NEUROPHYSIOLOGICAL INVESTIGATION OF THE FUNCTIONAL INTERACTIONS BETWEEN MANUAL ACTION CONTROL AND WORKING MEMORY

Rümeysa Gündüz Can

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Neurophysiological Investigation of the Functional Interactions between Manual Action Control and Working Memory

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MSc. Rümeysa Gündüz Can

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Supervisor

Prof. Dr. Thomas Schack[1,2,3]

Reviewers

Prof. Dr. Thomas Schack[1,2,3]

Prof. Dr. Dirk Koester [4]

[1]Faculty of Psychology and Sports Science,
Department of Sports Science,
Neuro-cognition and Action-Biomechanics Research Group,
Bielefeld University
[2] Cluster of Excellence-Cognitive Interaction Technology (CITEC),
Bielefeld University
[3] Research Institute for Cognition and Robotics (CoR-Lab),
Bielefeld University
[4] Faculty of Business and Management,
Department of Business Psychology,
Business School Berlin

Candidate's Declaration

I hereby declare that the current dissertation with the title “Neurophysiological investigation of the functional interactions between manual action control and working memory” is presented according to the doctoral regulations of the Faculty of Psychology and Sports Science. This dissertation is my own original work unless otherwise referenced or acknowledged. This dissertation has not been submitted for degree in this institution or any other professional qualifications at elsewhere.

Bielefeld, May 2, 2019 Rümeysa Gündüz Can

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To my beloved parents and husband

The current dissertation is based on the following manuscripts which have been published or submitted for publication:

CHAPTER 2

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CHAPTER 3

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CHAPTER 4

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Summary

Manual actions are the key motor actions interacting with the physical world around us. In a day, we perform a huge variety of skilled manual actions to interact with and manipulate objects, communicate with people through gestures or written text messages as well as do sports, play musical instruments and execute dance figures. In natural environments, we perform manual actions generally with other motor or cognitive tasks such as grasping a coffee cup while having a conversation. Moreover, in natural environments, individual physiological or cognitive states such as action goals or environmental situations such as target object location can change unexpectedly. Therefore, in natural environments, action flexibility is an important cognitive ability which provides rapid and precise manual actions suiting to desired action outcomes. Accordingly, performing skilled manual actions which are efficiently performed with other tasks as well as rapidly adapted to changing action demands require the close engagement of the sensory, motor and cognitive systems. The current thesis aims to further the understanding of the neuro-cognitive mechanisms underlying manual action control including action flexibility. That is, how the human brain orchestrates the sensorimotor systems with cognitive processes to plan, execute and adapt a variety of skilled manual actions in natural environments. For this aim, the current thesis focuses on grasping movements as the most frequently performed, yet the most complex manual actions requiring cognitive processes, and working memory (WM) as the core cognitive process guiding goal-directed behavior.

The current thesis particularly investigated the neurophysiological correlates of the functional domain interactions between manual action control (grasping movements) and cognition (WM). For this investigation, a cognitive-motor dual-task paradigm which required the concurrent performance of WM task and manual task was integrated into an electroencephalography (EEG) setting. For a profound investigation of the domain interactions, in three experimental studies, different movemet phases (execution, re-planning), WM domains (verbal, visuospatial), processes (encoding, maintenance, retrieval) and response modalities (manual, vocal) were focused. EEG was recorded while participants were performing the experimental tasks. Event-related potentials (ERPs) were extracted from the EEG recordings.

Study 1 investigated the neurophysiological correlates of the domain interactions between movement execution and WM. That is, whether the execution of a prepared movement without additional planning requirements interferes with WM, and where the locus of the interference is, i.e., encoding or retrieval process of verbal and visuospatial domains. In a dual-task scenario, participants either performed verbal and visuospatial WM tasks alone (single-task condition) or concurrently with a manual task which required grasping a sphere, holding it and placing it on a motor target, i.e., grasp-and-place movement (dual-task condition). ERPs were extracted for encoding and retrieval processes in verbal and visuospatial tasks. Both the

behavioral memory performance and ERPs were compared between single-task and dual-task conditions. The behavioral analyses showed that memory performance was lower in the dual-task compared to the single-task for the visuospatial task, but not for the verbal task. That is, concurrent movement execution interfered only with visuospatial domain and decreased memory performance only for the visuospatial task, i.e., *domain-specific movement execution costs*. ERP analyses showed the different ERP patterns in the dual-task compared to the single-task only during the encoding process in the visuospatial task. That is, domain-specific interference of movement execution was also obtained at the neurophysiological level, which was further specific to the encoding process of visuospatial domain, i.e., *domain and process-specific movement execution costs.*

Study 2 investigated the neurophysiological correlates of the domain interactions between movement re-planning and WM. That is, whether changing the prepared movement plan of an ongoing movement interferes with WM, and where the locus of the interference is, i.e., maintenance or retrieval process of verbal and visuospatial domains. In the dual-task scenario, participants performed verbal and visuospatial tasks concurrently with grasp-and-place movement which required either executing the initially prepared movement plan (prepared movement condition) or changing it with a new alternative plan for reversing the movement direction (re-planned movement condition). ERPs were extracted for maintenance and retrieval processes in verbal and visuospatial tasks. Both the behavioral memory performance and ERPs were compared between prepared movement and re-planned movement conditions. The behavioral analyses showed that memory performance was lower in the re-planned condition compared to the prepared condition in both verbal and visuospatial tasks. That is, concurrent movement re-planning interfered with both verbal and visuospatial domains and decreased memory performance for both WM tasks, i.e., *domain-general movement re-planning costs*. ERP analyses showed the different ERP patterns in the re-planned condition compared to the prepared condition during the maintenance process, but not the retrieval process, in verbal and visuospatial tasks. That is, domain-general interference of movement re-planning was also obtained at the neurophysiological level, which was further specific to the maintenance process of verbal and visuospatial domains, i.e., *domain-general, but process-specific movement re-planning costs.*

Study 3 investigated the role of the WM response modality in the neurophysiological correlates of the movement re-planning-WM interactions. That is, whether the neurophysiological interactions between movement re-planning and WM depend on the particular pairing of stimulus-response modalities within WM tasks as well as on the response modality overlap between WM tasks and manual task. The experimental procedure was the same as in Study 2. Participants performed verbal and visuospatial tasks concurrently with grasp-and-place movement which required executing the initially prepared movement plan for some trials (prepared movement condition) and changing it for other trials (re-planned movement condition). Different from Study 2 in which WM tasks included manual response modality, the current WM tasks included vocal response modality, i.e., spoken report of memory items. Both the behavioral memory performance and ERP analyses showed the similar results compared to the results obtained with manual response modality (Study 2). Namely, movement re-planning interfered with both verbal and visuospatial domains and decreased memory performance for both WM tasks, i.e., *domain-general movement re-planning costs.* Moreover, prepared and re-planned movements generated different ERPs only during the maintenance process of verbal and visuospatial domains, i.e., *domain-general, but process-specific movement re-planning costs.*

Taken together, the current studies have provided the first systematic investigations of the neurophysiological correlates of the functional domain interactions between manual action control and WM. The current findings have shown that manual action-WM interactions are complex and dependent on a variety of factors such as movement phases (execution, re-planning), WM domains (verbal, visuospatial) and processes (encoding, maintenance, retrieval). Nevertheless, the current findings have pointed out the functional role of WM in the execution and re-planning of manual actions, and thus the importance of investigating the domain interactions between manual action control, WM and human neurophysiology.

In general, the current thesis, by bringing together the human movement science (grasping movements), cognitive science (working memory) and neurophysiology (EEG), contributes to the understanding of the neuro-cognitive mechanisms underlying manual action control which has enabled humans to develop species-specific manual skills, and thus to achieve social, cultural and technological progress. Accordingly, the current thesis mainly relates to the human manual intelligence, and then also provides inputs to the other related fields such as cognitive robotics.

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Abbreviations

BACs	: Basic Action Concepts
CAA-A	: Cognitive Action Architecture Approach
EEG	: Electroencephalography
ERP	: Event Related Potential
IFC	: Inferior Frontal Cortex
IPL	: Inferior Parietal Lobe
ISI	: Inter-Stimulus Interval
ITC	: Inferior Temporal Cortex
LRP	: Lateralized Readiness Potential
LTM	: Long-Term Memory
MCO-M	: Multi-Component Model
PFC	: Prefrontal Cortex
PMC	: Premotor Cortex
PPC	: Posterior Parietal Cortex
Pre-SMA	: Pre-supplementary Motor Area
ROI	: Region-of-Interest
SMA	: Supplementary Motor Area
SPL	: Superior Parietal Lobe
WM	: Working Memory
TBRS-M	: Time-Based Resource Sharing Model

1 GENERAL INTRODUCTION

CHAPTER 1

“The hand can become a claw, a fist, a horn or spear or sword or any other weapon or tool. It can be everything because it has the ability to grasp anything or hold anything.”

Aristotle (384-322 BC)

Motor action control has been a great importance in mastering and adapting to the environment throughout the course of evolution (e.g., Berthoz, 2000; Cisek & Kalaska, 2010). Competent motor control enables animals to behave efficaciously with respect to the meaningful properties of the environment such as for moving through and investigating the environment safely, adapting to the ever-changing environmental demands, manipulating the objects and learning new skills. Humans particularly master a great deal of voluntary and purposeful motor actions. That is, humans perform actions to achieve certain action goals which reflect physiological and psychological needs, motivations and experiences in the short and long-term. Moreover, humans have the ability to flexibly adapt actions to the changing individual physiological and cognitive states as well as environmental demands. Action flexibility is an important cognitive ability which provides the rich repertoire of motor actions and enables the precise actions suiting to the desired action outcomes (e.g., Verbruggen, McLaren, & Chambers, 2014). Hence, human motor control brings together the sensory, motor and cognitive systems, and thus enables actions which satisfy desired outcomes accurately and rapidly given certain action goals and provide the flexibility for adapting to the changing individual and environmental demands (e.g., Gentsch, Weber, Synofzik, Vosgerau, & Schütz-Bosbach, 2016).

Manual actions, which constitute a vast amount of the human motor action repertoire, have provided the evolutionary advantage for humans among other animals (e.g., MacDougall, 1905; Tocheri, Orr, Jacofsky, & Marzke, 2008). With the development of upright body position, i.e., bipedality, human hands became free to develop as the environmental perception organ as well as the constructive and manipulative instrument (e.g., Leakey, Tobias, & Napier, 1964). Relative to other primate hands, human hands have shorter palms, straighter but shortened fingers and more importantly the longer, stronger and fully opposable thumb (e.g., Young, 2003; see Figure 1.1). This hand anatomy has provided humans with the species-specific manual skills such as forceful precision grips, and thus enabled humans to develop sophisticated manual interactions with the environment (e.g., Fragaszy & Crast, 2016; Napier, 1956). The superiority of the human hand with the ability to produce a huge variety of precise and flexible actions emerged not only due to the hand's anatomical features such as opposable thumb, but also due to the close engagement of the motor and cognitive systems. With the free and intelligent hands, humans have mastered the environment by exploring and shaping it, protecting themselves by building objects as well as achieved the social, cultural and technological progress (e.g., Ko, 2016; Osiurak, 2014).

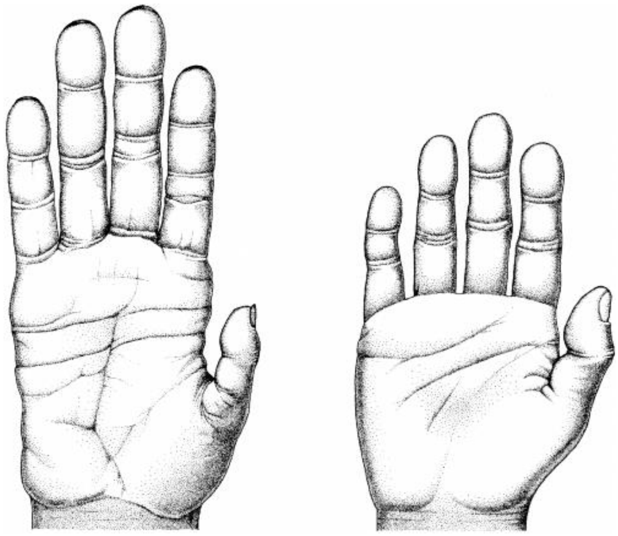

Figure 1.1. Comparison between a chimpanzee hand (left) and a human hand. Adapted from Young, 2003, p: 166. Copyright 2003 by Anatomical Society of Great Britain and Ireland.

So far it has not been well understood how the human brain integrates the sensory, motor and cognitive systems to achieve robust manual actions and action flexibility. Considering the importance of manual actions in everyday life as well as in the social, cultural and technological progress, it is important to understand how the manual actions are planned, executed and, when necessary, adapted. The current thesis, therefore, aims to contribute to the understanding of how the human brain orchestrates the sensorimotor systems with cognitive processes to produce rapid, precise and flexible manual actions in dynamic natural environments. Specifically, the current thesis focuses on grasping movements which are the most sophisticated manual actions and working memory which is the core cognitive process guiding complex behavior. Accordingly, the current thesis brings the movement science and cognitive science together with the brain research (electroencephalography) and investigates the neurophysiological correlates of the functional domain interactions between manual action control (grasping movements) and cognition (working memory).

This general introduction chapter will present an overview of the theoretical framework and previous research related to manual action control, working memory and human neurophysiology. Such an overview will guide towards the goal and research questions of the current thesis. In the section 1.1, I will outline the relevant principles of manual action control including the movement planning and online control phases (section 1.1.1) as well as the movement re-planning phase as a way of action flexibility (section 1.1.2). In the section 1.2, I will present the relevant principles of working memory including the theoretical framework (section 1.2.1), working memory domains and processes (section 1.2.2). In the section 1.3, I will elaborate on the theoretical framework for the domain interactions between manual action control and working memory. I will present the relevant principles of dual-task paradigms in the section 1.4, and previous dual-task research on the manual action-working memory interactions in the section 1.4.1. I will present the relevant principles of human neurophysiology in the section 1.5, and previous neurophysiological research on manual action control and working memory in the section 1.5.1 and section 1.5.2, respectively. I will close the general introduction chapter by presenting an overview of the goal, methodology and research questions of the current thesis (section 1.6).

1.1 Principles of manual action control

We use our hands intensively for performing almost any daily life activities such as eating, drinking, moving around the environment by using vehicles, communicating with people, even performing any seemingly pure cognitive tasks such as writing a thesis. Accordingly, we perform a rich repertoire of skilled manual actions such as pointing to and reaching for objects at different distances, grasping and lifting objects with different sizes, shapes and weight, as well as typewriting and gesturing. We perform manual actions for achieving overarching goals such as grasping a coffee cup for drinking coffee to awake up in the morning or perform manual actions concurrently with other motor or cognitive tasks such as grasping a pen while holding a mobile phone at the same time or grasping the coffee cup while having a conversation. Moreover, we also flexibly adapt actions to the changing action demands in dynamic natural environments.

Manual actions are grouped into prehensile actions such as grasping and non-prehensile actions such as typewriting based on the requirements of object manipulation (e.g., Fragaszy & Crast, 2016; Jones & Lederman, 2006). The current thesis focuses on the prehensile manual actions, particularly on grasping movements which are the most frequently performed, yet the most complex manual actions requiring the close engagement of the sensory, motor and cognitive systems (e.g., Castiello, 2005; Grafton, 2010).

In his pioneering work on the human grasping, Napier (1956) provided first insights into the intelligence of human hand and complexity of grasping movements. According to Napier (1956), human hand with the opposable thumb provides a variety of postures and orientations with the high precision and strong force which are then grouped into two main grip types, precision grip and power grip (see Figure 1.2). While the precision grip is performed by opposing the thumb to index finger, the power grip is performed by opposing the thumb to all fingers, i.e., whole hand (for recent grasp taxonomies created based on the object geometry and associated hand configurations, see Feix, Romero, Schmiedmayer, Dollar, & Kragic, 2016; Stival et al., 2019). Importantly, Napier (1956) further added that grip type is chosen not only based on physical object properties such as size, but also based on action goals. That is, an object can be grasped with one of the two grip types or combination of them based on the movement requirement (see Figure 1.2). Accordingly, the variety of grasping movements are not the expression of different grip types, but rather the expression of different purposive actions performed every day.

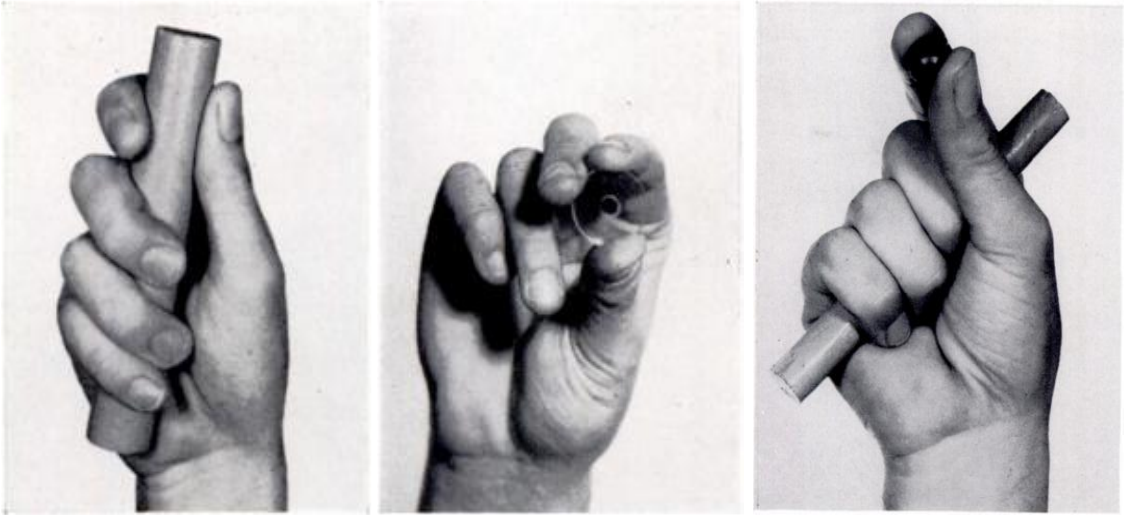

Figure 1.2. Human grip types. As suggested by Napier (1956), humans perform different grip postures including power grip (left), precision grip (middle) and combined grip (right). Adapted from Napier, 1956, p: 907, 911.

Grasping movements consist of a stereotyped sequence of events during which the hand comes to the vicinity of the object and aligns with the object orientation, and the fingers shape on the object by an initial straightening and a following closure until the object is perfectly matched (e.g., Jeannerod, 1984). All these events require sensorimotor transformations during which the physical object properties are transformed into the appropriate motor command in conjunction with the visual, proprioceptive and tactile input from the body (e.g., Desmurget, Pelisson, Rossetti, & Prablanc, 1998). Accordingly, the appropriate motor command necessitates the information about the intrinsic (e.g., size, shape and weight) and extrinsic (e.g., location and orientation) object properties (e.g., Smeets & Brenner, 1999; for recent research on the role of physical object properties in grasping movements, see Ansuini et al., 2016; Desanghere & Marotta, 2015; Schot, Brenner, & Smeets, 2010).

Besides the sensorimotor factors, the competent object grasping also requires a variety of cognitive factors. For example, it has been suggested that previous experiences and conceptual object knowledge affect the way people grasp objects (e.g., Herbort & Butz, 2011; Herbort, Butz, & Kunde, 2014; Herbort, Mathew, & Kunde, 2017; Klatzky, McCloskey, Doherty, Pellegrino, & Smith, 1987). Klatzky and colleagues (1987) showed that participants had conceptual knowledge about the class of the hand shape (e.g., clench, pinch, poke or palm) that they used to grasp an object. Moreover, the perceived function of an object (i.e., affordance) also shapes the way the object is grasped, for example, knowing that a hammer is used for pounding a nail, and thus is grasped with a power grip (e.g., Rounis, Van Polanen, & Davare, 2018; Tucker & Ellis, 1998, 2001). Nevertheless, people perform grasping movements flexibly based on the action context, intentions and goals. Therefore, the same hammer can be grasped differently for passing it to someone instead of pounding the nail.

The action intentions, i.e., what the person intents to do with an object after grasping, affect grasping movements in a way that planning and execution of an initial grasp is adjusted to the requirements of subsequent actions. For example, it has been shown that initial grasp kinematics differ when an object is grasped to lift or pour (e.g., Ansuini, Giosa, Turella, Altoè, & Castiello, 2008; Crajé, Lukos, Ansuini, Gordon, & Santello, 2011), to throw, place or pass to someone (e.g., Ansuini et al., 2008; Armbrüster & Spijker 2006; Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987), to move or use (e.g., Valyear, Chapman, Gallivan, Mark, & Culham, 2011). Similarly, Rosenbaum and colleagues showed that participants grasped a bar object with an initial awkward posture to ensure a comfortable hand posture at the movement end (e.g., Rosenbaum et al., 1990; Rosenbaum, Vaughan, Barnes, & Jorgensen, 1992; for the grasp height effect, see Cohen & Rosenbaum, 2004). That is, the initial grasp was planned and executed based on the anticipation of future task demands. Following such investigations, the term *end-state comfort effect* has been used for referring to the goal-directedness and anticipatory control of grasping movements (e.g., Rosenbaum et al., 1990; for a review, see Rosenbaum, Chapman, Weigelt, Weiss, & Van der Wel, 2012).

In line with the importance of cognitive factors on grasping movements, it has been also shown that grasping movements interact with different cognitive processes such as attention, perception and language (e.g., Baldauf & Deubel, 2010; Bruno & Franz, 2009; Glover, Rosenbaum, Graham, & Dixon, 2004; Koester & Schack, 2016). For example, Glover and colleagues (2004) used a task in which participants grasped a wooden block after reading the names of different graspable objects. The authors found that irrespective of the real size of the block, grip aperture was larger when participants read a word presenting a large object (e.g., apple) compared to a word presenting a small object (e.g., grape). That is, the word reading, and thus language processing, interacted with the motor system and affected the grasp aperture. In the sections 1.3 and 1.4.1, the interactions of grasping movements with working memory will be presented in detail.

The complexity of grasping movements has been also supported by the existence of a sophisticated frontal-parietal cortical network controlling not only the sensorimotor transformations, but also the cognitive operations (e.g., Begliomini et al., 2014; Cavina-Pratesi et al., 2018; for reviews, see Castiello & Begliomini, 2008; Filimon, 2010; Gallivan & Culham, 2015; Olivier, Davare, Andres, & Fadiga, 2007). For example, the premotor cortex (PMC) is involved in the configuration of fingers on a target object (e.g., Begliomini, Caria, Grodd, & Castiello, 2007) as well as in the action understanding and imitation (e.g., Chouinard & Paus, 2006). The posterior parietal cortex (PPC) is involved in the coding of grip type (e.g., Begliomini, Wall, Smith, & Castiello, 2007) as well as in the representation of object affordance and action goals (e.g., Hinkley, Krubitzer, Padberg, & Disbrow, 2009).

Moreover, the cross-talk between ventral and dorsal streams, which are otherwise separate visual systems supporting object recognition and visuomotor control, has been shown to be required for grasping movements (e.g., Budisavljevic, Dell' Acqua, & Castiello, 2018; for a review, see Milner, 2017; for the dual-stream theory, see Milner & Goodale, 2008). That is, to satisfy the desired outcome during a grasping movement, the ventral stream provides the information about the conceptual object knowledge and action goals, and the dorsal stream uses this information on a moment-to-moment basis to plan and execute the movement. The cross-talk between two streams is also in line with the literature which has suggested the close functional connections between the grasping network and the cortical regions supporting the conceptual object knowledge (e.g., the inferotemporal cortex, IT) and action goals and decisions (e.g., the prefrontal cortex, PFC; Andersen & Cui, 2009; Fagg & Arbib, 1998).

