600	-600 -500	-500 -400	-400 -300	-300 -200	-200 -100	-100 0	0 100
F(4,92)	0.92	1.50	2.11	**4.54**	**5.12**	**5.16**	**4.61**	**3.65**	2.62
t(23)				-2.47 AntZ -2.29 CentZ -2.16 PostZ		-2.38 AntZ -2.37 CentZ -2.09 CentR -2.12 PostZ	-2.08 PostZ		
Time window	100 200	200 300	300 400	400 500	500 600	600 700	700 800	800 900	900 1000
F(4,92)	3.02	2.69	**3.48**	**4.06**	**3.96**	**3.72**	**3.80**	**3.73**	**3.75**
t(23)						2.13 AntR	2.49 AntR	3.07 AntR	2.09 AntL 3.12 AntR
Time window	1000 1100	1100 1200	1200 1300	1300 1400	1400 1500	1500 1600	1600 1700	1700 1800	1800 1900
F(4,92)	**4.29**	**3.74**	2.98	3.00	3.31	3.20	3.28	3.17	2.64
t(23)	3.17 AntR	2.76 AntR							

Table A3.7: 100 ms-time-step-analyses time-locked to movement onset. F-Values for the 3-way interactions of the ANOVAs with the factors Condition, Front-Back, and Left-Right; significant values in bold face ($p < 0.05$). ROIs and t-values are reported only for significant effects of Condition (specified goal vs. free goal; $p < 0.05$) as follow-up analyses for significant 3-way interactions.

The ANOVA for 600 to 1200 ms time-locked to movement onset revealed a significant 3-way interaction for Condition, Front-Back, and Left-Right, $F(4, 92)=3.96$, $p<0.05$. A significant positivity for the specified goal condition compared to the free goal condition was present in the AntR-ROI, $t(23)=2.97$, $p<0.05$. No significant effects were found for the remaining ROIs.

Time window	-800 -700	-700 -600	-600 -500	-500 -400	-400 -300	-300 -200	-200 -100	-100 0	0 100
F(4,92)	1.21	1.70	0.97	0.86	0.18	0.17	0.26	0.58	0.74
t(23)									
Time window	100 200	200 300	300 400	400 500	500 600	600 700	700 800	800 900	900 1000
F(4,92)	0.74	0.74	0.66	0.90	1.25	1.36	1.25	1.12	0.86
t(23)									
Time window	1000 1100	1100 1200	1200 1300	1300 1400	1400 1500	1500 1600	1600 1700	1700 1800	1800 1900
F(4,92)	0.78	0.92	0.89	1.13	1.08	1.24	1.19	1.47	1.75
t(23)									

Table A3.8: 100 ms-time-step-analyses time-locked to movement onset. F-Values for the 3-way interactions of the ANOVAs with the factors Condition, Front-Back, and Left-Right; significant values in bold face ($p < 0.05$). ROIs and t-values are reported only for significant effects of Condition (specified grip vs. free grip; $p < 0.05$) as follow-up analyses for significant 3-way interactions.

7.3 Supplementary material related to chapter 4

Time window	-2100 -2000	-2000 -1900	-1900 -1800	-1800 -1700	-1700 -1600	-1600 -1500	-1500 -1400	-1400 -1300	... ...
F(4,108)	1.32	1.42	2.19	2.47	1.78	1.67	1.46	1.12	
t(27)									
Time window	-1300 -1200	-1200 -1100	-1100 -1000	-1000 -900	-900 -800	-800 -700	-700 -600	-600 -500	... ...
F(4,108)	0.98	1.05	0.87	0.88	0.61	0.69	0.67	0.81	
t(27)									
Time window	-500 -400	-400 -300	-300 -200	-200 -100	-100 0	0 100	100 200	200 300	... ...
F(4,108)	0.97	1.07	1.35	1.37	1.48	1.75	2.01	2.17	
t(27)									
Time window	300 400	400 500	500 600	600 700	700 800	800 900	900 1000	1000 1100	1100 1200
F(4,108)	2.24	2.24	2.30	2.40	2.30	2.42	2.45	2.30	2.17
t(27)									

Table A4.1: 100 ms-time-step-analyses time-locked to rotation onset. F-Values for the 3-way interactions of the ANOVAs with the factors Condition, Front-Back, and Left-Right; significant values in bold face ($p < 0.05$). ROIs and t-values are reported only for significant effects of Condition (thumb toward vs. thumb away; $p < 0.05$) as follow-up analyses for significant 3-way interactions; see also text. On average 30 trials per participant for the thumb toward condition and 29 trials for the thumb away condition entered analyses.

Time window	-2100 -2000	-2000 -1900	-1900 -1800	-1800 -1700	-1700 -1600	-1600 -1500	-1500 -1400	-1400 -1300	... ...
F(4,108)	0.35	0.19	0.06	0.18	0.19	0.20	0.66	0.30	
t(27)									
Time window	-1300 -1200	-1200 -1100	-1100 -1000	-1000 -900	-900 -800	-800 -700	-700 -600	-600 -500	... ...
F(4,108)	0.33	0.27	0.34	0.29	0.18	0.27	0.33	0.52	
t(27)									
Time window	-500 -400	-400 -300	-300 -200	-200 -100	-100 0	0 100	100 200	200 300	... ...
F(4,108)	0.72	1.00	1.13	1.10	0.94	0.89	0.82	0.47	
t(27)									
Time window	300 400	400 500	500 600	600 700	700 800	800 900	900 1000	1000 1100	1100 1200
F(4,108)	0.50	0.53	0.50	0.39	0.63	0.67	0.73	0.94	0.91
t(27)									

Table A4.2: 100 ms-time-step-analyses time-locked to rotation onset. F-Values for the 3-way interactions of the ANOVAs with the factors Condition, Front-Back, and Left-Right; significant values in bold face ($p < 0.05$). ROIs and t-values are reported only for significant effects of Condition (free grip vs. specified grip; $p < 0.05$) as follow-up analyses for significant 3-way interactions; see also text. On average 60 trials per participant for the free grip condition and 59 trials for the specified grip condition entered the analyses.