Taken together, the human ability for competent grasping movements comes about by the engagement of a variety of sensorimotor and cognitive factors such as physical object properties, conceptual object knowledge as well as action context, intentions and goals (e.g., Van Elk, Van Schie, & Bekkering, 2015).

1.1.1 Planning and online control phases of manual actions

The planning and online control movement phases were introduced for the first time by Woodworth (1899) as the underlying principle of goal-directed motor actions. In the two-component model, Woodworth (1899) argued that during an upper limb movement, pre-programmed initial impulse brings the hand to the vicinity of the object, while the feedback-based current control evaluates the ongoing movement and performs the corrections when the hand approaches to the object (for reviews see, Elliott et al., 2010; Elliott, Helsen, & Chua, 2001; Elliott et al., 2017). This model has then inspired other two-component models, such as optimized sub-movement model (e.g., Meyer, Abrams, Kornblum, Wright, & Smith, 1988), as alternatives to the pure pre-programmed models (e.g., Henry & Rogers, 1960; Keele, 1968; Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979) and the pure feedback models (e.g., Adam, 1971). Glover (2004) introduced a recent version of the two-component model, the planning and online control model, which has also proposed two separate, but complementary movement phases, of which the planning precedes the online control.

Planning phase serves the movement as an executive controller which determines movement parameters before the movement onset by considering a variety of sensorimotor and cognitive factors, and hereby translates abstract action goals into concrete movements (e.g., Miller, Galanter, & Pribram, 1960; Morsella, 2009). During planning, decision-making processes regarding which movement to produce, when to produce and how to produce require the information about the physical and non-physical object properties, action context, intentions and goals (e.g., Wolpert & Landy, 2012; Wong, Haith, & Krakauer, 2014). For example, uncertainty in the environment (e.g., Gallivan, Barton, Chapman, Wolpert, & Flanagan, 2015; Haith, Huberdeau, & Krakauer, 2015) as well as anticipatory action effects are incorporated in movement plans (for reviews, see Hommel, Brown, & Nattkemper, 2016; Rosenbaum et al., 2012). Accordingly, during planning, a variety of movement parameters such as to-be-moved effector (e.g., Rosenbaum, 1980), direction (e.g., Rosenbaum, 1980), duration (e.g., Vidal, Bonnet, & Macar, 1995), force (e.g., MacKay & Bonnet, 1990) and timing (e.g., Deecke, Kornhuber, Lang, Lang, & Schreiber, 1985) are precisely determined (for reviews, see Leuthold, Sommer, & Ulrich, 2004; Vidal, Burle, & Hasbroucq, 2018). Hereby, the optimal motor program which satisfies the desired action outcome is decided during planning phase.

Online control phase serves the movement with the execution and monitoring of plan to the completion, i.e., execution phase (e.g., Morsella, 2009). Online control makes use of several sources of information including the visuospatial object information, the visual and proprioceptive information from the body and the efference copy, i.e., copy of the initial motor command delivered from planning centers to online control centers. The object and body information are rapidly and continuously analyzed and compared with the efference copy. Hereby, during online control, any difference between the planned and current movement state can be detected, and thus any error can be minimized (e.g., Elliott et al., 2017; Glover, 2004).

Planning and online control rely on different perceptual and cognitive representations (e.g., Glover, 2004; Goodale & Haffenden, 1998). Planning operates based on the context-dependent representations which bring the visuospatial object information together with the conceptual object knowledge, surrounding context and action goals. Hence, planning is part of a high-level cognitive network. Online control operates based on the context-independent, moment-to-moment, metric representations of the visuospatial object information in relation to the body. In line with the separate representations, it has been shown that planning compared to online control is more susceptible to the cognitive-based, task-irrelevant information such as perceptual illusions (e.g., Franz, Scharnowski, & Gegenfurtner, 2005; Glover & Dixon 2001, 2002a), semantics (e.g., Glover & Dixon, 2002b; Liu, Chua, & Enns, 2008) and numerical magnitude (e.g., Namdar & Ganel, 2018).

The separation between planning and online control has been also supported by the neuroimaging studies showing that two phases activate different parts of the frontal-parietal cortical network (e.g., Begliomini et al., 2014; Glover, Wall, & Smith, 2012; Grol et al., 2007). While the planning activates the cortical regions, such as the inferior parietal lobe (IPL) and PFC, which integrate the visuospatial object information with the conceptual object knowledge and action goals, the online control activates the regions, such as the superior parietal lobe

(SPL) and PMC, which monitor the movement based only on the visuospatial object information (e.g., Glover, 2004).

1.1.2 Re-planning phase of manual actions

Manual actions are performed based on certain action goals in certain environmental contexts. In natural environments, however, achieving action goals can be prevented not only because of the noise inherited in the movement organization, but also because of the unexpected perceptual events such as a change in target object location (e.g., Shadmehr, Smith, & Krakauer, 2010; Wessel & Aron, 2017). The unexpected events rarely call for the complete inhibition of an ongoing movement, but rather call for the adaptation of the movement to the new action demand. Therefore, in natural environments, desired action outcomes are satisfied not only by the competent movement planning and execution, but also by the continuous monitoring and, when necessary, suitable adaptations of movements to the changing action demands (e.g., Morsella, 2009). Action flexibility is the cognitive ability which enables to organize, monitor and adapt movements with minimal time and effort. Accordingly, action flexibility is a major competent of cognitive control for meeting the challenges in natural environments (e.g., Verbruggen et al., 2014).

Perturbation paradigms have served as a reliable experimental method for investigating the action flexibility, i.e., whether and how the motor system is able to adapt ongoing movements to changing action demands (for reviews, see Gaveau et al., 2014; Prablanc, Desmurget, & Gréa, 2003; Smeets, Oostwoud Wijdenes, & Brenner, 2016). In perturbation paradigms, movement properties are unexpectedly changed concurrently with or after the movement onset (after the movement is planned). Since these changes occur only for a small number of trials, participants plan the movement as if no change would occur. When the change occurs, participants need to adapt the ongoing movement to the new action demand by modifying some movement parameters such as speed or distance. Accordingly, perturbation paradigms provide insights into how rapidly and effectively a prepared, ongoing movement can be adapted to a different action outcome.

Perturbation studies have shown that movement adaptations occur without additional costs in response to the perturbations in a variety of movement properties such as object location (e.g., Paulignan, MacKenzie, Marteniuk, & Jeannerod, 1991a), object size (e.g., Paulignan et al., 1991b) and visual representation of the hand (e.g., Brenner & Smeets, 2003; for a recent review, see Sarlegna & Mutha, 2015). That is, movements can be adapted rapidly as short as 100-150 ms (e.g., Goodale, Pélisson, & Prablanc, 1986) as well as automatically without visual input from the hand (e.g., Komilis, Pélisson, & Prablanc, 1993) and conscious awareness (e.g., Goodale et al., 1986). Moreover, movement adaptations are resistant to cognitive control (e.g., Day & Lyon 2000; Pisella et al., 2000). For example, Day and Lyon

(2000) showed that participants could not refrain from adapting the movement to the direction opposite to the perturbation. Accordingly, the rapid and automatic movement adaptations (i.e., online adjustments) which are achieved without changing the internal structure of a movement support the idea that continuous monitoring and flexibility is embedded within the motor system (e.g., Scott, 2004).

Online adjustments have been suggested to utilize feedforward and feedback control mechanisms (for a detailed explanation regarding the internal models of motor control, see Wolpert, Ghahramani, & Jordan, 1995; Wolpert & Kawato, 1998). During planning phase, feedforward motor command is issued by predicting the sensory consequence of a movement without actual sensory feedback. Then, the efference copy of this initial motor command is delivered to online control centers. During online control phase, sensory feedback from the object and body is continuously compared with the efference copy (and thus with the initial motor command). Based on this continuous comparison, a corrective motor command can be issued when there is a mismatch between the initial motor command and current movement state. Accordingly, prepared, ongoing movements can be rapidly and automatically adapted without detriment to the internal movement structure. The PPC has been shown to be involved in online adjustments by predicting the sensory consequences of movements as well as by detecting the mismatches between planned and current movement states (e.g., Desmurget & Grafton, 2000).

In some situations, however, rapid and automatic online adjustments cannot satisfy new action demands. In those situations, such as a reversal in movement direction, rather than the modification of movement parameters, the corrective update of prepared, ongoing movements is required (e.g., Elliott et al., 2001; Quinn & Sherwood, 1983). One way to achieve corrective movement update is changing the initially prepared movement plan with a new plan, i.e., movement re-planning. In the current thesis, based on the abort-and-reprogram model, movement re-planning is defined as the cancellation of an initially prepared movement plan, and the selection and implementation of a more appropriate alternative plan (e.g., Georgopoulos, Kalaska, & Massey, 1981; Larish & Stelmach, 1982; Prablanc & Martin, 1992; Soechting & Lacqueaniti, 1983).

Movement re-planning requires a multiplicity of cognitive operations for controlling the implementation of a new plan in the face of a more dominant initial plan (e.g., Pouget, Murthy, & Stuphorn, 2017; Verbruggen, Schneider, & Logan, 2008). For example, cancelling a prepared, but inappropriate plan requires understanding the error that ongoing movement is not satisfying the desired outcome (e.g., Wei & Körding, 2008). Hence, the ongoing movement must be inhibited, for example, by suppressing the stimulus-response mappings. Subsequently, a new plan must be selected to prepare and execute a new movement (e.g., Aron, Robbins, & Poldrack, 2014; Verbruggen, 2016). Accordingly, movement re-planning is involved in high-level cognitive control such as decision-making and conflict resolution between the expectancy and preparation of the ongoing movement and the need to override it by a new movement (e.g., Botvinick, Braver, Barch, Carter, & Cohen, 2001; Steinhauser & Yeung, 2010). Moreover, required cognitive operations have to be well-monitored for a rapid cancellation of the initially prepared plan, yet with an adequate time for the efficient selection and implementation of a new plan (e.g., Stinear, Coxon, & Byblow, 2009).

People can effectively re-plan ongoing movements and meet changing action demands. However, in contrast to the rapid and automatic online adjustments, movement re-planning is a time consuming and cognitively demanding process (e.g., Ullsperger, Danielmeier, & Jocham, 2014). Accordingly, movement re-planning induces motor costs such as longer reaction times (RT) and execution times (ET). For example, pre-cue paradigms, in which participants prepare movements based on a cue which provides either the valid or invalid advance information about the movement parameters such as direction or amplitude, have shown that invalid information in contrast to valid information result in longer RT (e.g., Leuthold, 2003; Leuthold & Jentzsch, 2002; Rosenbaum & Kornblum, 1982). The longer RT has been explained by the additional operations that are present during invalid conditions such as new response selection at pre-motor stage (e.g., Larish, 1986; Zelaznik, Shapiro, & Carter, 1982) or movement programming at late motor stage (e.g., Larish & Frekany, 1985; Lépine, Glencross, & Requin, 1989). Longer ET has been also shown for the movements requiring plan updates, especially when the movement direction is reversed (e.g., Barrett & Glencross, 1989; Oostwoud Wijdenes, Brenner, & Smeets, 2013; Sparrow & Newell, 1998; for a review see, Elliott, Hansen, Mendoza, & Tremblay, 2004). Longer ET has been explained by both the changes in the muscles involved in reversing movement direction and the increased attention demands (e.g., Brebner, 1968).

Movement re-planning also induces cognitive costs such as memory costs (e.g., Logan & Fischman, 2015; Spiegel, Koester, & Schack, 2013, 2014; Spiegel, Koester, Weigelt, & Schack, 2012; Weigelt, Rosenbaum, Huelshorst, & Schack, 2009). It has been suggested that cognitive costs of movement re-planning can be reduced by re-using former movement plans instead of changing them with new plans each time (e.g., Rosenbaum, Cohen, Jax, Weiss, & Van der Wel, 2007). Accordingly, to avoid cognitive costs, people keep the former motor plans by employing a variety of strategies such as recalling previous grasp postures (e.g., Hughes & Seegelke, 2013) or hand paths (e.g., Jax & Rosenbaum, 2007; Van der Wel, Fleckenstein, Jax, & Rosenbaum, 2007). In the section 1.4.1, the interactions of manual action re-planning with working memory and the related cognitive costs will be presented in detail.

The complexity of movement re-planning has been also supported by the involvement of a variety of the frontal and parietal cortical regions, besides the PPC (e.g., Desmurget et al., 1999; Pisella et al., 2000; Reichenbach, Bresciani, Peer, Bülthoff, & Thielscher, 2010). For example, the inferior frontal cortex (IFC; e.g., Mars, Piekema, Coles, Hulstijn, & Toni, 2007;

Neubert, Mars, Buch, Olivier, & Rushworth, 2010) and the pre-supplementary motor area (pre-SMA: e.g., Mars et al., 2009; Neubert, Mars, Olivier, & Rushworth, 2011) are involved in changing inappropriate movement plans with new plans under the time pressure. The dorsal PMC is involved in selecting and executing new movements by rapidly forming new stimulus-response mappings (e.g., Hartwigsen et al., 2012; Hartwigsen & Siebner, 2015).

1.2 Principles of working memory (WM)

Working memory (WM) is the cognitive process which stores and manipulates the limited amount of information for a brief period of time (e.g., Cowan, 2017). In human research, Miller and colleagues (1960) introduced the term *working memory* and defined it as a part of cognition which stores information for planning the actions, completing the goals, and thus operating successfully in life. In fact, the concept of WM dates back to Ebbinghaus (1885/1913) who introduced the term *immediate memory* referring to the limited amount of information stored for a short time (for a review, see Cowan, 2008). Later, Atkinson and Shiffrin (1968) introduced the short-term memory model which has conceptualized short-term memory as the temporary storage receiving the information directly from the sensory input, manipulating it, and transferring it into the long-term memory (LTM). This model, then, inspired the first WM model, the multi-component model (MCO-M; Baddeley & Hitch, 1974), which has described WM as a dynamic system including both the storage and executive functions. Although there are different views on what constitutes WM, the consensus is that WM provides a mental workspace not only for storing, but also for actively manipulating information (for a review, see Norris, 2017).

WM is the core cognitive process which engages in a range of complex behavior from perception to motor control (e.g., Nyberg & Eriksson, 2016). WM enables representing immediate past experience mentally, tracking moment-to-moment changes in the environment, acquiring new knowledge, and thus enables solving problems as well as formulating and acting on action goals. Relatedly, WM is involved in a variety of executive functions such updating the information, inhibiting the irrelevant information, and thus storing the relevant information in the presence of distraction, focusing or shifting the attention and coordinating different tasks (e.g., Miyake, Friedman, Emerson, Witzki, & Howerter, 2000; Unsworth & Engle, 2007; Vandierendonck, 2016).

The current thesis focuses on the functional role of WM in manual action control, particularly in a scenario where a manual task and a WM task are performed concurrently. Given that WM is not a unitary construct, but rather operates on different information domains and cognitive processes, manual action-WM interactions are investigated considering different WM domains and processes.

1.2.1 Theoretical framework for WM

Broadly, there have been two classes of WM models, system models and state models, which differ from each other in terms of the arguments regarding the separation between WM and LTM, existence of separate stores for different information domains, and role of attention in WM (for reviews, see Adams, Nguyen, & Cowan, 2018; Ma, Husain, & Bays, 2014).

One of the influential system models is the MCO-M which has described WM as a system which is separate from LTM, and thus is involved in the information storage and manipulation with own storage and executive capacities (Baddeley & Hitch, 1974; Baddeley, 2000; see Figure 1.3). According to the model, WM consists of two domain-specific, capacity-limited temporary storage buffers dedicated to the particular type of information; a domain-general attention controller, the central executive, manipulating the information and coordinating the buffers; a domain-general store, the episodic buffer, forming an interface between the buffers, central executive and LTM for the multi-dimensional binding of information (for reviews, see Baddeley, Hitch, & Allen, 2018; Repovš & Baddeley, 2006).

The phonological loop (i.e., verbal domain) is the storage buffer dedicated to the verbal information in phonological format. It has two components. The first is a passive, auditory-based phonological store in which the information is registered but fades in a few seconds if not rehearsed. The second is an active, motor-based phonological output buffer in which the information is maintained by a subvocal rehearsal mechanism (i.e., articulatory rehearsal). The visuospatial sketchpad (i.e., visuospatial domain) is the storage buffer dedicated to the visual (pictorial) and spatial (location) information. With an analogy to the articulatory rehearsal within the phonological loop, Baddeley (1986) proposed an eye movement-based active rehearsal mechanism for the visuospatial sketchpad, i.e., oculomotor rehearsal hypothesis. Later, Logie (1995) proposed two visuospatial sketchpad components. The passive visual store, the visual cache, deals with the static properties of visual images such as color, shape or luminance. The active rehearsal mechanism, the inner scribe, helps for maintaining the information in the visual cache by motor-based rehearsal (e.g., Logie, 2011). Moreover, the phonological loop and the visuospatial sketchpad work closely with the central executive which manipulates the information by focusing, dividing and switching attention as well as relating to the content of WM to LTM, and thus coordinates complex behaviors such as dual-task operations (Baddeley, 1996; Logie, 2016).

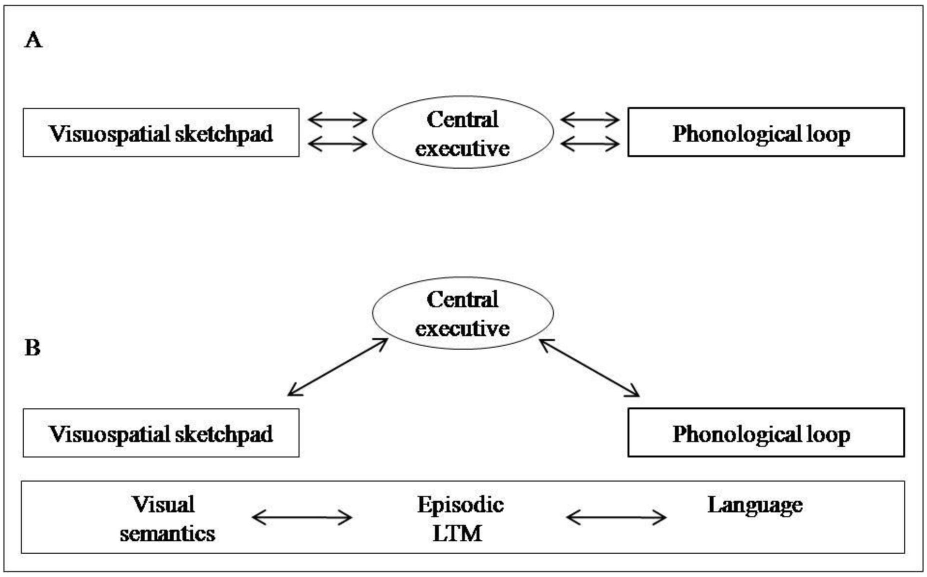

Figure 1.3. The multi-component model of WM. (A) Initial three-component model by Baddeley and Hitch (1974) with two storage buffers and attention controller. (B) The further developed model by Baddeley (2000). The episodic buffer allows for the interaction between storage buffers and LTM. Adapted from Baddeley, 2000, p: 418. Copyright 2000 by Elsevier Science Ltd.

State models have described WM as an emergent property of the interactions between attention and LTM. That is, WM is the active representations of LTM, which is controlled by attention (e.g., Barrouillet, Bernardin, & Camos, 2004; Cowan, 1988, 1999; Ericsson & Kintsch, 1995; McElree, 2001; Oberauer, 2002). State models have not proposed the structural separation between the domain-specific storage buffers and the domain-general central executive, but rather proposed that attention is the capacity-limited storage and manipulation mechanism working on any kind of information.

The embedded process model by Cowan (1988, 1999) has been the representative state model which introduced the idea of the capacity-limited focus of attention (FoA) as the core of WM. According to the model, attention allows for selecting the limited amount of information that is relevant for the task at hand, bringing and maintaining the selected information into the focus, and preventing the decay. Hence, two distinct states emerge, the capacity-limited FoA where the information is immediately available and the activated portion of LTM from where the information is put into the focus (see Figure 1.4). Cowan (2001) suggested that only four chunks of information can be stored and processed into the FoA at any time. Similar to the MCO-M, the embedded process model has suggested that information with similar features compete for the access to the FoA and interfere with each other.

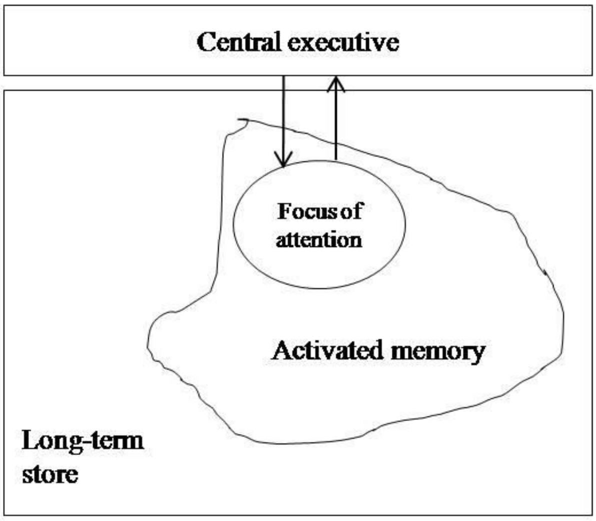

Figure 1.4. The embedded process model of WM. The model has proposed two distinct states of information, focus of attention and activated portion of LTM. Adapted from Cowan, 1988, p: 180.

Oberauer's three embedded process model (2002) has also accepted the idea that information exists in varying states of accessibility in memory, i.e., FoA, direct access region and activated portion of LTM. Different from Cowan's model, this model has suggested that the FoA has a limited capacity of one chunk at any time, with the ability to switch information in and out of the direct access region by attention.

The time-based resource sharing model (TBRS-M, Barrouillet et al., 2004; Barrouillet, Bernardin, Portrat, Vergauwe, & Camos, 2007) has also proposed that attention is the capacity-limited, domain-general mechanism involving both in the information storage and manipulation, also by focusing on how attention is shared in a time-based manner between them. According to the model, storage and manipulation cannot be performed at the same time since both use the common capacity-limited attention resources. Moreover, regardless of the information domain, any concurrent task capturing the attention resources for its performance would divert attention away from the storage and manipulation, and thus result in the disruptive effect for WM. Different from other state models, but similar to the MCO-M, the TBRS-M has proposed different rehearsal mechanisms for verbal and visuospatial domains. Namely, the domain-general attention refreshing is involved in the maintenance of both verbal and visuospatial information, and the domain-specific articulatory rehearsal is involved in the maintenance of verbal information, but not visuospatial visuospatial (Camos, Lagner, & Barrouillet, 2009).

Neural WM models have also supported the state models by suggesting that WM is represented by a distributed cortical network which also controls attention and LTM (e.g., Christophel, Klink, Spitzer, Roelfsema, & Haynes, 2017; Postle, 2006; for a review, see D' Esposito & Postle, 2015). For example, the emergent property view (Postle, 2006) has suggested that WM is the result of the interactions between several cortical regions which are activated based on task requirements. Accordingly, the same cortical regions are activated in response to the encoding and storage of information in a variety of goal-directed behavior including motor actions.

The current thesis, as in line with the MCO-M, conceptualizes WM as a dynamic system which consists of domain-specific storage systems supported by a domain-general attention controller. Nonetheless, the current thesis does not disregard the importance of the functional interactions of WM with LTM or the importance of the cross-talk between two storage buffers, which has been also suggested by the recent modifications of the MCO-M (e.g., Baddeley et al., 2018). Moreover, the current thesis also conceptualizes WM as a system which comprises separate, but overlapping cognitive processes for encoding, maintaining and retrieving information (e.g., Jonides et al., 2008).

1.2.2 WM domains and processes

The early support for the domain specificity of WM came from the behavioral studies which applied dual-task scenarios (e.g., Farmer, Berman, & Fletcher, 1986; Logie, Zucco, & Baddeley, 1990). These studies compared the memory performances for verbal and visuospatial tasks in various task conditions, e.g., tasks were performed alone, concurrently with same-domain task, concurrently with other-domain task. The underlying assumption of these studies was that if verbal and visuospatial domains pertain to the common capacity-limited resources, they would interfere with each other when verbal and visuospatial tasks are performed concurrently, and thus result in a memory performance decline. The succeeding dual-task studies have also shown that concurrent verbal and visuospatial tasks result in little or no interference with each other compared to concurrent two verbal tasks or visuospatial tasks (e.g., Alloway, Kerr, & Langheinrich, 2010; Cocchini, Logie, Della Sala, MacPherson, & Baddeley, 2002; Thalmann & Oberauer, 2017; for a recent computational approach for the domain specificity, see Poirier et al., 2018; for an alternative theoretical model suggesting the domain specificity, see Oberauer, Lewandowsky, Farrell, Jarrold, & Greaves, 2012). The lack of interference, therefore, has supported the idea that verbal and visuospatial domains are functionally separate, pertaining to separate resources.

The separation between verbal and visuospatial domains has been also supported by different rehearsal mechanisms. As first introduced by the MCO-M, verbal information is rehearsed by the inner-speech like articulatory rehearsal, while visuospatial information is rehearsed by the eye movement-based rehearsal (Baddeley, 1986). Accordingly, execution of a concurrent eye movement interferes with visuospatial domain, but not with verbal domain, and thus decreases memory performance only for visuospatial task (e.g., Pearson, Ball, & Smith, 2014; Postle, Idzikowski, Della Sala, Logie, & Baddeley, 2006). Movement interference with visuospatial domain has been also shown by other movement forms such as sequential tapping (e.g., Salway & Logie, 1995; Smyth, Pearson, & Pendleton, 1988; Smyth & Pendleton, 1989), pointing (e.g., Dodd & Shumborski, 2009; Rossi-Arnaud, Spataro, & Longobardi, 2012) and arm movements (e.g., Quinn & Ralston, 1986).

According to Logie (1995), movement interference is induced due to the inner scribe which is involved in both the active rehearsal of visuospatial information and the employment of this information for the planning and execution of concurrent movement. Consequently, the concurrent movement occupies the inner scribe, and thus hinders the storage of visuospatial information. Alternatively, the attention-based rehearsal hypothesis has suggested that spatial attention plays a functional role in active rehearsal of visuospatial information (e.g., Awh, Armstrong, & Moore, 2006). The experimental findings have supported both hypotheses by showing that visuospatial domain, but not verbal domain, shares resources with movement and spatial attention (for a review, see Quinn 2008).

Verbal and visuospatial domains are involved in different cognitive and motor tasks. For example, verbal domain engages in the language-related abilities such as vocabulary development and acquisition of reading skills (for a review, see Baddeley, 2017). Moreover, through the articulatory rehearsal, verbal domain engages in the task-switching by tracking sequential action plans (e.g., Liefooghe, Barrouillet, Vandierendonck, & Camos, 2008) as well as storing and, when necessary, recalling relevant action goals from LTM (e.g., Emerson & Miyake, 2003; Saeki & Saito, 2004; for a review, see Logan 2004). Relatedly, verbal domain also engages in the understanding and following task instructions (e.g., Jaroslawska, Gathercole, Logie, & Holmes, 2016). Differently, visuospatial domain engages in the binding or grouping of visual stimulus features (e.g., Luria & Vogel, 2014), visual search (e.g., Woodman & Luck, 2004), mental rotation (e.g., Prime & Jolicoeur, 2010) as well as visuomotor adaptation and sequence learning in motor skill acquisition (e.g., Anguera, Reuter-Lorenz, Willingham, & Seidler, 2011; De Kleine & Van der Lubbe, 2011). Moreover, developmental studies have also supported the separation between verbal and visuospatial domains by showing the lack of correlation between the domains for coordinating different cognitive abilities such as reading and arithmetic (e.g., Alloway, Gathercole, & Pickering, 2006; Bayliss, Jarrold, Gunn, & Baddeley 2003; Gathercole et al., 2016).

Brain research has also supported the functional separation between verbal and visuospatial domains. For example, neuropsychological studies have shown that damage to different cortical regions results in dissociable verbal and visuospatial domain deficits, i.e., some patients exhibit deficits in verbal domain with intact visuospatial domain, other patients show the opposite (e.g., De Renzi & Nichelli, 1975; Hanley, Young, & Pearson, 1991; Vallar & Baddeley, 1984). Neuroimaging studies have also shown that verbal and visuospatial domains recruit separate cortical regions (e.g., Gruber & von Cramon, 2003; Lee, Kravitz, & Baker, 2013). While verbal domain recruits predominantly a left lateralized cortical network (e.g., Awh et al., 1996; Kirschen, Chen, & Desmond, 2010; Narayanan et al., 2005; Paulesu, Frith, & Frackowiak, 1993), visuospatial domain recruits predominantly a right lateralized cortical network (e.g., Courtney, Petit, Maisog, Ungerleider, & Haxby, 1998; Silk, Bellgrove, Wrafter, Mattingley, & Cunnington, 2010).

Besides the domains, WM also comprises different processes, encoding, maintenance and retrieval, which engage in separate, but overlapping operations of information and recruit separate cortical regions (e.g., Baddeley, 1986; Cohen, Sreenivasan, & D' Esposito, 2014). During encoding, information to-be-remembered is extracted based on the stimulus-evoked sensory processes, and representation of this information is generated and transferred into WM. During maintenance, information is stored and protected from the interference and decay by sustained rehearsal mechanisms. During retrieval, the stored information is reactivated and used for performing the task at hand (e.g., Jonides et al., 2008).

Different research lines such as behavioral studies (e.g., Baddeley, Lewis, & Eldridge, 1984; Craik, Govoni, Naveh-Benjamin, & Anderson, 1996) and neuroimaging studies (e.g., Geiger et al., 2018; Landau, Schumacher, Garavan, Druzgal, & D' Esposito, 2004; Rypma, Berger, & D' Esposito, 2002) have shown that each process requires the cognitive resources such as attention to a different extent. Accordingly, memory load such as the presence of a concurrent task interferes with each process differently. For example, it has been shown that encoding is an active process requiring high attention resource both in verbal (e.g., Cowan & Morey, 2007) and visuospatial tasks (e.g., Vogel, Woodman, & Luck, 2005). Relatedly, encoding of verbal domain (e.g., Craik, Eftekhari, & Binns, 2018) and visuospatial domain (e.g., Logie & Marchetti, 1991) are disrupted by attention demanding concurrent tasks. In contrast, it has been shown that retrieval is an automatic process requiring limited attention resource, and thus can be performed concurrently with other tasks without any disruptive effect for memory performance (e.g., Baddeley et al., 1984; Landau et al., 2004; Weeks & Hashler, 2017). Relatedly, it has been also shown that focusing attention on to-be-remembered stimulus during encoding, but not during retrieval, enhances the subsequent memory recall (e.g., Damiano & Walther, 2019).

Each process has been also shown to activate separate, but overlapping cortical regions (e.g., Cairo, Liddle, Woodward, & Ngan, 2004; Cohen et al., 2014; Li, Christ, & Cowan, 2014; Manoach, Greve, Lindgren, & Dale, 2003). However, due to the limitations regarding the temporal resolution of neuroimaging techniques, not many studies have experimentally separated each process. Consequently, there has been a limited systematic investigation of the cortical regions involved in encoding, maintenance and retrieval processes of verbal and visuospatial domains.

WM is not a unitary construct, but rather consists of functionally separate, but overlapping domains and processes. Although the domains have been investigated elaborately, the processes have not been given such importance, particularly in relation to differences across the domains. Nevertheless, the processes have been also shown to represent different operations of information and to recruit different cortical regions. Accordingly, to investigate the domain interactions between manual action control and WM, it is also important to clarify how and what extent the separate processes, along with separate domains, are involved in the manual action control.

1.3 Theoretical framework for manual action - WM interactions

In the previous two sections, the principles of manual actions and WM have been presented as two separate domains. To understand how humans plan, execute and adapt manual actions, it is also critical to bring these domains together and determine how they interact and influence one another. The current section, therefore, presents different theoretical perspectives and related research on the manual action-WM interactions.

From the WM perspective, WM models which have conceptualized WM being involving not only in the cognitive, but also in the motor processes have supported the domain interactions between manual actions and WM (e.g., Fuster, 2009; Postle, 2006; Theeuwes, Belopolsky, & Olivers, 2009; for a review, see Nyberg & Eriksson, 2016). For example, the emergent property view (Postle, 2006) has suggested that WM plays a functional role in movement planning and execution by storing both the movement-related visuospatial information and future action goals and intentions. That is, WM serves as a bridging period for the movement with retrospective and prospective motor codes (e.g., Ikkai & Curtis, 2011). Similarly, Theeuwes and colleagues (2009), by investigating the functional interactions between WM, attention and motor control, have proposed that “the possibility that working memory is 'nothing more' than the preparation to perform an action, whether it be oculomotor, manual, verbal, or otherwise” (pp: 198-199).

Accordingly, it has been shown that WM plays a functional role in selection and execution of movement plans (e.g., Fournier, Gallimore, Feiszli, & Logan, 2014; Gallivan, Bowman, Chapman, Wolpert, & Flanagan, 2016; Mattson & Fournier, 2008). For example, Mattson and Fournier (2008) showed that executing a movement was delayed when another movement plan was stored into WM, particularly when the current movement shared a feature with the stored plan such as a left-hand response. Differently, Gallivan and colleagues (2016) showed that not only a first movement plan stored into WM influenced an upcoming new movement, but also the new movement influenced the initially stored movement plan, and accordingly changes the kinematics of the first movement. Accordingly, this retrospective influence of the second plan on the stored plan has suggested that movement plans are stored into WM and, when necessary, re-visited and changed based on the subsequent movements, which also supporting the role of WM in movement re-planning, and thus in action flexibility.

Memory-guided grasping paradigms, in which the visual feedback of a target object is not available during movement execution, have shown that WM keeps grasp-related object information active for converting it into a motor program (e.g., Hesse & Franz, 2009, 2010; Hesse, Miller, & Buckingham, 2016; Kirsch, Hennighausen, & Rösler, 2009; Kohler, Isenberg, Schönle, Inbar, & Conrad, 1989; for a review, see Schenk & Hesse, 2018). For example, it has been shown that WM keeps the visuospatial object information for 2 seconds during the period between the vision of the object and the movement onset, and thus enables the movement execution when the object vision is unavailable. Moreover, decay characteristic of the object information is similar to those observed in memory research (e.g., Hesse & Franz, 2010). Additionally, Hesse and colleagues (2016) showed that decay characteristics are different for the object size and location information, of which the former resistant to the decay more than the latter. Neuroimaging studies have also supported the role of WM in keeping the grasp-related object information. That is, the same frontal-parietal cortical regions which are involved in immediate grasping movements also show a sustained activation during delayed movements for keeping the object information active (e.g., Fiehler et al., 2011; Singhal, Monaco, Kaufman, & Culham, 2013).

The embedded cognition approach, which has suggested a close engagement of the motor and cognitive systems, has also supported the manual action-WM interactions. According to this approach, cognition is built from the bodily experiences and dynamic interactions with the physical environment (e.g., Dijkstra & Post, 2015; Glenberg, 1997; Wilson, 2002). Like in many other cognitive processes such as language (for a review, see Pulvermüller, 2018), it has been shown that motor representations, particularly of grasping movements, play a functional role in WM (e.g., Downing-Doucet & Guérard, 2014; Guérard, Guerrette, & Rowe, 2015; Mecklinger, Gruenewald, Besson, Magnie, & von Cramon, 2002; Mecklinger, Gruenewald, Weiskopf, & Doeller, 2004). For example, Mecklinger and colleagues (2004) showed that affordances related to object use enhanced WM storage and activation of the related cortical regions for manipulable objects compared to nonmanipulable objects. That is, motor simulation regarding the object grasping facilitates WM operations. Moreover, it has been also shown that spatial-motor representations improve WM performance for remembering task instructions (e.g., Allen & Waterman, 2015; Jaroslawska, Gathercole, Allen, & Holmes, 2016; Plancher, Mazeres, & Vallet, 2018). For example, Jaroslawska and colleagues (2016) showed that the recall of instructions such as 'pick up a black pencil' were enhanced when participants enacted the instructions in addition to processed them verbally. The role of motor representations in WM is also in line with the MCO-M which has proposed the motor-based active rehearsal mechanisms for both verbal domain (e.g., inner-speech like articulatory rehearsal) and visuospatial domain (e.g., eye movement-based rehearsal; Baddeley et al., 2018).

From the motor control perspective, a variety of perceptual-cognitive theories have focused on the cognitive control of motor actions (e.g., the ideomotor approach, Prinz, 1992; the theory of event coding, Hommel, 1998; Hommel, Müsseler, Aschersleben, & Prinz, 2001; the cognitive action architecture approach, CAA-A, Schack, 2004; Schack & Mechsner, 2006). According to these theories, people plan and execute actions based on what they desire to produce as perceptual effects in the environment based on certain action goals. Memory plays a functional role in motor control by storing the representations of perceptual action effects. The stored representations then enable anticipatory control of future actions which would also result in desired effects. Hereby, cognitive control of motor actions is achieved by the anticipations of perceptual action effects. Rosenbaum and colleagues (e.g., Rosenbaum & Jorgensen, 1992; Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001; also see Cohen & Rosenbaum, 2011) have also suggested the role of memory in motor control in the theory of motor planning. According to the theory, recently adopted motor solutions are stored in memory and used again for future tasks. This way, the stored solutions provide computationally efficient movement planning for new, yet comparable actions.

Although the role of memory in motor control has been suggested by different perceptual-cognitive motor theories, only the CAA-A (Schack, 2004) has explicitly discussed the role of WM in planning and execution of complex movements. According to the CAA-A, there are four building blocks of a movement, namely levels of the sensorimotor and mental control with the own levels of the sensorimotor and mental representations. For a given movement, multidirectional communications between the hierarchically organized levels are required. The mental representation level contains the basic action concepts (BACs), the major representation units stored in LTM, which bring together the sensory (e.g., perceptual action effects) and cognitive (e.g., action goals) movement features. Hence, BACs provide the basis for action anticipation, and thus cognitive control by linking high-level action goals with low level perceptual effects. The functional structure of BACs can change with motor learning and expertise, as shown for a variety of sport settings such as golf (e.g., Kim, Frank, & Schack, 2017) as well as dance (e.g., Bläsing, Tenenbaum, & Schack, 2009; for reviews, see Land, Volchenkov, Bläsing, & Schack, 2013; Seegelke & Schack, 2016). Moreover, the CAA-A has suggested that WM contributes to the functional structure of BACs by competently extracting and chunking the relevant information for a given movement. Therefore, both LTM and WM operations are required for skilled complex movements.

The current thesis applies a cognitive-motor dual-task paradigm for investigating the functional role of WM in manual action control. Therefore, next, I will present first the theoretical framework for dual-task paradigms (section 1.4) and related research on the manual action-WM interactions (section 1.4.1).

1.4 Principles of dual-task paradigms

In everyday life, to achieve a common action goal, it is inescapable to perform motor and cognitive tasks at the same time such as grasping a mobile phone while writing a text, driving while attending traffic signs, or walking through a grocery shop while recalling items from a shopping list (for a review on the importance of dual-tasking in a variety of natural environments, see Logie, Law, Trawley, & Nissan, 2010). Therefore, cognitive-motor dual-task paradigms, in which a cognitive task and a motor task are performed concurrently, are highly relevant to everyday living and suitable for the investigation of cognitive requirements of motor tasks (e.g., McIsaac, Lamberg, & Muratori, 2015; Plummer et al., 2013; for a review on the neural correlates, see Leone et al., 2017). In the current thesis, the dual-task paradigm is conceptualized in a way that a WM task not necessarily requiring a speeded response is combined and temporally overlapped with a continuous manual task (e.g., Jolicoeur & Dell' Acqua, 1998; Kee, Barthus, & Hellige, 1983; for a review on the different dual-task paradigms, see Watanabe & Funahashi, 2018). Accordingly, the current dual-task paradigm enables that "two tasks can be performed independently, measured separately and have distinct goals" (McIsaach et al., 2015, p: 2).

In experimental context, dual-task paradigms are well-suited to investigate whether two tasks are functionally correlated, i.e., whether the operations required for one task affect the performance of another task. Functionally correlated tasks generally interfere with each other and result in dual-task costs which refer to the task performance differences between single-task and dual-task conditions. Dual-task costs can be observed either as the performance decline for both tasks or as the performance trade-off in which the performance of one task is preserved at the expense of the performance of another task (e.g., Plummer et al., 2013).

One theoretical approach to explain dual-task interference is the structural bottleneck theories which have proposed that only one task can be processed at a time due to the processing limitation of the human cognitive system, so-called bottleneck (e.g., Pashler, 1994). When two tasks are performed concurrently, especially the central operations such as response selection must be delayed for one of the tasks while the bottleneck is occupied by another task. The extended version of the bottleneck theories has further proposed that dual-task interference occurs not only due to the central operations, but also due to the peripheral operations at the motor output stage if concurrent tasks require common motor output structures, i.e., peripheral bottleneck (e.g., Bratzke, Rolke, & Ulrich, 2009; Bratzke et al., 2008; De Jong, 1993; Ulrich et al., 2006). Accordingly, it has been shown that overlapping effector systems of the concurrent tasks, for example, co-activated hands during bimanual tasks, lead to erroneous transmission of motor codes due to the motor contrainst, and thus result in dual-task interference (e.g., Heuer, 1996; Heuer, Kleinsorge, Spijkers, & Steglich, 2004; Swinnen & Wenderoth, 2004).

The resource sharing theories have suggested that dual-task interference occurs due to the capacity-limited cognitive resources shared between concurrent tasks. According to the modality-general theories (e.g., Kahneman, 1973; Tombu & Jolicoeur, 2003), there is a domain-general resource, such as attention, for which each task competes. If concurrent tasks are not cognitively demanding, they can be performed at the same time. However, when the concurrent performance of the tasks requires the resources which exceed the available capacity, fewer resources are allocated to each task. Consequently, tasks are performed less efficiently with a performance decline. If one of the tasks is prioritized, more resources are allocated to that task for preserving the task performance at the expense of the performance of the non-prioritized task. Alternatively, the modality-specific theories (e.g., Navon & Gopher, 1979; Wickens, 1980) have suggested that there are multiple resources with own limited capacity rather than a general structure or resource shared by any task. Hence, dual-task interference occurs only if concurrent tasks share the common capacity-limited resources, otherwise tasks are performed concurrently without interference. Accordingly, both the task difficulty and common resources affect the dual-task interference.

The multiple resource theory (Wickens, 1980; Wickens, Sandry, & Vidulich, 1983) has further suggested that each task requires resources related to particular dimensions such as input modality (i.e., sensory channels for stimuli such as visual or auditory input), central codes (i.e., codes of central processing such as spatial or verbal) and output modality (i.e., response channels such as manual or vocal response). Therefore, the concurrent tasks requiring the common resources for any of these dimensions interfere with each other more than the tasks requiring separate resources. Moreover, Wickens, Vidulich and Sandry-Garza (1984) introduced the concept of the within-task modality compatibility. That is, there are preferred combinations of the input and output modalities (i.e., stimulus-response modalities) such as visual stimulus with manual response. The combinations of the stimulus-response modalities, whether they are compatible or incompatible within a task, then determine the resistance of the task to the dual-task interference.

Accordingly, it has been shown that modality compatibility affects the extent of dual-task interference more than it affects the single-task performance (e.g., Hazeltine & Ruthruff, 2006; Hazeltine, Ruthruff, & Remington, 2006; for a review, see Huestegge & Hazeltine, 2011). For example, Hazeltine and colleagues (2006) showed that two compatible tasks (e.g., visual-manual and auditory-vocal tasks) resulted in less dual-task interference compared to incompatible tasks (e.g., visual-vocal and auditory-manual tasks). However, the authors showed that the modality compatibility did not play a role in the single-task performance. The stimulus-response compatibility has been explained as a natural tendency to pair certain sensory modalities with certain motor modalities, supporting the idea of ideomotor principle (e.g., Greenwald, 1972; Hommel et al., 2001). Accordingly, preferred processing pathways for certain pairings decrease the required cognitive resources, and thus decrease the dual-task interference between concurrent tasks.

Recently, dual-task interference has been explained in relation to WM (e.g., Göthe, Oberauer, & Kliegl, 2016; Halvorson & Hazeltine, 2015; Hazeltine & Wifall, 2011; Maquestiaux, Ruthruff, Defer, & Ibrahime, 2018; Pieczykolan & Huestegge, 2017). For example, Hazeltine and Wifall (2011) investigated whether dual-task interference occurs due to the competition between concurrent tasks for the common capacity-limited WM resources. The authors paired a WM task including the tones or locations as stimuli with a choice reaction task including the visual stimuli with either vocal or manual response. It was found that independent of the stimulus modality of the choice task (visual stimulus), the vocal choice task interfered with the tones while the manual choice task interfered with the locations. By manipulating only the response modality of the choice task (vocal or manual response), the authors further showed that the interference with WM was determined by the response modality. In line with the MOC-M, these findings have suggested that dual-task interference occurs when the concurrent tasks compete for the common WM resources. Therefore, WM requirements of the concurrent tasks are critical for determining the dual-task interference particularly at the response stage.

Moreover, dual-task advantage of the modality compatibility has been also explained in relation to the MOC-M (e.g., Göthe et al., 2016; Maquestiaux et al., 2018). When the stimulus-response modalities overlap within a task, but not between tasks, modality codes of each task are stored in separate WM systems, either in the phonological loop or the visuospatial sketchpad. In contrast, when the stimulus-response modalities do not overlap within a task, modality codes of each task are partially stored in same WM systems. For example, the visuospatial sketchpad would contain a stimulus code for a visual-vocal task and a response code for an auditory-manual task. Accordingly, when two incompatible tasks are performed concurrently, the dual-task interference occurs due to the competition for the common WM resources in the same WM system.

1.4.1 Manual action - WM interactions in dual-task paradigms

Cognitive-motor dual-task paradigms have been also used for investigating the manual action-WM interactions, and have shown a complex pattern for the WM involvement in the planning, execution and re-planning of grasping movements (e.g., Guillery, Mouraux, & Thonnard, 2013; Guillery, Mouraux, Thonnard, & Legrain, 2017; Logan & Fischman, 2011, 2015; Pardhan & Zuidhoek, 2013; Spiegel et al., 2013, 2014; Spiegel et al, 2012; Voelcker-Rehage & Alberts, 2007; Weigelt et al., 2009).

Guillery and colleagues (2013), for example, showed that a concurrent WM task including visual search and counting interfered with a grasping movement including grasping, lifting and holding an object. Moreover, WM task interfered both with movement planning and execution as shown by the increased duration of initial force scaling during planning and the increased application of grip force during execution. Differently, Pardhan and Zuidhoek (2013) showed that a concurrent WM task including counting interfered only with planning of a grasping movement as shown by the increased movement onset time.

Other studies have shown the interference of grasping movements with WM, resulting in memory performance decline (e.g., Logan & Fischman, 2011, 2015; Spiegel et al., 2013; Spiegel et al., 2012; Weigelt et al., 2009). For example, Weigelt and colleagues (2009) investigated the interactions between movement planning and memory processes by applying a perceptual-motor task together with a verbal memory task. Participants had to open a drawer, grasp a cup located in the drawer, get the letters as memory stimuli from the inside of the cup and memorize the letters. The authors found that planning requirements of the manual task, particularly abandoning a movement plan in favor of another, interfered with memorizing the letters and eliminated the recency effect which is otherwise a robust tendency for remembering the recent memory items better than the earlier items. Differently, Logan and Fischman (2011) found that not only the planning, but also the execution of a concurrent grasping movement, regardless of the movement complexity, interfered with memorizing the letters, which they interpreted as a basic concurrence cost.