Time window	-3100 -3000	-3000 -2900	-2900 -2800	-2800 -2700	-2700 -2600	-2600 -2500	-2500 -2400	-2400 -2300	-2300 -2200
F(4,108)	0.07	0.79	0.74	0.93	0.71	0.56	0.56	0.83	0.66
t(27)									
Time window	-2200 -2100	-2100 -2000	-2000 -1900	-1900 -1800	-1800 -1700	-1700 -1600	-1600 -1500	-1500 -1400	-1400 -1300
F(4,108)	0.92	1.11	0.97	0.99	0.73	0.83	0.84	0.73	0.86
t(27)									
Time window	-1300 -1200	-1200 -1100	-1100 -1000	-1000 -900	-900 -800	-800 -700	-700 -600	-600 -500	-500 -400
F(4,108)	1.01	1.01	1.12	1.84	2.08	2.00	2.69	**3.16**	**3.31**
t(27)								2.07 AL 2.19 AR	2.14 AL 2.11 AR
Time window	-400 -300	-300 -200	-200 -100	-100 0	0 100	100 200	200 300		
F(4,108)	**3.36**	**3.50**	**3.70**	**4.20**	**4.31**	**3.94**	**4.10**		
t(27)	2.40 AL 2.30 AR	2.44 AL 2.29 AR	2.44 AL 2.19 AR	2.43 AL 2.08 AR	2.24 AL	2.08 AL			

Table A4.3: 100 ms-time-step-analyses time-locked to rotation end. F-Values for the 3-way interactions of the ANOVAs with the factors Condition, Front-Back, and Left-Right; significant values in bold face ($p < 0.05$). ROIs and t-values are reported only for significant effects of Condition (thumb toward vs. thumb away; $p < 0.05$) as follow-up analyses for significant 3-way interactions; see also text. On average 60 trials per participant for the thumb toward condition and 58 trials for the thumb away condition entered the analyses.

Time window	-3100 -3000	-3000 -2900	-2900 -2800	-2800 -2700	-2700 -2600	-2600 -2500	-2500 -2400	-2400 -2300	-2300 -2200
F(4,108)	0.32	0.32	0.39	0.96	1.16	0.89	0.92	1.01	0.79
t(27)									
Time window	-2200 -2100	-2100 -2000	-2000 -1900	-1900 -1800	-1800 -1700	-1700 -1600	-1600 -1500	-1500 -1400	-1400 -1300
F(4,108)	0.64	0.75	0.87	0.74	0.87	0.89	0.65	0.83	1.05
t(27)									
Time window	-1300 -1200	-1200 -1100	-1100 -1000	-1000 -900	-900 -800	-800 -700	-700 -600	-600 -500	-500 -400
F(4,108)	1.01	0.94	0.98	0.76	0.62	0.60	0.53	0.50	0.57
t(27)									
Time window	-400 -300	-300 -200	-200 -100	-100 0	0 100	100 200	200 300		
F(4,108)	0.52	0.62	0.62	0.62	0.68	0.69	0.90		
t(27)									

Table A4.4: 100 ms-time-step-analyses time-locked to rotation end. F-Values for the 3-way interactions of the ANOVAs with the factors Condition, Front-Back, and Left-Right; significant values in bold face ($p < 0.05$). ROIs and t-values are reported only for significant effects of Condition (free grip vs. specified grip; $p < 0.05$) as follow-up analyses for significant 3-way interactions; see also text. On average 60 trials per participant for the free grip condition and 58 trials for the specified grip condition entered the analyses.

7.4 Supplementary material related to chapter 5

Experiment (described in chapter)	Time window	Time-locking event	ROIs	Effect	Possible functional processing
1 (2)	-600 -200	Grasping	PL, PM, PR	Negativity for immediate vs final goal-cued	Anticipated sensory representations of movement effects
1 (2)	-700 -200	End	AR	Positivity for immediate vs final goal-cued	Planning & control
2 (3)	-1100 -700	Grasping	AZ, CZ	Negativity for specified vs free goal	Planning
2 (3)	-500 0	Grasping	AZ, CZ, PZ	Negativity for specified vs free goal	Planning (AZ) / Control or generation of movement intentions (PZ)
2 (3)	-1900 -1400	End	AR	Positivity for specified vs free goal	Planning & anticipation
3 (4)	-600 200	End	AL, AR	Negativity for thumb away vs thumb toward	Planning & control

Table A5.1: Major effects. The table shows the number of the experiment and in which chapter this experiment is described, the time window in which the effects occurred, in relation to which time-locking event, in which region of interest, what kind of effect was observed and its possible functional processing.

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