Spiegel and colleagues (2012, 2013, 2014) conducted a series of experiments focusing on the different movement phases and different WM domains. Accordingly, the authors applied a dual-task paradigm in which a manual task including grasping an object and placing it on a motor target was combined with a WM task. First, Spiegel and colleagues (2012) investigated the functional domain interactions between movement re-planning and verbal domain. The authors found that concurrent movement re-planning interfered with memorizing verbal information and decreased memory performance. The following study (Spiegel et al., 2013) investigated whether movement execution would result in similar interference patterns with WM. Accordingly, the authors compared the memory performances for verbal and visuospatial tasks in the movement execution and re-planning conditions. It was found that concurrent movement execution interfered with memorizing visuospatial information, but not verbal information, and decreased memory performance only for visuospatial task. Differently, concurrent movement re-planning interfered with memorizing both verbal and visuospatial information and decreased memory performances both for verbal and visuospatial tasks. Spiegel and colleagues (2013) interpreted these findings to suggest that movement execution generates domain-specific dual-task interference with visuospatial domain, while movement re-planning generates domain-general dual-task interference both with verbal and visuospatial domains. Accordingly, movement re-planning and execution are different movement phases which recruit distinct WM capacities, and thus interact with WM domains to a different extent.

Although Spiegel and colleagues (2012, 2013) have provided the first systematic investigations of the manual action-WM interactions by focusing on the different movement phases and WM domains, to the best of my knowledge, the current thesis provides the first systematic neurophysiological investigations of such interactions. Before going into the details of the goal and research questions of the current thesis, I will present the relevant principles of human neurophysiology and ERP research on the manual action-WM interactions in the next section.

1.5 Principles of human neurophysiology

EEG is a direct and non-invasive measurement technique for recording the electrical activity of the human brain (e.g., Luck & Kappenman, 2012). EEG recordings reflect the summation of the synchronous activity of thousands of neurons which are aligned parallel to each other. The electrical activity is recorded by the electrodes which are positioned along the scalp based on the international 10-20 system (e.g., Oostenveld & Praamstra, 2001). EEG has a high temporal resolution in order of milliseconds, therefore allowing the immediate recordings of the electrical activity over a period of time.

ERPs are small voltage changes which are extracted from the continuous EEG recordings in response to a particular internal or external event such as a stimulus or motor response (e.g., Coles & Rugg, 1995; Hillyard & Kutas, 1983). ERPs are obtained by time-locking the continuous recordings either to the presentation of a stimulus (stimulus-locked) or to the movement onset (response-locked). While the stimulus-locked ERPs generally reflect the cognitive processes such as stimulus evaluation, response-locked ERPs reflect the motor processes such as movement preparation. Accordingly, ERPs can describe the processes either preceding or succeeding a particular event (e.g., Luck & Kappenman, 2012).

ERPs are embedded in the large EEG signals which also include the noise signal unrelated to the event. Therefore, ERP signals should be differentiated from the noise signal by the signal averaging. The idea behind signal averaging is that signals related to the identical events, but not the noise signal, are often associated with similar cortical activity. Accordingly, with the repetitions of identical events, the noise signal varies randomly and averages to zero, and leaves only the signals representing the cortical activity related to the event. Since the ERP amplitude is much smaller than the EEG amplitude, a high number of repetitions of the event is required for a high signal-to-noise ratio (e.g., Donchin, 1979).

ERPs are characterized by three dimensions, amplitude, latency and scalp distribution (e.g., Bressler, 2002). Amplitude is the index of the extent of the cortical activity which functionally responds to the event. Latency is the index of the time at which the peak activity occurs following the event. Scalp distribution is the index of the pattern of the voltage changes which occur over the scalp in response to the event. Although the ERPs have low spatial resolution, the scalp distribution can still provide useful and complementary information to the amplitude and latency. That is, comparisons of the scalp distribution of the ERPs elicited by different events allow for inferring whether two events generate different patterns of the cortical activity and reflect different functional processes (e.g., Hillyard & Kutas, 1983). Accordingly, ERPs provide information about which cortical regions are activated for how long and in which order.

ERPs consist of characteristics voltage deflections, the components. ERP components are defined by the polarity (positive or negative voltage deflections) and the latency. Therefore, ERP components are generally named by a letter (N/P) indicating the polarity and a number indicating the latency in millisecond (e.g., Münte, Urbach, Düzel, & Kutas, 2000). For example, N100 refers to the negative going deflection peaking at 100 ms after the event. Moreover, some components are named based on the event properties. For example, the contingent negative variation is an ERP component which appears when the contingency of the second stimulus on the first stimulus is established. ERP components can reflect either the stimulus driven processes, the exogenous components, or the cognitive or motor processes related to a certain task, the endogenous components (e.g., Luck & Kappenman, 2012).

One of the most investigated endogenous ERP components is the P300 which is a positive going deflection with peak latency of 300-1000 ms (e.g., Chapman & Bragdon, 1964; Sutton, Braren, Zubin, & John, 1965; Sutton, Tueting, Zubin, & John, 1967; for a review, see Polich, 2012). It has two subcomponents. The P3a is an early deflection appearing over the frontal-central scalp regions. The P3a engages in the involuntary attention shifts to unexpected task-irrelevant changes in the environment. The P3b is a late deflection appearing over the central-parietal scalp regions. In many cases, the term *P300* refers to the P3b (e.g., Polich, 2007). P300 engages in many cognitive processes such as stimulus evaluation and categorization, stimulus-response mappings and context updating in the tasks that require some form of overt or covert actions (e.g., Donchin & Coles, 1988; Kok, 2001; Niewenhuis, Aston-Jones, & Cohen, 2005; Verleger, Jaskowski, & Wascher, 2005). Moreover, P300 is sensitive to the probability and individual expectancy of the event, task relevance of the stimulus and difficulty of the task. Accordingly, P300 indexes the mental effort related to the task (e.g., Kok, 1997; Sirevaag, Kramer, Coles, & Donchin, 1989).

Besides the components, ERPs can also consist of the slow waves which last for hundreds of milliseconds or even seconds and reflect the complex information processing during a variety of tasks such as sustained attention, WM, movement preparation and execution (e.g., Birbaumer, Elbert, Canavan, & Rockstroh, 1990; Rösler, Heil, & Glowalla, 1993). Like the components, slow waves are also defined based on the polarity of voltage deflections, negative and positive slow waves. Generally, it has been suggested that negative slow waves indicate the excitability of the underlying cortical region, and thus the amplitude of the negative slow wave indicates the task difficulty (e.g., Rösler, Heil, & Röder, 1997). However, in experimental context, slow waves are not defined in an absolute way, but always as a voltage deflection for one condition relative to other conditions. Moreover, slow waves have task-specific scalp distributions. That is, a certain slow wave appears over a certain scalp region depending on the task demand. For example, tasks activating the frontal cortical regions generate slow waves over anterior scalp regions, while tasks activating the parietal cortical regions generate slow waves over posterior scalp regions.

1.5.1 ERP correlates of manual action control

ERPs have provided a reliable method for investigating the critical aspects of motor actions such as effector selection or movement direction encoding (for a review, see Shibasaki & Hallett, 2006). However, because of potential movement artefacts, ERP research has been mostly restricted to the preparation (pre-execution) phase of simple movements such as finger tapping. Recently, ERPs have been successfully applied to the investigation of overt, complex manual actions (e.g., Bozzacchi, Cimmino, & Di Russo, 2017; De Sanctis, Tarantino, Straulino, Begliomini, & Castiello, 2013; Van Schie & Bekkering, 2007; Westerholz, Schack, & Koester, 2013, 2014; Westerholz, Schack, Schütz, & Koester, 2014; for reviews, see Armstrong, Sale, & Cunnington, 2018; Di Russo et al., 2017; Koester, Schack, & Westerholz, 2016). Accordingly, these studies have provided insight into the activation patterns of the frontal-parietal cortical regions involved in the planning and execution of manual actions such as timing of the activation or the interactions with cognitive domains.

For example, Van Schie and Bekkering (2007) for the first time investigated the ERP correlates of overt manual actions. By comparing the conditions in which either the immediate action goal (how to grasp and transport an object) or final action goal (where to place the object) was specified, the authors found that grasping of the same object generated different slow waves. Namely, the immediate action goals generated the posterior slow waves over the parietal-occipital cortical regions, while the final goals generated the anterior slow waves over the frontal cortical regions. The authors explained these findings to suggest that involvement of the frontal-parietal cortical regions in manual actions depends on the action goal, but not on the movement kinematics, since both conditions require the same precision grip. Moreover, Westerholz and colleagues (2013) found similar anterior and posterior slow waves for the grasping movements requiring power grips. Therefore, like behavioral and neuroimaging research, the ERP research has also supported the manual action-cognition interactions by showing the goal-directedness and anticipatory control of manual actions.

In contrast to the planning and execution of manual actions, to the best of my knowledge, there has not been any ERP research on the re-planning of overt, complex manual actions. However, ERPs have provided a reliable method for investigating the action flexibility for simple actions, particularly by allowing the separation in time of different cognitive operations such as error detection (e.g., Navarro-Cebrian, Knight, & Kayser, 2016; Padrón, Fernández-Rey, Acuña, & Pardo-Vazquez, 2016; Rodríguez-Fornells, Kurzbuch, & Münte, 2002), motor inhibition (e.g., Kok, Ramautar, De Ruiter, Band, & Ridderinkhof, 2004; Swann et al., 2009) and plan update per se (e.g., Chase, Swainson, Durham, Benham, & Cools, 2011; Fleming, Mars, Gladwin, & Haggard, 2009; Krämer, Knight, & Münte, 2011; Leuthold, 2003; Leuthold & Jentzsch, 2002; Randall & Smith, 2011; Trewartha, Spilka, Penhune, Li, & Phillips, 2013; Vidal et al., 1995).

Fleming and colleagues (2009) investigated the neurophysiological activity underlying the flexibility of actions which are either freely chosen or instructed. In a button press task, participants prepared a left or right movement either based on an arrow pointing to left or right (instructed) or a bidirectional arrow pointing to both directions (freely chosen). Then, a keep/change cue was presented after the participants prepared, but not initiated the movement yet. While the keep cue asked for performing the prepared movement, the change cue asked for reversing the movement direction, and thus asked for changing the initial movement plan with a new plan (i.e., movement re-planning). The authors found that the unpredictable change cue compared to the keep cue generated a larger P300, particularly during the movements which were planned based on the instruction. Accordingly, the authors interpreted these findings to suggest that instructed movement plans are more difficult to change than the freely chosen plans, and thus result in a larger P300.

P300 has been also shown to be involved in updating the internal action representations in the presence of a mismatch between planned movements and desired action outcomes (e.g., Krigolson & Holroyd, 2007; Krigolson, Holroyd, Van Gyn, & Heath, 2008; Ullsperger, Fischer, Nigbur, & Endrass, 2014). Moreover, task-switching research has also shown the involvement of P300 in plan updates by suggesting that P300 reflects the operations related to the updating of response context upon the receipt of a change cue (e.g., Barceló & Cooper, 2018).

1.5.2 ERP correlates of WM domains and processes

ERPs have provided a reliable method for tracking the time course and scalp distribution of WM operations in a variety of paradigms (for reviews, see Friedman & Johnson, 2000; Ruchkin, Grafman, Cameron, & Berndt, 2003). The first demonstration of the ERPs during WM maintenance was reported by Ruchkin, Johnson, Canoune and Ritter (1990) who showed a negative slow wave which was persistent during the retention interval and sensitive to the memory load. The succeeding studies have also shown that this negative slow is sensitive to a variety of information attributes such as information domain (e.g., Lang, Starr, Lang, Lindinger, & Deecke, 1992; Rämä, Carlson, Kekoni, & Hämäläinen, 1995; Ruchkin et al., 1997a; Ruchkin, Johnson, Grafman, Canoune, & Ritter, 1992, 1997b) and information amount (e.g., Löw et al., 1999; Löw, Rockstroh, Harsch, Berg, & Cohen, 2000; Ruchkin, Canoune, Johnson, & Ritter, 1995).

Regarding the information domain, it has been shown that verbal and visuospatial domains generate the slow waves with different timing and scalp distribution, supporting the idea that verbal and visuospatial domains are functionally separate systems controlled by separate cortical regions. For verbal domain, the widely reported slow waves have been the left anterior negativity and the right posterior positivity (e.g., Kiss, Watter, Heisz, & Shedden, 2007; Kusak, Grune, Hagendorf, & Metz, 2000; Ruchkin et al., 1997a; Ruchkin et al., 1992; Watter, Heisz, Karle, Shedden, & Kiss, 2010). The left anterior negativity shows the sustained activity during the retention interval and locates in the vicinity of the cortical regions involving in the speech production. Accordingly, it has been suggested that the left anterior negativity may reflect the processes related to the articulatory rehearsal mechanisms during maintenance process. Differently, the short duration right posterior positivity may reflect the processes related to the encoding of visually presented information into the phonological loop. For visuospatial domain, the widely reported slow wave has been a posterior negativity which is generally right lateralized over the parietal-occipital cortical regions (e.g., Löw et al., 1999; Löw et al., 2000; Ruchkin et al., 1992, 1997b; Watter et al., 2010). Moreover, it has been suggested that the posterior negativity is generated not only over the right cortical regions, but over the regions which are contralateral to the position of to-be-remembered memory items (e.g., Klaver, Talsma, Wijers, Heinze, & Mulder, 1999; Vogel & Machizawa, 2004).

Further, it has been suggested that when the capacity of domain-specific slow waves is exceeded due to the high memory load such as a high number of memory items, long retention intervals or distracters, domain-general slow waves are generated in response to WM maintenance. For example, it has been shown that the left anterior negativities or posterior negativities reflecting attention mechanisms are generated under high memory load, independent of the information domain (e.g., Bosch, Mecklinger, & Friederici, 2001; Kiss et al., 2007; Kusak et al., 2000; Löw et al, 1999; Peters, Suchan, Zhang, & Daum, 2005).

ERPs have been also applied to the investigation of the spatio-temporal characteristics of separate encoding, maintenance and retrieval processes (e.g., Berti, 2016; Bledowski et al., 2006; Chapman, Gardner, Mapstone, Dupree, & Antonsdottir, 2015; Getzmann, Wascher, & Schneider, 2018; Gulbinaite, Johnson, De Jong, Morey, & Van Rijn, 2014; Hönegger et al., 2011; Makovski, Sussman, & Jiang, 2008; Pinal, Zurrón, & Díaz, 2014; Van der Ham, Van Strien, Oleksiak, Van Wezel, & Postma, 2010). These studies have generally focused on the cognitive operations involved in each process, rather than focusing on the domain-specific slow waves generated in separate processes. For example, it has been shown that both in verbal and visuospatial tasks, a P300 is generated reflecting the executive functions such as attention switching or distracter inhibition (e.g., Berti, 2016; Chapman et al., 2015). Moreover, it has been shown that the P300 generation depends on the memory load. For example, decreased P300 amplitude has been shown with increased memory load both in encoding and retrieval processes (e.g., Bledowski et al., 2006; Getzmann et al., 2018).

1.6 Goals and research questions of the current thesis

Human motor action control is the result of several processes which are highly interconnected to the sensory information, motor system and cognition. Although, previous research has pointed out the functional domain interactions between manual action control and WM, to the best of my knowledge, there has not been any research on the cortical mechanisms underlying such interactions. Accordingly, the goal of the current thesis is to contribute to a better understanding of the neuro-cognitive mechanisms underlying manual action control. Towards this goal, the current thesis, for the first time, investigates the neurophysiological correlates of the functional domain interactions between manual action control and WM. To provide an in-depth investigation and to clarify the variables that shape the manual action-WM interactions, different movement phases (execution, re-planning), different WM domains (verbal, visuospatial) and processes (encoding, maintenance, retrieval) as well as different response modalities (manual, vocal) are considered. Hereby, the current thesis provides a systematic investigation of how the human brain orchestrates the sensorimotor systems with cognitive processes to plan, execute and adapt a variety of skilled manual actions.

The current thesis applies a cognitive-motor dual-task paradigm in which a manual task is concurrently performed with a WM task (verbal and visuospatial versions). The manual task requires grasping an object, holding it and placing it on a motor target requiring high precision, i.e., grasp-and-place movement. The verbal WM task requires memorizing the identity of letters positioned in a letter string, and the visuospatial WM task requires memorizing the identity and location of symbols positioned in a matrix. In Study 1, movement is performed as initially planned in all trials, i.e., prepared movement without additional planning requirements. In Study 2 and Study 3, movemet is performed as initially planned in some trials, but in other trials, movement direction is reversed, and thus movement is performed by changing the initially prepared movement plan with a new plan, i.e., re-planned movement. In Study 1 and Study 2, WM tasks include manual response modality which requires written report of memory items. In Study 3, WM tasks include vocal response modality which requires spoken report of memory items. In each study, EEG is recorded during the experimental task and ERPs are analyzed.

ERPs provide a reliable method for investigating the rapid dynamics of the spatio-temporal characteristics of the manual action-WM interactions. This is feasible not only because ERPs have high temporal resolution in order of milliseconds, but also because ERPs have characteristics latency, amplitude and scalp distribution. Hence, ERPs allow for the isolation of the effect of a given experimental manipulation in time and spatial domain. In the current studies, ERPs have the potential to separate the operations related to different movement phases as well as WM domains and processes. For example, in the case of WM processes, each process shows the stable time relationships to the separately defined reference event, such as stimulus presentation (encoding), offset of stimulus presentation (maintenance) or recall (retrieval). Accordingly, as advantage over pure behavioral measures reflecting the summed contributions of all processes, ERPs provide the distinct interaction patterns between movement phases and each WM process.

In the dual-task setting, the current thesis investigates whether manual action control are functionally related to WM, and thus the operations of manual task interfere with the operations of WM task at behavioral and neurophysiological level. At the behavioral level, dual-task costs are defined as the memory performance differences between single-task and dual-task conditions (Study 1), or between two dual-task conditions requiring and not requiring movement re-planning (Study 2 and Study 3). At the neurophysiological level, dual-task costs are defined as the ERP differences between the conditions. The extent of dual-task costs would depend on whether and how manual actions and WM share common cognitive resources (e.g., Kahneman, 1973; Wickens, 1980), central structures (e.g., Pasher, 1994) or motor output structures (e.g., De Jong, 1993; Heuer, 1996).

Study 1 (Chapter 2) provides the initial neurophysiological investigation of the domain interactions between manual action control and WM. Therefore, this study focuses on a basic question and investigates the neurophysiological correlates of the dual-task interference between movement execution and WM. That is, whether the execution of a prepared movement without additional planning requirements interferes with WM, and where the locus of the interference is, i.e., the encoding or retrieval process of verbal and visuospatial domains. In this study, memory costs of concurrent movement execution for WM are named *movement execution costs* both at the behavioral and neurophysiological level.

Study 2 (Chapter 3) investigates the neurophysiological correlates of the dual-task interference between movement re-planning and WM. That is, whether changing the initially prepared movement plan with a new plan interferes with WM, and where the locus of the interference is, i.e., maintenance or retrieval process of verbal and visuospatial domains. In this study, memory costs of concurrent movement re-planning for WM are named *movement re-planning costs* both at the behavioral and neurophysiological level. This study, together with Study 1, also provides the information about whether movement execution (performing a movement in a prepared direction) and re-planning (performing a movement by reversing the direction) engage in similar WM capacities.

Study 3 (Chapter 4) investigates whether the WM response modality affects the dual-task interference between movement re-planning and WM. That is, whether the neurophysiological correlates of the movement re-planning costs change when the WM tasks require a vocal response instead of a manual response (Study 2). The potential role of the WM response modality in dual-task interference is considered from two separate, but complementary points of views.

First, it has been suggested that the compatibility of stimulus-response modalities within a task determines the extent of dual-task interference (e.g., Hazeltine et al., 2006; Wickens et al., 1984). In Study 2, manual response modality is more compatible for visuospatial stimulus compared to verbal stimulus. In contrast, in Study 3, vocal response modality is more compatible for verbal stimulus compared to visuospatial stimulus. Accordingly, balancing the particular pairings of stimulus-response modalities across two studies allows for investigating whether the interactions between movement re-planning and WM depend on the particular stimulus-response modalities within WM tasks. Second, it has been suggested that besides the common central structures or resources, common motor output structures such as overlapping effector systems can also lead to dual-task interference due to the response modality overlap at the motor output stage (e.g., Bratzke et al., 2008; De Jong, 1993; Heuer, 1996). Different from Study 2, in Study 3, vocal response modality separates the effector systems between WM tasks and manual task. Accordingly, Study 3 also allows for investigating whether the interactions between movement re-planning and WM depend on the response modality overlap (i.e., overlapping effector systems) between WM tasks and manual task. Taken together, Study 3 allows for the comprehensive investigation of the domain interactions between movement re-planning and WM.

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2 ERP CORRELATES OF THE FUNCTIONAL INTERACTIONS BETWEEN MANUAL ACTION EXECUTION AND WM

CHAPTER 2

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Movement Interferes with Visuospatial Working Memory during the Encoding: An ERP Study

Rumeysa Gunduz Can^{1,2*}, Thomas Schack^{1,2,3}, Dirk Koester^{1,2}

[1] Neurocognition and Action - Biomechanics Research Group, Faculty of Psychology and Sport Science, Bielefeld University, Bielefeld, Germany

[2] Cognitive Interaction Technology - Center of Excellence (CITEC), Bielefeld University, Bielefeld, Germany

[3] Research Institute for Cognition and Robotics (CoR-Lab), Bielefeld University, Bielefeld, Germany

*** Correspondence:**

Corresponding Author

ruemeysa.guenduez@uni-bielefeld.de

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Author Contributions

Conceived and designed the study: RGC, TS, DK. Performed data collection: RGC. Analyzed and interpreted data: RGC, DK. Contributed to the interpretation and preparation of the manuscript: RGC, TS, DK.

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Abstract

The current study focuses on the neurophysiological correlates of the functional domain interactions between manual action execution and WM. Particularly, the neurophysiological correlates of the dual-task costs of movement execution for WM domains (verbal, visuospatial) and processes (encoding, retrieval) are investigated. Thirty participants were tested in a cognitive-motor dual-task paradigm which included a WM task (verbal and visuospatial versions) and a manual task (grasping a sphere and placing it on a motor target, i.e., grasp-and-place movement). To examine movement execution costs, a single-task condition (verbal or visuospatial task) was compared with a dual-task condition (concurrent performance of WM task and manual task). ERPs were analyzed separately for encoding and retrieval processes in verbal and visuospatial tasks both in single-task and dual-task conditions. The behavioral analyses show that grasp-and-place movement interfered with WM and decreased memory performance. The performance decrease was larger for the visuospatial task compared to the verbal task, i.e., domain-specific movement execution costs. The ERP analyses show the domain-specific execution costs also at the neurophysiological level, which is further process-specific to the encoding. That is, comparing the WM-related ERPs in the single-task and the dual-task, visuospatial ERPs changed only during the encoding process when the grasp-and-place movement was performed at the same time. Generally, the current study shows an evidence for domain and process-specific interactions of movement execution with WM (visuospatial domain during encoding process). This study, therefore, provides an initial neurophysiological characterization of the manual action-WM interactions in a cognitive-motor dual-task setting, and contributes to a better understanding of the neuro-cognitive mechanisms underlying manual action control.

2.1 Introduction

The vast majority of interaction with the everyday environment is accomplished through manual actions. For example, we reach for objects at different distances, we grasp and lift objects with different shapes, weight and texture, and we manipulate objects depending on our goals while keeping our current tasks available (in WM). Planning and executing skilled manual actions require precise motor control, which is provided by the integration of not only the sensory and motor systems, but also the cognitive systems (e.g., Castiello, 2005). The current study focuses on the functional domain interactions between manual action control and cognition. Particularly, in a dual-task setting, the neurophysiological correlates of the domain interactions between a grasp-and-place movement (grasping an object and placing it on a target) and WM are investigated.

The way how we interact with and manipulate an object is shaped by both the external and internal factors. External factors refer to the intrinsic object properties such as size, shape and texture, and the extrinsic properties such as location and orientation (e.g., Castiello, 2005). In natural environments, manual actions are not performed solely based on the external factors. Indeed, they are performed also based on the internal factors which are mainly cognitive variables (for reviews, see Glover, 2004; Rosenbaum, Chapman, Weigelt, Weiss, & Van der Wel, 2012; Rosenbaum, Herbort, Van der Wel, & Weiss, 2014).

For example, action goals, intentions about the object use, familiarity with the object, and affordances the object provides also shape the way how we interact with and manipulate objects (e.g., Ansuini, Giosa, Turella, Altoè, & Castiello, 2008; Creem & Proffitt, 2001; Grèzes, Tucker, Ellis, & Passingham, 2003; Herbort & Butz, 2010, 2011; Tucker & Ellis, 2001, 2004). Think about a manual action toward a fork. We reach for and grasp the fork differently depending on whether we place it in a cupboard or use it for eating. Moreover, in natural environments manual actions are often performed concurrently with other cognitive tasks. For example, we can engage in a conversation while interacting with the fork in that particular context. Therefore, considering the required sensory, motor and cognitive systems, it can be suggested that manual actions and cognition are not functionally independent, but rather there may be a cross-talk between them.

WM is one of the cognitive processes, besides, for example, language (e.g., Glover, Rosenbaum, Graham, & Dixon, 2004; Lindemann, Stenneken, Van Schie, & Bekkering, 2006) or perception (e.g., Deubel, Schneider, & Paprotta, 1998), being shown to interact with manual actions. WM is the cognitive process which temporarily stores and manipulates information for coordinating various activities such as maintaining an action goal (grasping the fork to place it in the cupboard) and holding a conversation (Baddeley, 2003).

WM and motor actions have close domain interactions, which has been shown for different actions such as finger tapping (e.g., Smyth, Pearson, & Pendleton,1988; Smyth & Pendleton, 1989), pointing (e.g., Hale, Myerson, Rhee, Weiss, & Abrams, 1996), arm movements (e.g., Lawrence, Myerson, Oonk, & Abrams, 2001; Quinn & Ralston, 1986) as well as eye movements (e.g., Lawrence et al., 2001; Postle, Idzikowski, Della Sala, Logie, & Baddeley, 2006). WM for objects with affordances depend on the activation of motor programs associated with object use, which in turn, reflects the involvement of motor processes in WM (e.g., Mecklinger, Gruenewald, Besson, Magnie, & von Cramon, 2002; Mecklinger, Gruenewald, Weiskopf, & Doeller, 2004). Moreover, WM is involved in complex motor actions including sequences such as dance movements (e.g., Cortese & Rossi-Arnaud, 2010). WM is employed during grasping movements, for example, to keep the grasp-related object information for the subsequent execution of grasp (e.g., Fiehler et al., 2011; Fournier, Behmer, & Stubblefield, 2014). Accordingly, execution of grasping movements after a delay depends on WM (e.g., Binsted, Rolheiser, & Chua, 2006; Hesse & Franz, 2010; Kohler, Isenberg, Schönle, Inbar, & Conrad,1989; Singhal, Culham, Chinellato, & Goodale, 2007).

Cognitive-motor dual-task paradigms have been used to investigate the motor action-WM interactions **(**e.g., Guillery, Mouraux, & Thonnard, 2013; Logan & Fischman, 2011; Spiegel, Koester, & Schack, 2013, 2014; Spiegel, Koester, Weigelt, & Schack, 2012; Voelcker-Rehage & Alberts, 2007; Weigelt, Rosenbaum, Huelshorst, & Schack, 2009). The logic of dual-task paradigms is that concurrent performance of two tasks would result in interference between the tasks if both tasks compete for the common capacity-limited cognitive resources. This interference would be demonstrated by means of decreases in performance of either of the tasks or both (e.g., Pashler, 1994; Wickens, 2008). Studies employing dual-task paradigms have shown that motor tasks requiring manual actions recruit the capacity-limited cognitive resources which are also required for a concurrent memory task. That is, concurrent motor tasks interfere with WM and decrease memory performance (e.g., Logan & Fischman, 2011; Spiegel et al., 2013; Spiegel et al., 2012; Weigelt et al., 2009).

Weigelt and colleagues (2009) combined a perceptual-motor task (opening a sequence of drawers to grasp cups in the drawers) with a verbal memory task (recalling a sequence of letters positioned in the cups). By doing so, the authors investigated whether and how the motor planning and verbal memory interact with each other. Weigelt and colleagues (2009) showed that motor planning eliminated the recency effect, i.e., the tendency of recent items to be recalled better than earlier items in a list, which otherwise is a robust memory effect. The authors interpreted this finding as to suggest that motor planning recruits the capacity-limited cognitive resources which are also required for performing the memory task. Logan and Fischman (2011), in a complex everyday task setup, showed that not only the motor activity requiring complex planning, but also the motor activity requiring no or limited planning could eliminate the recency effect.

Recently, Spiegel and colleagues (2013) investigated the manual action-WM interactions in a cognitive-motor dual-task paradigm taking two points into consideration. First, goal-directed actions consist of two functionally separate phases, i.e., planning and online control (execution), which rely on different perceptual and cognitive representations (e.g., Elliott, Helsen, & Chua, 2001; Glover, 2004). Second, WM has functionally separate verbal and visuospatial domains, which are selectively interfered by motor actions (e.g., Baddeley, 2003; Baddeley & Hitch, 1974; Logie, 2011).

Spiegel and colleagues (2013) first investigated the dual-task interference of a prepared movement for WM by combining verbal and visuospatial versions of a WM task with a manual task which included the condition of grasping an object and placing it on a motor target. The authors showed that performing a prepared movement (execution) interfered more with memorizing visuospatial information compared to verbal information and decreased memory performance for visuospatial task, i.e., domain-specific movement execution interference. Second, Spiegel and colleagues (2013) investigated the dual-task interference of movement re-planning (i.e., changing the plan of an ongoing movement). Unlike the execution, movement re-planning interfered with memorizing both verbal and visuospatial information to a similar degree and decreased memory performance for both WM tasks, i.e., domain-general movement re-planning interference. These findings suggest that both movement phases recruit distinct WM capacities, and therefore lead to the unique interference with WM domains. While, movement execution shares the capacity-limited cognitive resources mainly with visuospatial domain, movement planning shares the cognitive resources with both domains.

As aforementioned, it has been shown that manual actions have a close domain interaction with WM, which is complex and dependent on a variety of factors (e.g., Spiegel et al., 2013). However, there is still lack of research investigating the underlying cortical activity. Therefore, the goal of the current study is to extend the knowledge for manual action-WM interactions to the neurophysiological level. Specifically, the current study investigates the neurophysiological correlates of dual-task costs of a grasp-and-place movement for WM.

The current cognitive-motor dual-task paradigm is adapted from the behavioral studies by Spiegel and colleagues (2012, 2013, 2014) to the EEG setting. This way, the current study can replicate previous behavioral findings and use an established experimental paradigm for the current investigation of the underlying neurophysiological activity (EEG). In a baseline single-task condition, participants perform verbal (recall of letters) or visuospatial (recall of symbols positioned in a 4 x 4 matrix) version of a WM task. In a dual-task condition, WM task is embedded in manual task. To investigate the neurophysiological correlates of dual-task costs, EEG data is recorded in both WM tasks in single-task and dual-task conditions.

The current study aims to determine the source of dual-task costs for WM domains. Depending on the function, WM has been suggested to have three cognitive processes (i.e., encoding, maintenance, retrieval) which represent distinct cognitive operations of information and arise from separate neural sources (e.g., Bledowski et al., 2006; Hale et al., 1996; Geffen et al., 1997; Manoach, Greve, Lindgren, & Dale, 2003; Pinal, Zurrón, & Díaz, 2014; Studer et al., 2010). Encoding is the process during which a stimulus is perceived and a representation of it is generated. Maintenance is the process during which the stimulus is retained active in memory when the perceptual input of the stimulus is not available. Retrieval is the process during which the stored stimulus is accessed for performing the task at hand (e.g., Jonides et al., 2008). Given the distinct cognitive operations in encoding, maintenance and retrieval processes, the manual task could interfere with WM domains uniquely in each process.

With the aim of determining the source of the dual-task costs for WM domains, the current study makes use of the ERPs which are the voltage fluctuations being extracted from EEG recordings in response to a cognitive or motor process (e.g., Friedman & Johnson, 2000; Hillyard & Kutas, 1983). ERPs have high temporal resolution in order of milliseconds, so they can be used to measure rapidly changing dynamics of any cognitive process (e.g., Pinal et al., 2014). ERPs also provide useful information about the scalp distribution of the cortical activity related to different cognitive processes. That is, comparisons of the spatial distribution of ERPs elicited by different experimental conditions could indicate whether these conditions entail different patterns of cortical activity, thus, likely reflect different cognitive processes (e.g., Woodman, 2010). Therefore, ERPs are particularly suitable for studying spatio-temporal characteristics of transient operations independently in each WM domain and process. This is feasible since each WM process shows stable time relationships to separately defined reference events, such as stimulus presentation (encoding process), offset of stimulus presentation (maintenance process) or recall (retrieval process; e.g., Friedman & Johnson, 2000).

Consistently, ERPs also provide a reliable method for investigating the distinct movement interference with each WM process, which would be very difficult to address only with behavioral data. The current study, therefore, investigates the WM processes during which the manual task interferes with WM, i.e., whether the interference arises during either of the encoding or retrieval of information or both. For this aim, ERPs are analyzed separately for encoding and retrieval processes in verbal and visuospatial WM tasks both in single-task and dual-task conditions.

The current study has three objectives: First aim is to replicate the findings of the behavioral study by Spiegel and colleagues (2013) in an EEG setting. Second aim, also the main objective, is to provide an initial neurophysiological characterization of the domain interactions between manual action control and WM by focusing on separate WM domains and processes. To the best of my knowledge, the current study is one of the few studies investigating the ERPs in an experimental setting requiring overt movement execution (e.g., Van Schie & Bekkering, 2007; Westerholz, Schack, & Koester, 2013; Westerholz, Schack, Schütz, & Koester, 2014) and the first study investigating the ERPs of the manual action-WM interactions in a dual-task setting. Therefore, in a more general level, the current study also aims to demonstrate whether reliable ERPs can be analyzed in complex experimental settings which involve movement execution such as grasping an object to place it on a target, and hand writing for reporting memory items. This, in turn, should encourage future research options with more sensitive measures such as ERPs as opposed to the pure behavioral measures for the investigation of multiple cognitive processes in manual action control.

Regarding the behavioral analyses, hypotheses are formulated based on the previous findings by Spiegel and colleagues (2013). It is expected that concurrent movement execution would interfere with WM and decrease memory performance, which would be larger for visuospatial task compared to verbal task. That is, the prepared grasp-and-place movement is expected to entail domain-specific movement execution costs.

Regarding the ERP analyses, given a lack of comparable ERP studies investigating the manual action-WM interactions, hypotheses are formulated based on the limited available ERP findings on either manual actions or WM. Most ERP studies have focused mainly on the maintenance process, although the gaining a complete understanding of the cortical activity involved in WM requires dissociating cognitive processes of encoding, maintenance, and retrieval (e.g., Jonides et al., 2008; Manoach et al., 2003). Importantly, the current study includes a joint processing of each WM process and grasp-and-place movement. Therefore, a starting point which can further provide hypotheses regarding the ERPs of the manual action-WM interactions is chosen. Hypotheses regarding the WM-related ERPs are formulated based on widely reported slow waves for each WM domain: The (left) anterior negative slow wave for verbal domain (e.g., Kiss, Watter, Heisz, & Shedden, 2007; Kusak, Grune, Hagendorf, & Metz, 2000; Ruchkin et al., 1997a; Ruchkin, Johnson, Canoune, & Ritter, 1990; Ruchkin, Johnson, Grafman, Canoune, & Ritter, 1992) and the (right) posterior negative slow wave for visuospatial domain (e.g., Bledowski et al., 2006; Geffen et al., 1997; Löw et al., 1999; Pinal et al., 2014; Ruchkin, Canoune, Johnson, & Ritter, 1995; Ruchkin et al., 1992; Ruchkin, Johnson, Grafman, Canoune, & Ritter, 1997b). Accordingly, in the single-task condition, the (left) anterior negativity for verbal domain compared to visuospatial domain and the (right) posterior negativity for visuospatial domain compared to verbal domain are expected.

In the dual-task condition, it is expected that concurrent movement execution would interfere with WM also at the neurophysiological level, particularly with visuospatial domain. Previous ERP studies have suggested two major slow waves for manual actions: The posterior negative slow wave reflecting the planning and execution of actions and the anterior negative slow wave reflecting the high-level cognitive operations such as planning sequences and supporting final action goals during sequential actions (e.g., Bozzacchi, Giusti, Pitzalis, Spinelli, & Di Russo, 2012; Van Schie & Bekkering, 2007; Westerholz et al., 2013; Westerholz et al., 2014; for a review, see Koester, Schack, & Westerholz, 2016). Considering the previously suggested slow waves for WM and manual actions in isolation, it is expected that the interactions between grasp-and-place movement and WM would be visible at the anterior and posterior scalp regions. Specifically, it is expected that visuospatial ERPs in the dual-task would demonstrate different patterns than the ERPs in the single-task, i.e., domain-specific movement execution costs at the neurophysiological level. Moreover, given distinct cognitive operations of information in each WM process, it is further expected that grasp-and-place movement would share the cognitive resources with each process in a process-specific manner. Consequently, execution costs would be non-identical for each WM process.

2.2 Methods

2.2.1 Participants

Thirty right-handed participants from students of Bielefeld University participated in the study. Due to the behavioral performance and EEG data quality, for the behavioral analyses 29 participants (21 females, 8 males, *M* age = 25 years, SD = 4.1), for the encoding process analyses 23 participants (20 females, 3 males, *M* age = 24.5 years, SD = 4), and for the retrieval process analyses 21 participants (18 females, 3 males, *M* age = 24.5 years, SD = 4.2) were entered into analyses.

All participants had normal or corrected-to-normal vision and no known neurological disorder. Participants provided written informed consent and received either 15 € or 2-hour of participation credits as compensation.

This study was conducted in accordance with the ethical standards of the sixth revision of the Declaration of Helsinki and approved by the ethics committee at Bielefeld University.

2.2.2 Materials

The stimulus events for the experimental task were presented on a 17-in flat-screen monitor with integrated speakers and a resolution of 1024 x 768 pixel.

The stimuli for the verbal task were eighty pseudo-randomly chosen letter sequences, each consisting of eight consonants of the Latin alphabet (each consonant was 2 cm in height and width). Neither any abbreviation nor alphabetic order among the consonants was allowed. In addition, frequency of the presentation of each consonant was controlled. Each letter sequence was presented along a vertical axis at the center of the monitor screen to avoid any possible visual field effect. The stimuli for the visuospatial task were eighty 4x4 symbol matrices. Each matrix consisted of a variation of eight symbols which were selected from three symbol types, i.e., triangle, circle, square (each symbol was 2 cm in height and width). The symbols were placed at any random eight of sixteen equiprobable positions of the matrix which was presented at the center of the monitor screen.

A task board (4 cm x 60 cm x 28 cm) was used for the manual task. The board consisted of three sticks (10 cm in height, 0.5 cm in width) as a start position and left and right motor targets requiring high precision movement. Motor targets were mounted 15 cm away from the center of the task board which was marked by a yellow cross. A sphere (6 cm in diameter with a hole of 10 mm) was used to be placed on one of the motor targets. The start position and motor targets were equipped with pressure sensitive micro switches which allowed for self-paced trial beginnings and ends (see Figure 2.1).

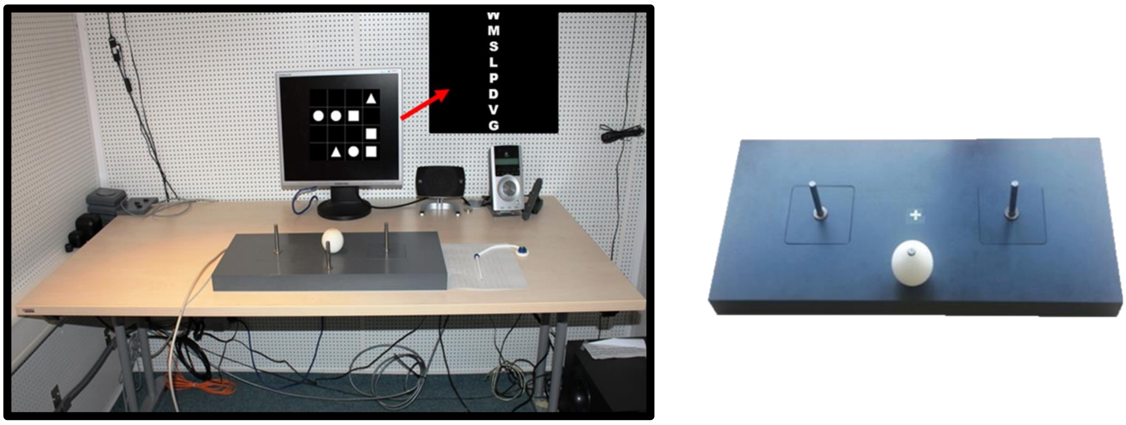

Figure 2.1. The experimental setup used for all the experimental studies in the current thesis. (Left) In the figure, setup includes an example stimulus for visuospatial task and verbal task and task board for manual task. (Right) Task board includes three sticks a start position (where the sphere is fitted onto) and two motor targets. Center of the task board is marked by a yellow cross.

2.2.3 Procedure and design

After giving written informed consent, participants seated comfortably in an electrically shielded cabin where the experiment took place (see Figure 2.1). Participants received instructions for the experimental task which also required maintaining stable posture and not blinking while executing the task. Single-task condition required participants to perform verbal and visuospatial tasks. Dual-task condition required participants to perform the WM tasks embedded in the manual task. Single-task and dual-task conditions had the same fixed sequence of stimulus events which were initiated and terminated by participants themselves.

In the single-task condition, participants initiated the fixed sequence of stimulus events by pressing down on the micro switch mounted on the start position (see Figure 2.2).

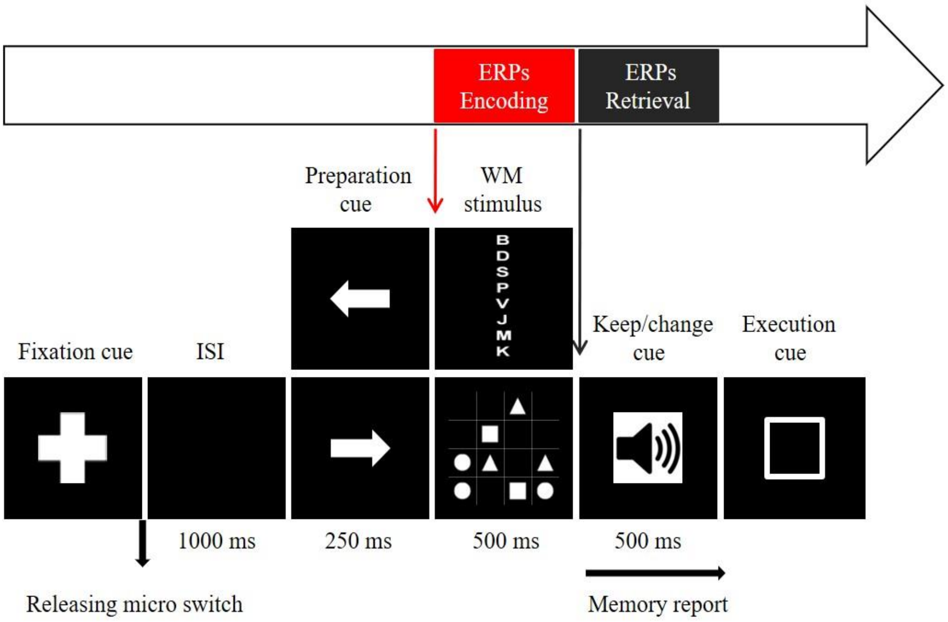

Figure 2.2. Fixed sequence of stimulus events and ERP reference events in the single-task condition. The onset of WM stimulus is the reference event for encoding process ERPs and the onset of keep/change cue is the reference event for retrieval process ERPs.

First, a fixation cross appeared at the center of the monitor screen. When participants released the micro switch, the fixation cross disappeared. After an inter-stimulus interval (ISI; 1000 ms duration) a movement preparation cue as a directional arrow was presented for 250 ms. Following the cue, a WM stimulus, either a letter sequence or a 4x4 matrix, was presented for 500 ms. During WM stimulus presentation, participants must encode the items into WM. The WM stimulus was followed by a keep/change cue as an auditory tone of either 400 Hz or 750 Hz (500 ms duration), and a movement execution cue. Since there was no manual task, participants ignored the preparation, keep/change and movement execution cues, and reported memory items directly following the WM stimulus presentation. After WM report, participants self-initiated the next trial.

In the dual-task condition, verbal and visuospatial tasks were combined with the manual task. The fixed sequence of stimulus events was identical to the sequence in the single-task (see Figure 2.3).

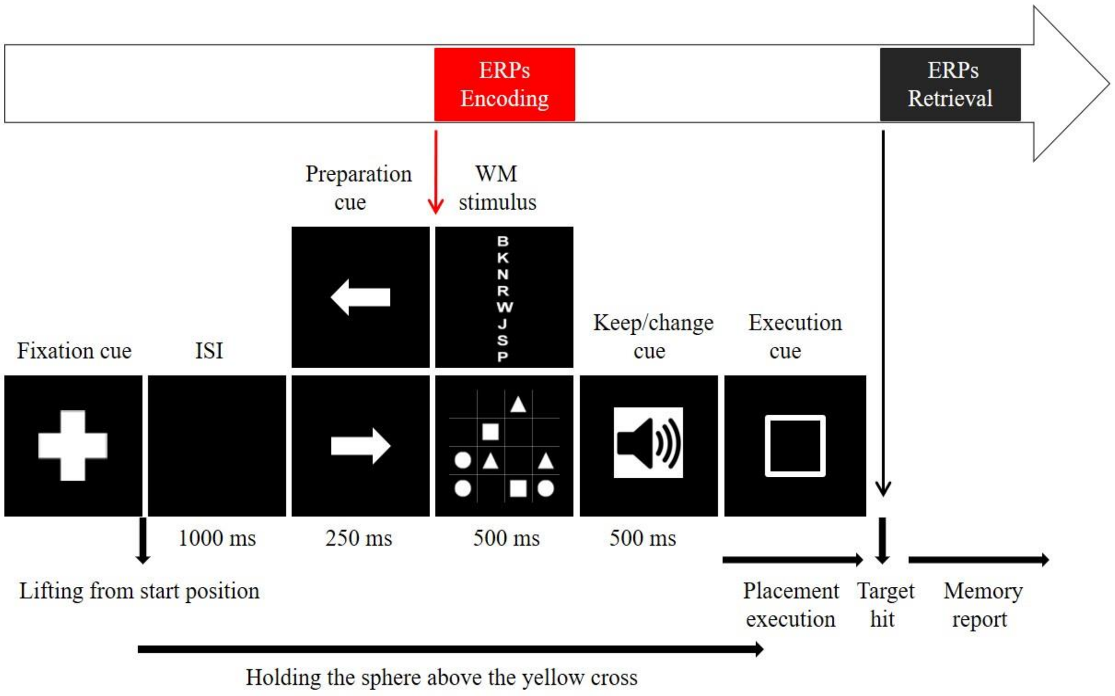

Figure 2.3. Fixed sequence of stimulus events and ERP reference events in the dual-task condition. The onset of WM stimulus is the reference event for encoding process ERPs and the target hit is the reference event for retrieval process ERPs.

Initially, the sphere was at the start position. Participants grasped the sphere and pressed it down on the start position to initiate the stimulus events. First, a fixation cross appeared at the center of the monitor screen. Lifting the sphere from the start position started ISI (1000 ms duration), during which participants transported the sphere to the center of the task board (yellow cross). Participants held the sphere above the yellow cross until the onset of the movement execution cue. While participants were holding the sphere above the yellow cross, they first received the movement preparation cue as a directional arrow pointing to left or right (250 ms duration). The arrow, thus, directed towards the motor target based on which the subsequent movement was planned.

Following the preparation cue, WM stimulus, either a letter sequence or a 4x4 matrix, was presented for 500 ms. Then, the keep/change cue, one of the auditory tones, was presented for 500 ms. In the current study, participants ignored the tone since it was only used to assure comparability with the behavioral study by Spiegel and colleagues (2013). After the tone, the movement execution cue was visually presented. With the onset of execution cue, participants transported the sphere from the yellow cross to the directed motor target and fitted the sphere onto the stick. Sphere placement on the target was referred as the target hit, regardless of whether the target was the correct one, and accepted as the termination of the manual task. After the target hit, participants reported memory items. After WM report, participants placed the sphere back on the start position for the next trial.

Participants were required to memorize as many letters or symbols as possible and move the sphere as quickly as possible but at a comfortable speed. Both verbal task and visuospatial task required written report on the answer sheets provided. The verbal task required to memorize as many letters as possible and recall them independently of the serial order (only the identity). The answer sheet consisted of rectangle blank boxes with a left to right orientation. The visuospatial task required to memorize as many symbols as possible and recall the correct symbol in the correct position within the matrix (identity and position). The answer sheet consisted of blank 4 x 4 matrices.

The study employed a 2x2 within-subject design with the factors task block (single block, dual block) and WM task (verbal task, visuospatial task). Each experimental condition (i.e., verbal task in single block, visuospatial task in single block, verbal task in dual block, visuospatial task in dual block) consisted of 40 trials, resulting in a total of 160 experimental trials. Different WM stimulus sets were used in single and dual blocks to avoid repetition effect. The order of WM stimuli in each experimental condition was randomized.

There were four versions of the experimental condition order (see Table 2.1). That is, the experiment could start with either single block or dual block, and each block could start with either verbal task or visuospatial task. Participants first performed two WM tasks within the first block, and then started with the second block. Four lists of a block sequence were created based on the experimental condition order, which were also used for dividing the participants into experimental groups. Participants were randomly assigned to one of the four experimental groups.

Table 2.1

Four Experimental Groups Based on the Block Sequence

	First Block		Second Block	
	WM Task 1	WM Task 2	WM Task 1	WM Task 2
Group A	Single Block Visuospatial Task	Single Block Verbal Task	Dual Block Visuospatial Task	Dual Block Verbal Task
Group B	Single Block Verbal Task	Single Block Visuospatial Task	Dual Block Verbal Task	Dual Block Visuospatial Task
Group C	Dual Block Visuospatial Task	Dual Block Verbal Task	Single Block Visuospatial Task	Single Block Verbal Task
Group D	Dual Block Verbal Task	Dual Block Visuospatial Task	Single Block Verbal Task	Single Block Visuospatial Task

Note: Four lists of the block sequence were created based on the experimental condition order.

2.2.4 EEG recordings

EEG was recorded by a 64-channel amplifier (ANT, www.ant-neuro.com). Ag/AgCL electrodes were arranged according to the international 10-20 system (Oostenveld & Praamstra, 2001) using WaveGuard EEG cap. Ocular artifacts were detected by four electrodes placed above and below the right eye and lateral to both eyes. Data were average-referenced during recording. EEG was band-pass filtered (DC-138 Hz) and digitized at 512 Hz. The impedance of all electrodes was kept below 5 kV.

2.2.5 Data analysis

Regarding the behavioral data, dependent variables were memory performance and movement execution time. For the verbal task, memory performance was defined as the number of correctly reported letters independently of the serial order in the letter sequence. For the visuospatial task, it was defined as the number of correctly reported symbols in the correct position within the matrix. Movement execution time was defined as the time from the onset of keep/change cue to the target hit (dual block).

Trials with placement errors were excluded from the memory performance, execution time and EEG analyses. In addition, trials deviating more than 2.5 SD from the individual mean execution time were also excluded from the dual-block analyses. For the memory performance analysis, a two-way repeated measure of analysis of variance (ANOVA) including the factors *task block* (single vs. dual) and *WM task* (verbal vs. visuospatial) was conducted on the arcsine transformed proportions of correct answers. For the execution time analysis, a paired sample t-test was conducted.

Regarding the EEG data, given a lack of comparable studies on the manual action-WM interactions, mainly a data driven approach seemed appropriate. EEG data from verbal and visuospatial tasks both in single and dual blocks were analyzed separately for encoding and retrieval processes. First, EEG data were band-pass filtered from 0.1 Hz to 30 Hz and re-referenced to the average mastoid electrodes. Then, stimulus-locked epochs for encoding and retrieval processes were extracted based on separate reference events (see Figure 2.2 and Figure 2.3).

Encoding process epochs both in single and dual blocks were extracted time-locked to the WM stimulus onset with a 100 ms pre-stimulus baseline. These epochs included the time interval over the period of WM stimulus presentation (500 ms duration). Retrieval process epochs were extracted time-locked to the different reference events in single and dual blocks. To provide comparability with the study by Spiegel and colleagues (2013), participants reported memory items directly after the stimulus presentation in the single block, but after the target hit in the dual block. Therefore, retrieval process epoch in the single block was extracted time-locked to the onset of keep/change cue with a 100 ms pre-stimulus baseline. Differently, dual block epoch was extracted time-locked to the target hit with a 100 ms pre-stimulus baseline. Bearing in mind that movement artifacts may arise during longer time intervals, the time interval for the retrieval process analyses was kept shorter than the actual time that might be required to complete retrieval process. Therefore, retrieval process epochs covered a duration of 1500 ms after the reference event.

Given that participants could start reporting memory items directly after the WM stimulus presentation in the single block, it was assumed that participants did not get into maintenance process, which is required for retaining the stimulus active when the perceptual input is not available (e.g., Jonides et al., 2008). The absence of maintenance process in the single block, thus, prevented the comparions between single and dual blocks for investigating the movement execution costs for the maintenance. Consequently, the current investigation was restricted to the encoding and retrieval.

Ocular correction was done using the correction procedure of Gratton, Coles and Donchin (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. Time epochs were visually double-checked for artifacts. If necessary, single bad channels causing the rejection of any epoch were interpolated. Then, data of the participants losing more than 50% of epochs of each experimental condition were excluded from further analyses. Therefore, encoding and retrieval analyses had different number of participants, but the participants were kept equal for single and dual block comparisons. For example, the encoding analyses had the same 23 participants both for single and dual block analyses. Afterwards, grand average ERPs were computed at all electrode sites separately for encoding and retrieval processes in verbal and visuospatial tasks both in single and dual blocks.

Four region-of-interests (ROI) were selected based on the previous ERP studies on WM (e.g., Kiss et al., 2007; Pinal et al., 2014; Studer et al., 2010) and manual actions (e.g., Van Schie & Bekkering, 2010; Westerholz et al., 2014). These ROIs were systematically aligned across the scalp: Left-anterior (LA), right-anterior (RA), left-posterior (LP), right-posterior (RP), and each included 6 recording electrodes. Electrodes for the LA were Fp1, AF7, AF3, F5, F3, F1. Electrodes for the RA were Fp2, AF8, AF4, F6, F4, F2. Electrodes for the LP were P5, P3, P1, PO7, PO5, PO3. Electrodes for the RP were P6, P4, P2, PO8, PO6, PO4.

Since there were different reference events for the retrieval process in single and dual blocks (for time-locking the ERPs), movement execution costs for verbal and visuospatial domains could be compared only qualitatively during retrieval. Moreover, for the consistency of encoding and retrieval processes, single and dual blocks were compared qualitatively also during encoding. Therefore, three-way repeated measures of ANOVAs were conducted for each process separately in single and dual blocks (four ANOVAs in total). These ANOVAs included the factors *WM task* (verbal vs. visuospatial), *hemisphere* (left vs. right) and *anterior-posterior orientation of ROI* (*AP*; anterior vs. posterior). Time intervals for statistical analyses were chosen as a combination of available ERP studies on WM and visual inspection of the grand average ERPs (e.g., Bledowski et al., 2006; Pinal et al., 2014; Ruchkin et al.,1992). Encoding process analyses included the time interval between 200-400 ms, and retrieval process analyses included an early (250-650 ms) and a late (800-1500 ms) time interval both in single and dual blocks. Comparisons of the ERPs of verbal and visuospatial tasks in single and dual blocks enabled the investigation of whether the ERP patterns change in the presence of the grasp-and-place movement.

2.3 Results

2.3.1 Behavioral results

In the dual block, participants executed the grasp-and-place movement correctly in 99% of trials in verbal and visuospatial tasks. Regarding the memory performance, verbal task yielded on average 4.08 (SD = 0.36) correct letters in single block and 3.98 (SD = 0.40) correct letters in dual block. Visuospatial task yielded on average 3.73 (SD = 0.69) correct symbols in single block and 3.07 (SD = 0.66) correct symbols in dual block (see Figure 2.4).

The two-way (*Task block x WM task*) ANOVA revealed main effects of task block ($F(1, 28) = 55.38$, $p < .001$, $\eta_p^2 = .66$), WM task ($F(1, 28) = 23.62$, $p < .001$, $\eta_p^2 = .46$), and a significant interaction ($F(1, 28) = 42.84$, $p < .001$, $\eta_p^2 = .61$). Follow-up paired sample t-tests indicated that for the visuospatial task, memory performance in dual block was lower compared to single block, $t(28) = 8.32$, $p < .001$. For the verbal task, the difference between the performances in single and dual blocks was not statistically significant, $t(28) = 1.76$, $p = .089$.

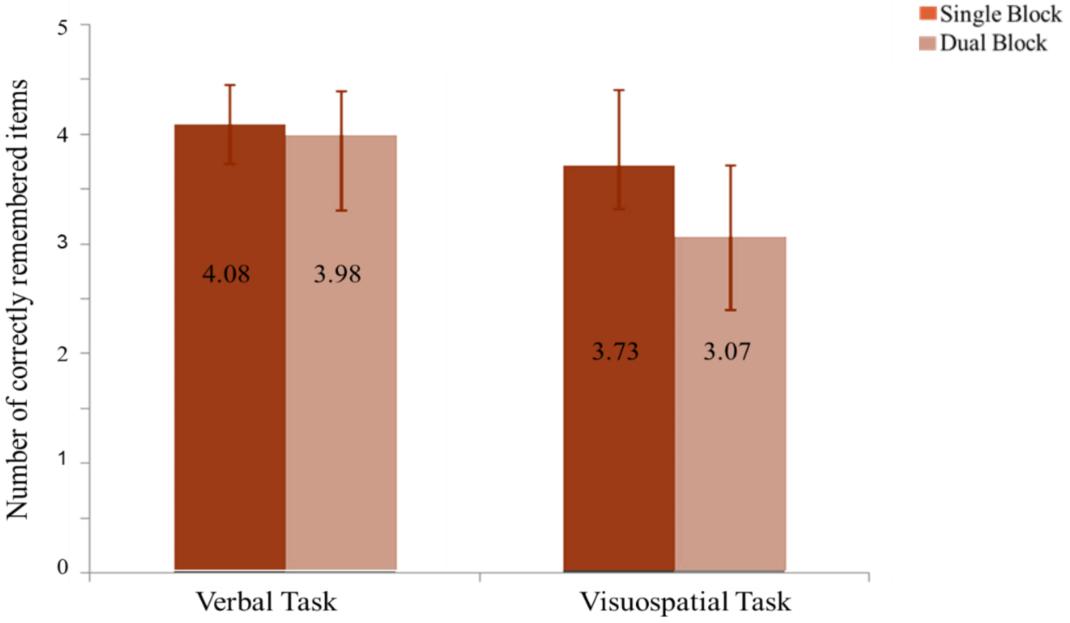

Figure 2.4. Mean memory performance for verbal and visuospatial tasks in single and dual blocks. Memory performance for the visuospatial task in the dual block is lower than the performance in the single block, i.e., domain-specific memory costs. Error bars attached to each column represent the standard deviation.

Regarding the movement execution time in the dual block, there was no difference between the verbal task (M ms = 2177.6, SD = 536) and visuospatial task (M ms = 2153.9, SD = 438), $t(28) = .24$, $p = .813$.

2.3.2 ERP analyses results

Encoding Process

For the single block, the three-way ANOVA (*WM task x Hemisphere x AP*) revealed a three-way interaction of WM task, hemisphere and AP between 200-400 ms, *F*(1, 22) = 17.74, $p < .001$, $\eta_p^2 = .45$. [1] Following this interaction, paired sample t-tests were performed for each ROI. Verbal task elicited larger anterior negative slow waves compared to visuospatial task over both hemispheres, ($t(22) = -2.80$, $p = .011$ for left and $t(22) = -4.24$, $p < .001$ for right). In addition, visuospatial task elicited a larger posterior negative slow wave compared to verbal task over the right hemisphere, $t(22) = 3.28$, $p = .003$, (for the ERP plots and scalp map, see Figure 2.5).

For the dual block, the three-way ANOVA revealed a two-way interaction of WM task and AP between 200-400 ms, *F*(1, 22) = 11.24, $p = .003$, $\eta_p^2 = .34$. Following this interaction, paired sample t-tests were performed for anterior and posterior ROIs separately. The t-tests showed that visuospatial task elicited the larger posterior negative slow waves compared to verbal task over both hemispheres, $t(22) = 2.40$, $p = .025$, (for the ERP plots and scalp map, see Figure 2.6).

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[1] An additional three-way ANOVA was conducted for the time interval between 200-500 ms considering that the encoding process may take longer. This ANOVA also revealed the same statistical pattern for the ERP effects as the 200-400 ms analysis.

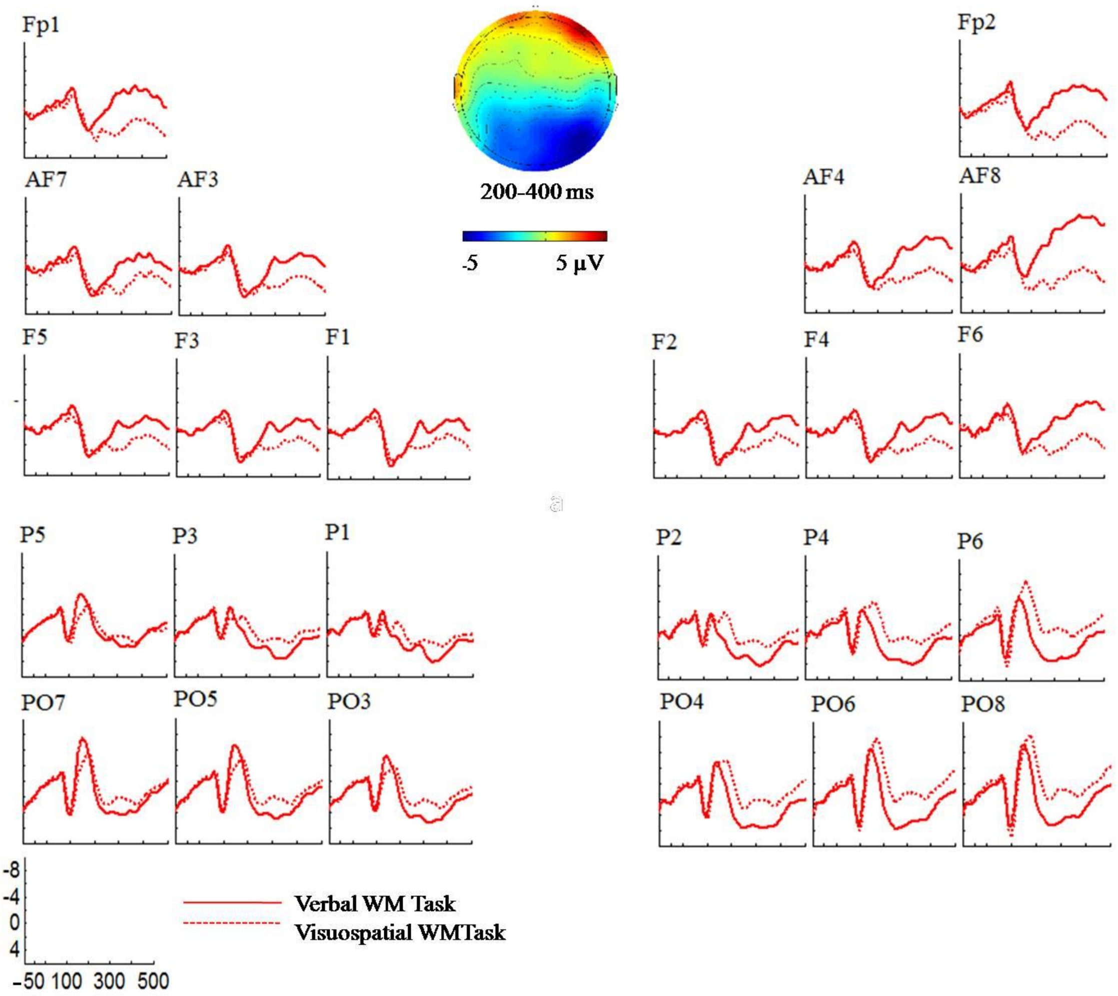

Figure 2.5. Grand average ERP plots and scalp map for the encoding process in the single block. ERPs are superimposed for verbal task (red solid line) and visuospatial task (red dotted line). Six electrodes from each ROI are shown and arrayed from left to right and from anterior to posterior as they were positioned on the scalp. Negativity is plotted upwards. Stimulus onset occurred at 0 ms which was the onset of WM stimulus in the single block. Encoding process analysis in the single block showed the ERP effect in the bilateral anterior ROIs and right posterior ROI. The scalp map, which is plotted by subtracting the ERPs of the verbal task from the visuospatial task, represents the spatial scalp distribution of the ERP effect between 200-400 ms.

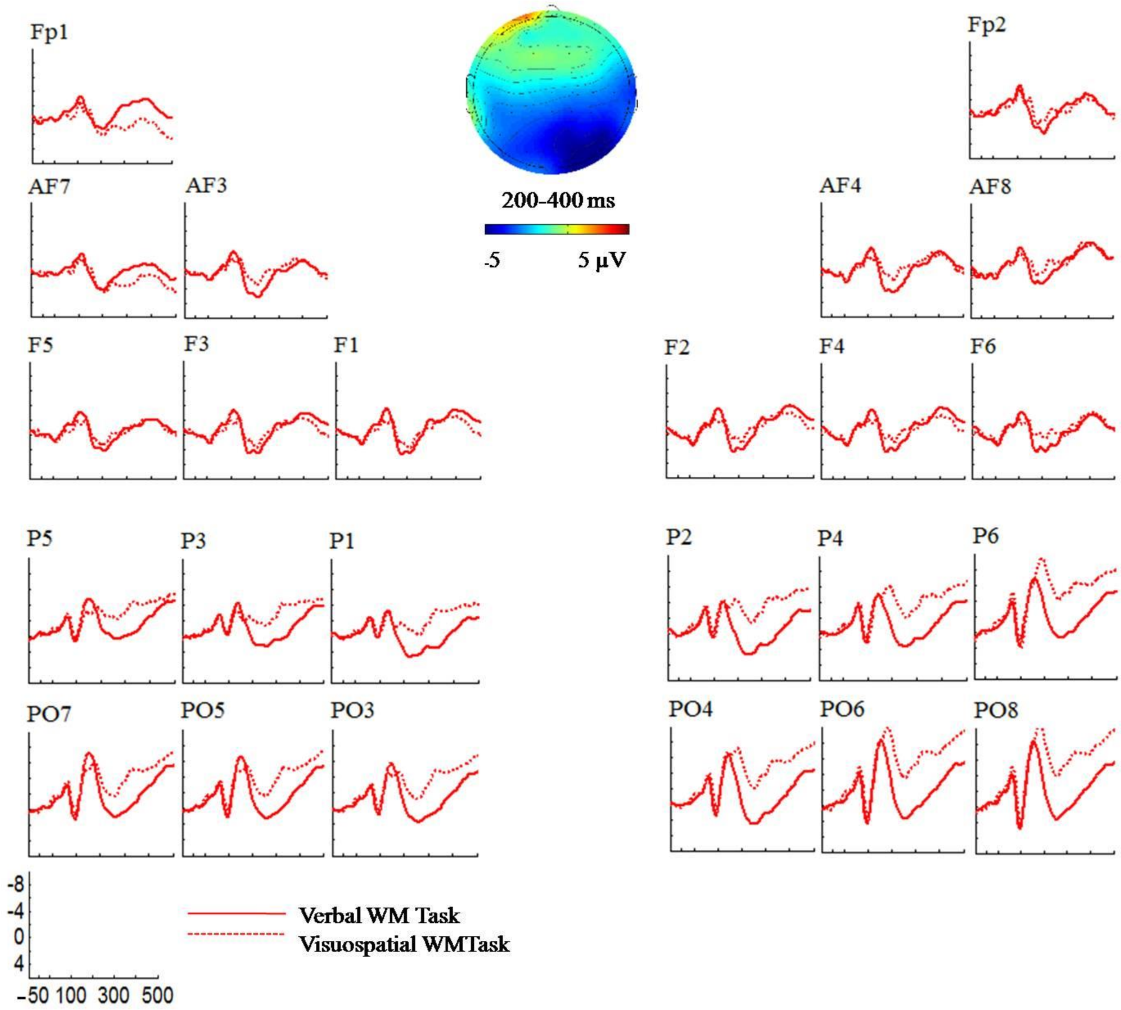

Figure 2.6. Grand average ERP plots and scalp map for the encoding process in the dual block. ERPs are superimposed for verbal task (red solid line) and visuospatial task (red dotted line). Six electrodes from each ROI are shown and arrayed from left to right and from anterior to posterior as they were positioned on the scalp. Negativity is plotted upwards. Stimulus onset occurred at 0 ms which was the onset of WM stimulus in the dual block. Encoding process analysis in the dual block showed the ERP effect in the bilateral posterior ROIs. The scalp map, which is plotted by subtracting the ERPs of the verbal task from the visuospatial task, represents the spatial scalp distribution of the ERP effect between 200-400 ms.

Retrieval Process

For the single block, the three-way ANOVA (*WM task x Hemisphere x AP*) revealed a two-way interaction of WM task and AP between 250-650 ms, $F(1, 20) = 12.40$, $p = .002$, $\eta_p^2 = .38$. Following this interaction, paired sample t-tests were performed for anterior and posterior ROIs separately. The t-tests showed that visuospatial task compared to verbal task generated larger posterior negative slow waves over both hemispheres, $t(20) = 2.19$, $p = .041$. Further three-way ANOVA in the late time window, 800-1500 ms, also revealed a two-way interaction of WM task and AP, $F(1, 20) = 9.124$, $p = .007$, $\eta_p^2 = .31$. Although the ERP plots and scalp map visually showed similar differences between the WM tasks in this time window, the paired sample t-tests showed differences neither for anterior nor for posterior ROIs (for the ERP plots and scalp map, see Figure 2.7).

For the dual-task block, the three-way ANOVAs showed neither a main effect nor interaction of the factors in any time window (for the ERP plots and scalp map, see Figure 2.8).

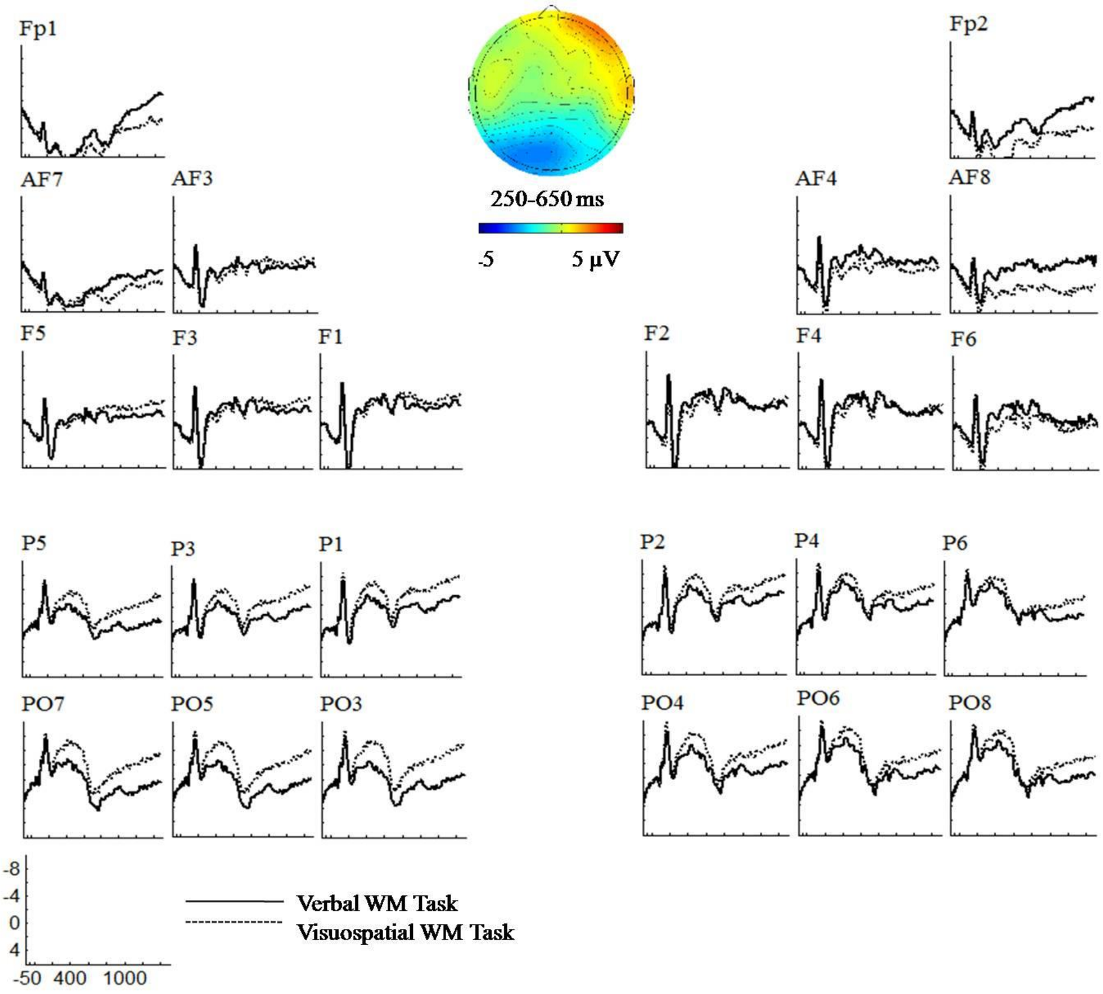

Figure 2.7. Grand average ERP plots and scalp map for the retrieval process in the single block. ERPs are superimposed for verbal task (black solid line) and visuospatial task (black dotted line). Six electrodes from each ROI are shown and arrayed from left to right and from anterior to posterior as they were positioned on the scalp. Negativity is plotted upwards. Stimulus onset occurred at 0 ms which was the onset of keep/change cue in the single block. Retrieval process analysis in the single block showed the ERP effect in the bilateral posterior ROIs between 250-650 ms. The scalp map, which is plotted by subtracting the ERPs of the verbal task from the visuospatial task, represents the spatial scalp distribution of the ERP effect between 250-650 ms.

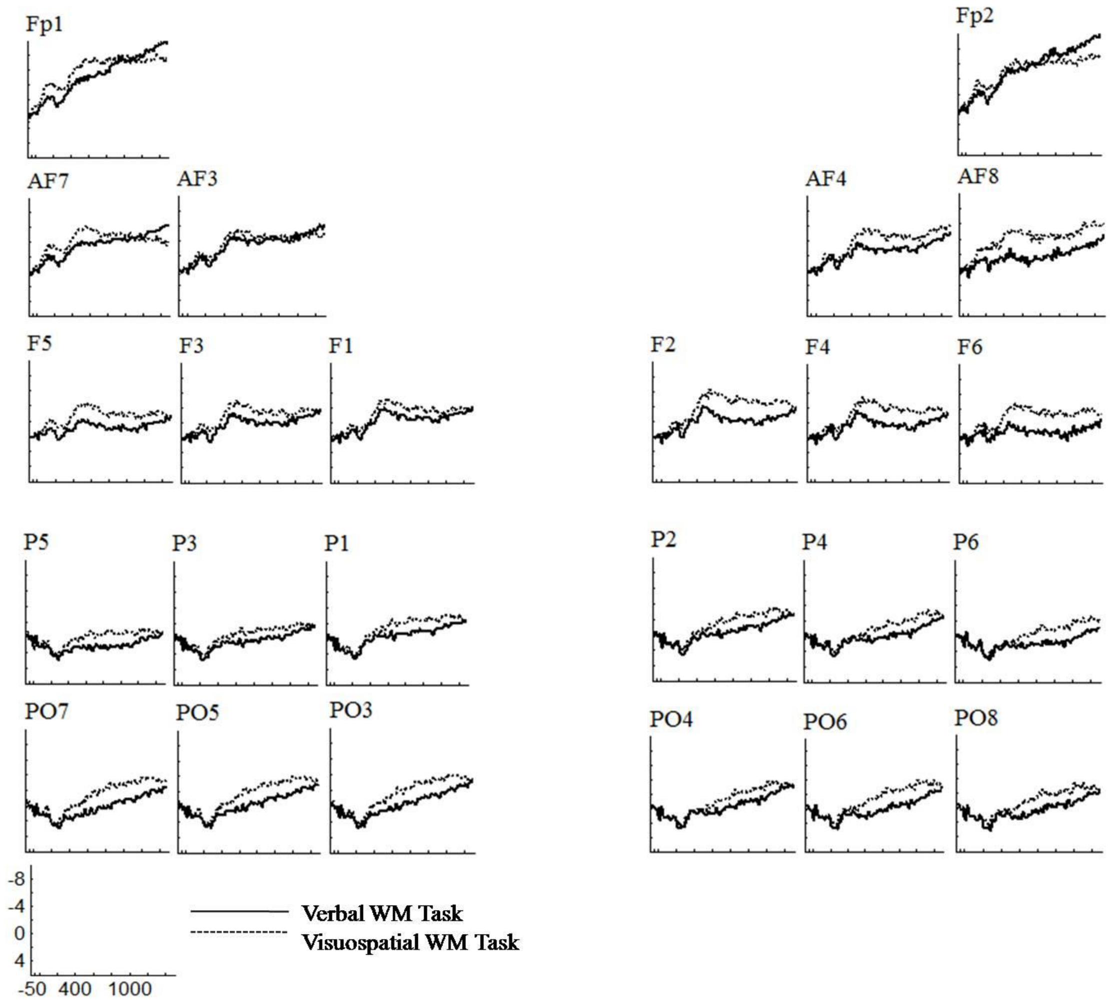

Figure 2.8. Grand average ERP plots and scalp map for the retrieval process in the dual block. ERPs are superimposed for verbal task (black solid line) and visuospatial task (black dotted line). Six electrodes from each ROI are shown and arrayed from left to right and from anterior to posterior as they were positioned on the scalp. Negativity is plotted upwards. Stimulus onset occurred at 0 ms which was the target hit in the dual block. Retrieval process analysis in the dual block showed no significant ERP effect.

Although the qualitative comparisons between single and dual blocks are considered to be appropriate due to the different task requirements in the current study, additional four-way repeated measures of ANOVAs were conducted separately for encoding and retrieval processes. These ANOVAs included the factors *task block, WM task, hemisphere* and *AP*. For the encoding process, the ANOVA revealed a significant four-way interaction between 200-400 ms, $F(1, 22) = 4.96$, $p = .036$, $\eta_p^2 = .18$. For the retrieval process, the ANOVA revealed a significant three-way interaction of task block, WM task and AP between 250-650 ms, $F\ (1, 20) = 12.64$, $p = .002$, $\eta_p^2 = .39$. Accordingly, both interactions also supported the current qualitative differences between single and dual blocks (for the mean ERP values entered in the four-way ANOVAs for encoding and retrieval process in single and dual blocks, see Supplementary Material).

2.4 Discussion

Here, the neurophysiological correlates of the functional domain interactions between manual action control and WM were investigated. More specifically, it was investigated whether the interference of a grasp-and-place movement pertains to the encoding and retrieval processes of verbal and visuospatial domains. The behavioral analyses, replicating the behavioral study by Spiegel and colleagues (2013), showed domain-specific movement execution costs for visuospatial domain. The ERP analyses showed the domain-specific costs also at the neurophysiological level, which is further process-specific to the encoding. In support of the current hypotheses, an initial neurophysiological evidence for the domain and process-specific interactions of movement execution with WM (with visuospatial domain during encoding process) is provided.

2.4.1 Behavioral movement execution costs

In the single block, memory performances for verbal and visuospatial tasks were on average 3-4 items, which is consistent with the proposed WM capacity (e.g., Cowan, 2001). Importantly, performing an additional prepared movement decreased memory performance for the visuospatial task. There was no marked memory performance decrease for the verbal task when comparing the single block and the dual block. That is, memory costs of the grasp-and-place movement seem to be specific to visuospatial domain. On the one hand, this domain specificity is in contrast with the 'basic concurrence cost' hypothesis which views the dual-task costs as general costs (Logan & Fischman, 2011). According to this hypothesis, memory performance should also decrease for the verbal task. On the other hand, the current findings are in line with the previous behavioral findings which also showed larger execution costs for visuospatial domain compared to verbal domain (Spiegel et al., 2013).

The selective interference of the grasp-and-place movement with visuospatial domain is consistent with the MCO-M positing separate verbal and visuospatial domains which draw on specialized cognitive resources (e.g., Baddeley, 2000). According to this model, both domains consist of a passive capacity-limited perceptual store and an active rehearsal mechanism which prevents material-specific information from decaying. For verbal domain the articulatory rehearsal mechanisms, and for visuospatial domain the motor processes was initially suggested to serve to maintain information into visuospatial store (e.g., Baddeley, 1986; Logie, 2011). Consistently, when performed concurrently, many forms of motor actions have been shown to produce interference with visuospatial domain. These include finger tapping (e.g., Smyth et al., 1988), pointing (e.g., Hale et al., 1996), eye movements (e.g., Lawrence et al., 2001), arm movements (e.g., Lawrence et al., 2001; Quinn & Ralston, 1986) and complex movements (e.g., Cortese & Rossi-Arnaud, 2010). Recently, attention has been also suggested as an alternative cognitive resource to serve to maintain information into visuospatial store (e.g., Godijn & Theeuwes, 2012; Postle, Awh, Jonides, Smith, & D' Esposito, 2004).

In the current study, performing the grasp-and-place movement required participants to shift attention not only for holding the sphere centrally while encoding memory items into WM, but also for placing the sphere on the motor target. Moreover, placing the sphere precisely on the target required oculomotor control (e.g., Spiegel et al., 2013). Therefore, it is suggested that attention and oculomotor control are the cognitive resources which are required both by visuospatial domain and grasp-and-place movement. The sharing of capacity-limited attention and oculomotor resources might provide a potential mechanism to explain the domain-specific movement execution costs.

An alternative explanation for domain-specific execution costs might be that the visuospatial character of the preparation cue (directional arrow), not the movement itself, interfered selectively with visuospatial domain. In the current dual-task paradigm, participants could plan the subsequent placement movement based on the directional arrow pointing to one of the motor targets. As an alternative, it might be suggested that the direction of the arrow was kept into WM as an abstract (i.e., symbolically coded) representation and not as a planned, subsequent placement movement. Therefore, the abstract representation of the arrow required the common capacity-limited cognitive resources which were also required for keeping the visuospatial memory items into WM. These shared capacity-limited cognitive resources, thus, resulted in the execution costs for the visuospatial task. However, for the following reasons, this explanation does not seem to be plausible as the main explanation of the current domain-specific execution costs.

A recent behavioral study by Spiegel and colleagues (2013), which used the same experimental setup and procedure, has shown that participants indeed used the arrow for planning the placement movement. Spiegel et al. (2013) investigated the interference of movement re-planning with verbal and visuospatial domains. As in the current study, participants were presented with a directional arrow depending on which they performed the placement movement towards either the left or right motor target. After the arrow, a WM stimulus was presented. Then, an auditory tone (either a high or low tone) serving as a keep/change cue was presented. Depending on the tone, participants placed the sphere either on the motor target pointed by the arrow (executing the initial plan) or on the other motor target (changing the initial plan for 20% of trials). The results revealed that changing the movement plan (re-planning) decreased memory performance both for verbal task and visuospatial task.

Now, if the arrow had been represented just as an abstract symbol, then one would expect that participants must, upon the tone, access the symbolic code, compute a motor target position and execute the movement. Consequently, no re-planning effect should be observed (as there would not have been any planning in the first place). However, such a re-planning effect was consistently found by Spiegel and colleagues (2012, 2013). Therefore, it is argued that the arrow was not represented as a symbol that interfered with visuospatial domain. Rather, it is suggested that the arrow was used for the planning and the planned movement itself interfered with visuospatial domain. Future research may confirm this suggestion by using, for example, different non-spatial cues for movement planning.

2.4.2 Neurophysiological movement execution costs

Encoding Process

In the single block, ERPs of verbal and visuospatial tasks started to diverge at bilateral anterior and right posterior recording sites about 200 ms following the onset of WM stimulus presentation (see Figure 2.5). ERP differences observed during this time interval showed the larger bilateral anterior negativities for the encoding of verbal information compared to visuospatial information, and the larger right posterior negativity for the encoding of visuospatial information compared to verbal information. The different scalp distribution suggests, consistent with the current hypotheses, that the encoding of verbal and visuospatial information are different cognitive processes and seem to arise from non-identical neural sources. These findings support previous ERP studies that have also shown different ERPs for the encoding of verbal and visuospatial information (e.g., Bosch, Mecklinger, & Friederici, 2001; Ruchkin et al., 1990; Ruchkin et al., 1992).

The right posterior negativity has been suggested to reflect the perception and identification of visuospatial information for encoding it into visuospatial store (e.g., Mecklinger, 1998; Ruchkin et al., 1995; Ruchkin et al., 1997b). Previously, the anterior negativity, particularly the left hemisphere dominant, has been suggested to reflect the articulatory rehearsal mechanisms for the maintenance of verbal information (e.g., Ruchkin et al., 1990; Ruchkin et al., 1992; Ruchkin et al., 1997a). The current study shows that an anterior negativity can also be elicited for the encoding of verbal information. This anterior negativity might reflect that participant started rehearsing the letters while stimuli were still present. Obviously, rehearsing may last longer than the actual analyzed epoch for the encoding. Therefore, this interpretation should be approached with caution.

In the dual block, ERP analyses showed a differential cortical activity for WM tasks at bilateral posterior recording sites between 200-400 ms (see Figure 2.6). This bilateral posterior ERP difference reflects the larger negativities for the encoding of visuospatial information compared to verbal information. There was no significant ERP difference between the tasks at anterior recording sites.

Comparing the single block and the dual block in terms of the patterns of ERP differences between verbal and visuospatial tasks, it is suggested that the posterior effect was not the same in single and dual blocks. Whereas the encoding of visuospatial information compared to verbal information elicited the larger right posterior negativity in the single block, it elicited the larger bilateral posterior negativities in the dual block. These findings fit to the findings in the literature that have shown either the right dominant or bilaterally distributed posterior negativity for the encoding of visuospatial information (e.g., Mecklinger, 1998; Ruchkin et al., 1995; Ruchkin et al., 1997b). In line with the previous findings, it is argued that the current posterior negativity reflects the encoding of visuospatial information into WM, and that additional grasp-and-place task changes the neuro-cognitive processes underlying this operation.

Regarding the anterior null effect in the dual block, on the one hand, it is highly unlikely that there was no or a reduced involvement of verbal domain since the high memory performance in the dual block showed that verbal information was still encoded. On the other hand, the visuospatial task, at least qualitatively, seems to elicit increased anterior negativity in dual block compared to single block (see Figure 2.5 and Figure 2.6). It can be assumed that the dual block was more complex and difficult than the single block. Therefore, it is possible that participants used, at least partly, verbalization strategies for the encoding of visuospatial information in the dual block. Another alternative could be that the more difficult (dual) task demanded more attention resources. Previous ERP studies have shown that high cognitive (attention) resources required for the encoding of visuospatial information in the presence of an increased memory load results in an increased anterior negativity (e.g., Awh, Anllo-Vento, & Hillyard, 2000; Luu et al., 2014; Ruchkin et al., 1995; Studer et al., 2010). In either case, encoding of visuospatial information in the current study should elicit an increased anterior negativity in dual block compared to single block. Consequently, the comparison of the verbal and the visuospatial ERPs at anterior recording sites may not result in a statistically significant amplitude difference. Hence, an increased task difficulty might explain the non-significant ERP effect at anterior recording sites. Further research is needed to confirm this suggestion.

These findings suggest that the ERP differences between verbal and visuospatial tasks qualitatively change from single block to dual block in terms of the scalp topography. This qualitative change is interpreted as reflecting the changes in the neuro-cognitive processes underlying the encoding of visuospatial information in the dual block (both at anterior and posterior recording sites). Hereby, these findings reflect the neurophysiological movement execution costs of grasp-and-place task for the encoding process of visuospatial domain.

Retrieval Process

In the single block, ERPs of verbal and the visuospatial tasks started to diverge at bilateral posterior recording sites about 250 ms following the offset of WM stimulus presentation and continued until 650 ms (see Figure 2.7). This bilateral posterior difference shows the larger negativities for visuospatial task compared to verbal task, and it is supposed to reflect the retrieval of visuospatial information. There was no significant ERP difference between the tasks at anterior recording sites.

The anterior null effect might suggest that the retrieval of verbal and visuospatial information is equally difficult, given that participants could retrieve verbal and visuospatial information. If this were so, there should not be any ERP difference for the retrieval process, but there was bilateral posterior effect reflecting the retrieval of visuospatial information. Such a posterior effect for the retrieval of visuospatial information, which is also in line with previous ERP findings, was expected (e.g., Bledowski et al., 2006; Pinal et al., 2014). Moreover, this posterior retrieval effect in the current study demonstrates that reliable ERPs can be obtained during overt movement execution in a complex experimental setting. Regarding the anterior null effect, it cannot be fundamentally ruled out that the retrieval process involves neural sources that are difficult to trace, and thus results in the null effect at anterior recording sites. Conceivably, frontal motor-related cortical activity may conceal retrieval effect (e.g., Westerholz et al., 2013; Westerholz et al., 2014). Future research is necessary to investigate this interpretation.

In the dual block, there was an ERP difference between verbal and visuospatial tasks neither at anterior nor posterior recording sites (See Figure 2.8). First, it should be noted that the retrieval ERPs in the dual block did not show early components (N1/P2) which were present for the retrieval ERPs in the single block. Instead, the dual block retrieval ERPs showed steady, more or less constant amplitude both at anterior and posterior recording sites. For the anterior recording sites, the null ERP effect in the dual block fits to the anterior null effect in the single block. In contrast, the bilateral posterior effect in the single block was not found in the dual block. Although, it is not fully understood yet, the persistent ERPs may be potentially a hint for ongoing cognitive activity that would be expected for retrieval processes. Conceivably, if there was a persistent amplitude difference between the verbal and visuospatial ERPs that was also present during the baseline period, one would artificially eliminate a constant ERP amplitude difference. Unfortunately, there is no preceding fixed duration event for time-locking that would permit a more appropriate retrieval ERP analysis in the dual block.

For the claim that the retrieval process is affected by the concurrent grasp-and-place movement, one would need to show changes in the ERP patterns between single and dual blocks. There was no anterior effect neither in the single nor in the dual block. That is, the ERP patterns at the anterior recording sites did not change. In contrast, in the single block, the bilateral posterior effect reflecting the retrieval of visuospatial information was observed, which was not observed in the dual block. Although, this seems to be a change in the ERP patterns, it is also conceivable that absence of a posterior effect in the dual block was due to methodological circumstances (e.g., a constant effect in the baseline) and not the absence of the difference between the retrieval processes of verbal and visuospatial domains. Moreover, analyzing the retrieval processes in single and dual blocks based on different reference events might have made it difficult to show the changes in ERP patterns in the presence of grasp-and-place movement. Therefore, the present evidence is not considered as sufficient for strictly concluding that the ERP patterns changed between single and dual blocks. Further research is needed to characterize the functional interactions between retrieval process and manual actions.

2.5 Conclusion

The current study provides evidence to extend the understanding of the neuro-cognitive mechanisms underlying manual action control. Here, grasping movement as one of the cognitively demanding manual actions and WM as one of the widely studied cognitive processes in relation to manual action control were focused. More importantly, as the main objective, the functional domain interactions between manual action control and WM, underlying cortical activity and the evaluation of them by means of ERPs are focused.

First, previous behavioral findings (Spiegel et al., 2013) are replicated by showing the domain-specific movement execution costs of prepared movement for visuospatial domain. Second, as the main objective, an initial neurophysiological characterization of the domain interactions between manual action control and WM are provided. The current findings have shown a difference between single and dual blocks for the encoding process of visuospatial domain. That is, the current study has neurophysiologically established that at least the encoding of visuospatial information is affected by the concurrent grasp-and-place movement. This finding points towards the functional importance of the encoding process with regard to the manual action interference with WM. Third, reliable ERPs are reported in a complex experimental setting including overt movement execution, which extends the situations of mere spoken language (e.g., Ganushchak, Christoffels, & Schiller, 2011; Koester & Schiller, 2008) and mere grasping (e.g., Westerholz et al., 2013; Westerholz et al., 2014).

Future investigations are required for characterizing the domain interactions between manual actions and both retrieval and maintenance processes. Moreover, future quantitative statistical comparisons beyond the qualitative comparisons of single and dual blocks are required. These investigations should provide a better understanding of the distinct spatio-temporal characteristics of neuro-cognitive resources shared between manual actions and separate WM processes, and functional interdependence of manual action control and WM. More generally, the current study points out the potential neurobiological underpinnings of motor action control and its interactions with WM.

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3 ERP CORRELATES OF THE FUNCTIONAL INTERACTIONS BETWEEN MANUAL ACTION RE-PLANNING AND WM

CHAPTER 3

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Rümeysa Gündüz Can, ruemeysa.guenduez@uni-bielefeld.de

Manual Action Re-planning Interferes with the Maintenance Process of Working Memory: An ERP Investigation

Rumeysa Gunduz Can[1], Thomas Schack[1,2], Dirk Koester[3]

[1]Faculty of Psychology and Sports Science, Department of Sports Science, Neurocognition and Action-Biomechanics Research Group, Bielefeld University, Bielefeld, Germany
[2]Center for Cognitive Interaction Technology (CITEC), Bielefeld University, Bielefeld, Germany
[3]Faculty of Business and Management, Department of Business Psychology, Business School Berlin, Berlin, Germany

Correspondence concerning this article should be addressed to Dr. Rumeysa Gunduz Can.
Contact: ruemeysa.guenduez@uni-bielefeld.de

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Conflicts of Interest:

The authors declare that they have no conflict of interest.

Ethics Approval:

The current study was performed in line with the principles of 1964 Helsinki Declaration and its later amendments. This study was approved by the ethics committee of Bielefeld University.

Consent to Participate:

Written informed consent was obtained from all individual participants included in the current study.

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Written informed consent was obtained from participants (not all) included in the current study for the publication of videos obtained during experimental task (if necessary).

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Not applicable.

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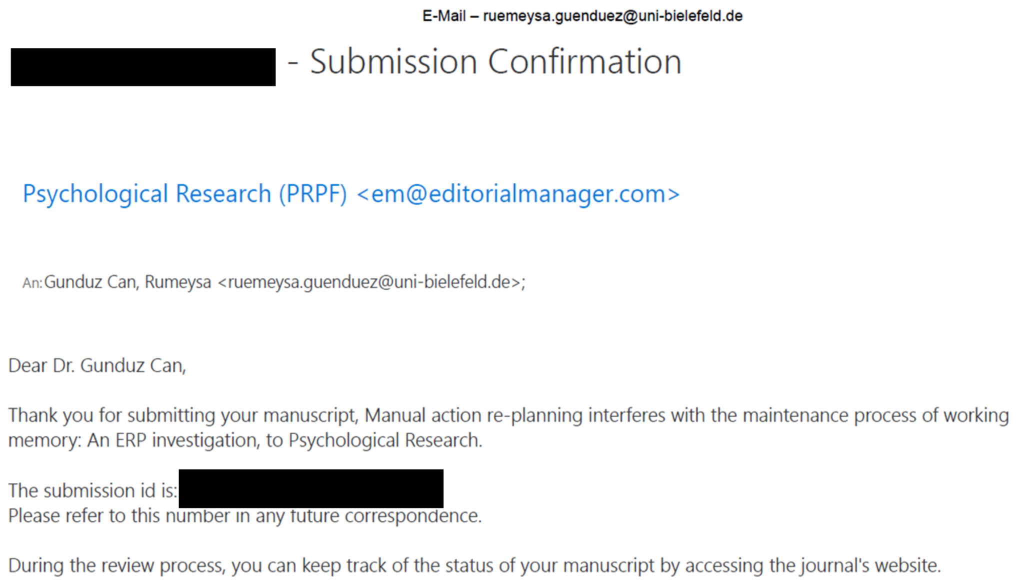

E-Mail – ruemeysa.guenduez@uni-bielefeld.de

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Psychological Research (PRPF) <em@editorialmanager.com>

An: Gunduz Can, Rumeysa <ruemeysa.guenduez@uni-bielefeld.de>;

Dear Dr. Gunduz Can,

Thank you for submitting your manuscript, Manual action re-planning interferes with the maintenance process of working memory: An ERP investigation, to Psychological Research.

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Abstract

The current study focuses on the domain interactions between manual action re-planning and working memory (WM), and the neurophysiological correlates underlying those interactions. Particularly, we investigated the neurophysiological characterization of the re-planning interference with WM domains (verbal, visuospatial) and processes (maintenance, retrieval). Thirty-six participants were tested in a cognitive-motor dual-task paradigm which included concurrent performance of verbal and visuospatial WM tasks with a manual task. Manual task required performing a grasp-and-place movement by either executing the initially prepared movement plan (planned movement condition) or changing the prepared plan to reverse movement direction (re-planned movement condition). ERPs were extracted for planned and re-planned movements separately during maintenance and retrieval processes in verbal and visuospatial tasks. Both the behavioral memory performance and ERPs were compared between planned and re-planned movement conditions. ERP analyses yielded similar effects in both WM tasks. In both tasks, during the maintenance, but not during the retrieval process, re-planned movements compared to planned movements generated a larger positive slow wave with a centroparietal maximum between 200-700 ms, which indicated a P300. We interpret this P300 re-planning effect as suggesting that movement re-planning interferes with the maintenance, but not with the retrieval process, of verbal and visuospatial domains, resulting in domain-general, but process-specific re-planning costs. The current study provides an initial neurophysiological characterization of the domain interactions between manual action re-planning and WM, and contributes to a better understanding of the neurocognitive mechanisms underlying manual action flexibility.

Key words: EEG, motor control, action flexibility, grasping, verbal memory, visuospatial memory

4 ROLE OF WORKING MEMORY RESPONSE MODALITY IN ACTION RE-PLANNING - WM INTERACTIONS

CHAPTER 4

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Rümeysa Gündüz Can, ruemeysa.guenduez@uni-bielefeld.de

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Rumeysa **Gunduz Can**[1,2], Thomas **Schack**[1,2], Dirk **Koester**[3]

1. Faculty of Psychology and Sports Science, Department of Sports Science, Neurocognition and Action-Biomechanics Research Group, Bielefeld University, Universitätsstraße 25, 33615 Bielefeld, Germany

2. Center for Cognitive Interaction Technology, Bielefeld University, Inspiration 1, 33619 Bielefeld, Germany

3. Faculty of Business and Management, Department of Business Psychology, Business School Berlin, Calandrellistrasse 1-9, 12247 Berlin, Germany

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Author Contributions

Conceived and designed the study: RGC, TS, DK. Performed data collection: RGC. Analyzed and interpreted data: RGC, DK. Contributed to the interpretation and preparation of the manuscript: RGC, TS, DK.

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Contact: ruemeysa.guenduez@uni-bielefeld.de

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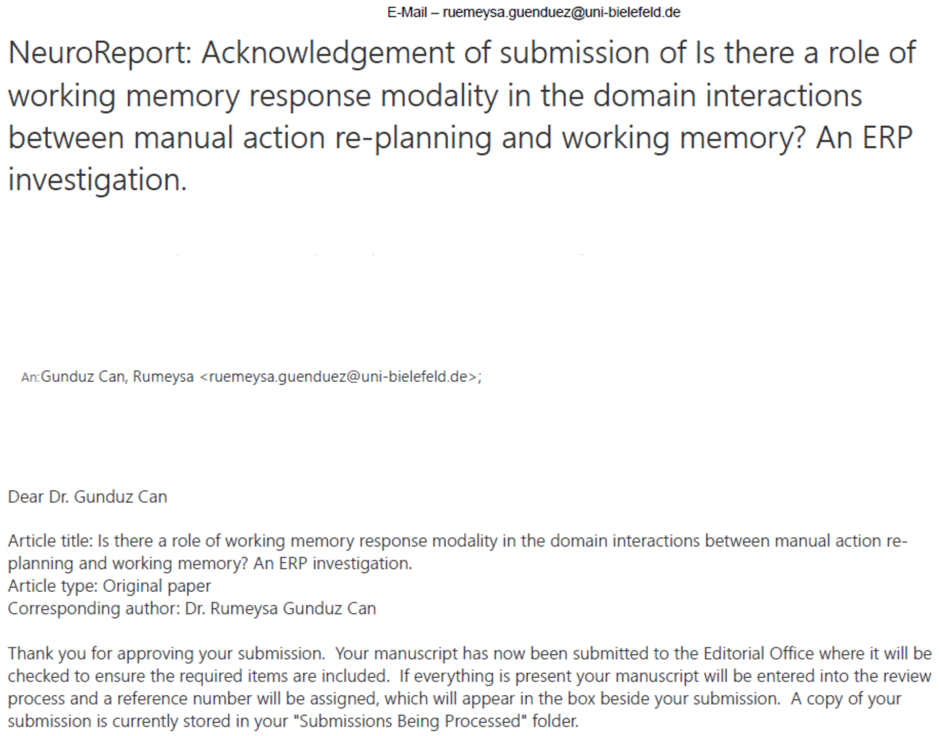

E-Mail – ruemeysa.guenduez@uni-bielefeld.de

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Abstract

The current study focuses on the neurophysiological correlates of the domain interactions between manual action re-planning and working memory (WM). Particularly, based on a previous dual-task study showing the neurophysiological domain interactions when a WM task and manual task required manual responses, the current study investigates the role of the WM response modality (vocal response instead of manual response) in manual action re-planning-WM interactions. In a 2x2 within-subject design with the factors WM task (verbal, visuospatial) and movement planning (planned, re-planned), thirty-six participants performed verbal and visuospatial WM tasks concurrently with a manual task which required performing a grasp-and-place movement by either executing the initially prepared movement plan (planned movement condition) or changing the plan to reverse movement direction (re-planned movement condition). ERPs were extracted for planned and re-planned movements during maintenance and retrieval processes in verbal and visuospatial tasks. ERP analyses showed that in both WM tasks, during the maintenance, but not during the retrieval, re-planned movements compared to planned movements generated a larger positive slow wave with a centroparietal maximum between 200-700 ms, which indicated a P300. We interpret this P300 re-planning effect as suggesting that movement re-planning interferes with the maintenance process of verbal and visuospatial domains, resulting in domain-general, but process-specific movement re-planning costs, which seem to be similar to the re-planning costs obtained with the written report. Accordingly, we argue that the neurophysiological domain interactions of movement re-planning with WM are independent of WM response modality, rather they determined by the central cognitive resources.

Key words: EEG, cognitive-motor dual-task, dual-task interference, motor control, action flexibility, grasping, cognition

5 GENERAL DISCUSSION

Manual actions constitute the great share of the motor action repertoire that people perform every day for achieving daily life routines, communication with other people, or doing sports and playing music instruments. Manual actions are mostly performed with other cognitive tasks such as grasping a coffee cup while having a conversation or hitting the ball in a volleyball game while giving attention to other players around. Moreover, it is also critically important to adapt manual actions to the changing individual physiological or cognitive states such as action goals as well as the changing environmental situations such as target object location. The action flexibility, therefore, is an important cognitive ability which provides rich action repertoire as well as enables precise actions suiting to the desired action outcomes (e.g., Verbruggen et al., 2014). Performing manual actions which achieve the action goals rapidly and accurately without interfering with concurrent tasks, and at the same time accommodate the sudden changes in action demands requires the close engagement of the sensory, motor and cognitive systems. Manual actions, bringing the motor control together with cognition, have provided the evolutionary advantages for humans among other animals, and contributed to the social, cultural and technological progress (e.g., Osiurak, 2014).

The current thesis, with the aim of advancing the understanding of the neuro-cognitive mechanisms underlying manual action control including action flexibility, focused on the manual action-cognition interactions and underlying cortical mechanisms. The current thesis, particularly, investigated the neurophysiological correlates of the functional domain interactions between grasping movements as one of the most cognitively demanding manual actions and WM as the core cognitive process guiding complex behavior.

In a cognitive-motor dual-task paradigm, a manual task requiring grasping an object, holding it, and placing it on a motor target, i.e., grasp-and-place movement was combined with a WM task. To investigate the manual action-WM interactions thoroughly, the current thesis focused on the different aspects of movement phases (execution, re-planning), WM domains (verbal, visuospatial), processes (encoding, maintenance, retrieval) and response modalities (manual response for Study 1 and Study 2 and vocal response for Study 3). In short, the current thesis systematically investigated the neurophysiological correlates of the functional role of WM in the execution and re-planning of manual actions.

Study 1 investigated the neurophysiological correlates of the domain interactions between movement execution and WM. In the dual-task scenario, participants either performed the verbal and visuospatial tasks alone (single-task condition) or concurrently with the manual task (dual-task condition). ERPs were analyzed separately for encoding and retrieval processes in verbal and visuospatial tasks. Both the behavioral memory performance and ERPs were compared between single-task and dual-task conditions. The memory performance was lower in the dual-task compared to the single-task for the visuospatial task, but not for the verbal task.

That is, concurrent movement execution interfered only with visuospatial domain and decreased the memory performance only for the visuospatial task.

In the single-task, encoding process, but not retrieval process, in verbal and visuospatial tasks generated different ERPs both at the anterior and posterior recording sites. Encoding of verbal information generated the left anterior slow wave while the encoding of visuospatial information generated the right posterior slow wave. In the dual-task, the ERP differences between verbal and visuospatial tasks were only at the posterior recording sites. The lack of anterior effect in the dual-task compared to the single-task was explained by an increased anterior slow wave generated in response to the encoding of visuospatial information in the presence of movement execution. The differences between the encoding-related ERPs for visuospatial task in single-task and dual-task conditions were interpreted as reflecting the interference of movement execution. Accordingly, these findings have suggested that executing the movement as initially planned requires the resources which are also required for the encoding process of visuospatial domain, and thus interferes with the encoding of visuospatial information into WM. This movement execution interference then results in domain and process-specific movement execution costs for visuospatial domain.

Study 2 investigated the neurophysiological correlates of the domain interactions between movement re-planning and WM. That is, at what extent changing the initially prepared plan of an ongoing movement is functionally correlated to WM domains and processes. In the dual-task scenario, participants performed the verbal and visuospatial tasks concurrently with the manual task. For some trials, a keep/change cue as an auditory tone asked for reversing the movement direction, and thus changing the initially prepared movement plan with an alternative. ERPs were analyzed separately for maintenance and retrieval process in both WM tasks. Both the memory performance and ERPs were compared between the movement condition which required performing the movement as initially planned (prepared movement condition) and the condition which required performing the movement by changing the initial plan for reversing the movement direction (re-planned movement condition).

The memory performance was lower in the re-planned condition compared to the prepared condition in both verbal and visuospatial tasks. That is, re-planning the ongoing movement interfered with both verbal and visuospatial domains and decreased memory performance for both WM tasks. ERP analyses showed that re-planned movements compared to prepared movements generated a larger P300 during maintenance process independent of WM task. This ERP difference was interpreted as reflecting the movement re-planning interference. Accordingly, these findings have suggested that changing the initially prepared plan of an ongoing movement requires the resources which are also required for the maintenance process of verbal and visuospatial domains, and thus interferes with the maintenance of verbal and visuospatial information. This movement re-planning interference then results in domain-general, but process-specific movement re-planning costs for both WM domains.

Study 3 investigated whether the WM response modality affects the neurophysiological correlates of the domain interactions between movement re-planning and WM. That is, whether the neurophysiological interactions of movement re-planning with WM depend on the particular pairings of stimulus-response modalities within WM tasks as well as on the response modality overlap between WM tasks and manual task. The experimental procedure was the same as in Study 2. Participants performed the verbal and visuospatial tasks concurrently with the manual task which required executing the prepared movement plan for some trials and changing it for other trials. The only difference was that both WM tasks included vocal response (spoken report) instead of manual response (written report). ERPs were analyzed separately for maintenance and retrieval processes in both WM tasks. Both the memory performance and ERPs were compared between prepared and re-planned movement conditions.

Both the behavioral and ERP analyses showed the similar results compared to the results obtained with written report (Study 2). Namely, movement re-planning interfered with both verbal and visuospatial domains and decreased the memory performance for both verbal and visuospatial tasks. Moreover, re-planned movements compared to prepared movements generated a larger P300 during the maintenance process independent of WM task. Accordingly, regardless of the WM response modality, movement re-planning entails domain-general, but process-specific re-planning costs for the maintenance process of both verbal and visuospatial domains.

The current studies together have provided a comprehensive investigation of the movement execution costs and re-planning costs for WM domains and processes, and of the re-planning costs across written and spoken reports. Hereby, the variables which shape the domain interactions between manual action control and WM, and the underlying neurophysiological correlates have been clarified. The current findings have shown that WM plays a functional role in manual action control. Importantly, these findings have shown that this role depends on a variety of factors such as movement phase (execution, re-planning), information domain (verbal, visuospatial) and information process (encoding, maintenance, retrieval).

Motor requirements of mere execution of a spatially directed movement and cognitive requirements of re-planning of an ongoing movement recruit distinct WM capacities. Consequently, movement execution and movement re-planning induce separate neuro-cognitive costs for WM domains and processes both at the behavioral and neurophysiological level. Accordingly, the current findings have supported the functional separation between movement execution and re-planning phases as well as between WM domains and processes.

The current thesis provides the first neurophysiological investigation of the domain interactions between manual action control and WM. Importantly, this thesis also uncovers the neuro-cognitive mechanisms underlying manual action flexibility which is the key for precise manual actions in natural environments. Moreover, the current thesis encourages future research methods with more sensitive measures such as ERPs for the investigation of the manual action-cognition interactions. Accordingly, the current thesis contributes to a better understanding of how the human brain achieves rapid, precise and flexible actions by orchestrating the sensorimotor systems with cognitive processes.

5.1 Variables which shape the manual action - WM interactions

The current findings have shown that WM plays a functional role in manual action control. Accordingly, these findings are in line with the WM theories suggesting the role of WM not only in cognitive control, but also in motor control (e.g., Postle, 2006; Theeuwes et al., 2009). Moreover, these findings are also in line with the motor control theories, particularly with the CAA-A which has explicitly suggested a role of WM in planning and execution of complex movements (Schack, 2004).

Moreover, the current findings have shown that movement execution and movement re-planning recruit distinct WM capacities. Namely, movement execution displays domain and process-specific WM interactions with the encoding process of visuospatial domain, and movement re-planning displays domain-general, but process-specific WM interactions with the maintenance process of verbal and visuospatial domains. These findings are in line with the two-component model which has stated that planning and online control are separate, but complementary movement phases (e.g., Glover, 2004; Woodworth, 1899; for a review, see Elliott et al., 2017).

Planning phase occurs prior to movement onset and reflects not only the immediate aspects, but also the invariant aspects of a movement such as conceptual object knowledge, action goals and anticipatory action effects (e.g., Hommel et al., 2016; Wong et al., 2014). Hereby, planning engages in high-level cognitive control by bringing together the motor and cognitive systems (e.g., Gentsch et al., 2016). Besides the planning, online control phase is also required for satisfying the desired action outcome by bringing the plan to the completion. During online control, the sensorimotor transformations are executed based on the sensory input from the object and body. Moreover, by integrating the sensory input with the efference copy, any mismatch between the planned and current movement state can be determined and corrected (e.g., Glover, 2004; Wolpert & Ghahramani, 2000). Moreover, planning and online control rely on different perceptual and cognitive representations, and thus interact with cognition to a different extent (e.g., Glover, 2004).

The current thesis suggests that besides planning and online control, re-planning is another movement phase which is required when the action demands change and ask for a plan update. Movement re-planning is achieved by cancelling the initally prepared plan of an ongoing movement and implementing a more appropriate alternative plan. Although movement re-planning is related to both planing and online control phases, it requires additional cognitive operations for achieving a balance between the prepared, ongoing movement and the inhibition of it for preparing a new movement. Consequently, movement re-planning with additional cognitive operations recruits different neuro-cognitive resources compared to mere movement execution. Detailed discussion about the neuro-cognitive costs of movement execution and movement re-planning for WM will be presented in the section 5.1.1 and 5.1.2.

The findings that different movement phases interact with different WM domains and processes are also in line with the literature suggesting the functionally separate WM domains and processes (e.g., Baddeley, 2012; Jonides et al., 2008). The separation between verbal and visuospatial domains was initially suggested by the MCO-M (Baddeley & Hitch, 1974), which then has been supported by different research lines such as data from children (e.g., Alloway et al., 2006), neuroimaging studies (e.g., Gruber & von Cramon, 2003) and ERP studies (e.g., Ruchkin et al., 1992; Watter et al., 2010). While the verbal domain is dedicated to verbal information in phonological format, the visuospatial domain is dedicated to visual (pictorial) and spatial (location) information. Accordingly, verbal and visuospatial domains are involved in different cognitive and motor tasks. For example, verbal domain is involved in storing, tracking and, when necessary, recalling the action plans from LTM (e.g., Logan, 2004) as well as in following the task instructions (e.g., Jaroslawska et al., 2016). Differently, visuospatial domain is involved in planning and execution of spatially directed movements as well as in constructing, manipulating and searching the visual images (for reviews, see Luria, Balaban, Awh, & Vogel, 2016; Morey & Bieler, 2013).

WM has been also shown to comprise encoding, maintenance and retrieval processes which are involved in separate, but overlapping cognitive operations of information (e.g., Jonides et al., 2008). During encoding, incoming information is evaluated whether it is relevant for the task at hand, and if it is relevant, a representation is generated and transferred into WM. During maintenance, information is stored and protected against distraction and decay. During retrieval, stored information is reactivated for performing the task at hand. Different research lines such as behavioral studies (e.g., Baddeley et al., 1984; Craik et al., 2018), neuroimaging studies (e.g., Landau et al., 2004) and ERP studies (e.g., Gulbinaite et al., 2014) have shown that each process requires different amount of cognitive resources, and thus is interfered by the memory load such as the presence of a concurrent task to a different extent.

The current findings have also shown that movement re-planning displays domain-general, but process-specific WM interactions independent of the WM response modality. In Study 2, both verbal and visuospatial tasks required written report with right hand (i.e., manual response modality). In Study 3, WM tasks required spoken report (i.e., vocal response modality). The manual task required a right hand response (i.e., manual response modality) both in Study 2 and Study 3. In Study 2, manual response provided the more compatible stimulus-response modality in visuospatial task (i.e., visuospatial stimulus-manual response) compared to verbal task (i.e., verbal stimulus-manual response). In contrast, in Study 3, vocal response provided the more compatible stimulus-response modality in verbal task (i.e., verbal stimulus-vocal response) compared to visuospatial task (i.e., visuospatial stimulus-vocal response; e.g., Hazeltine et al., 2006; Wickens et al., 1984). Moreover, in Study 2, both WM tasks and manual task required right-hand response, which then resulted in response modality overlap across the tasks due to the common motor structure (i.e., overlapping effector systems; e.g., Huestegge & Koch, 2010). Differently, in Study 3, vocal response separated the response modalities between WM tasks and manual task.

Despite the differences between Study 2 and Study 3 in terms of the particular pairings of stimulus-response modalities within WM tasks as well as the response modality overlap between WM tasks and manual task, movement re-planning showed the same interactions patterns with WM. Accordingly, the current findings do not support the literature suggesting that the particular pairing of stimulus-response modalities, and thus the modality compatibility within a task determines the extent of dual-task interference (e.g., Hazeltine et al., 2006; Wickens et al., 1984) or the literature suggesting that common motor structures are the source of dual-task interference (e.g., Bratzke et al., 2008; De Jong, 1993; Heuer, 1996).

Alternatively, the current findings support the literature suggesting that domain-general mechanisms such as central cognitive resources (e.g., Kahneman, 1973; Tombu & Jolicoeur, 2003) or central structures (e.g., Pashler, 1994) are the source of dual-task interference. Accordingly, the current findings are in line with the previous findings which have shown that concurrent tasks can interfere with each other even when the tasks include compatible sensory-motor modalities (e.g., Hazeltine & Wifall, 2011; Halvorson & Hazeltine, 2015; Pieczykolan & Huesttege, 2018; Stelzel & Schubert, 2011) or different effector systems such as vocal and manual responses (e.g., Dux, Ivanoff, Asplund, & Marois, 2006; Levy, Pashler, & Boer, 2006), oculomotor and manual responses (e.g., Huestegge & Koch, 2010; Pieczykolan & Huesttege, 2017, 2018), and foot and manual responses (e.g., Hiraga, Garry, Richard, Carson, & Summers, 2009). Accordingly, the current findings have shown that movement re-planning shares the domain-general cognitive resources (or structures) with WM domains. Importantly, the shared cognitive resources do not depend on the WM response modality.

5.1.1 ERP correlates of execution costs for WM

The mere execution of a grasp-and-place movement without additional planning requirements resulted in domain and process-specific neuro-cognitive costs for the encoding process of visuospatial domain. Domain-specific interactions of a variety of movement forms with visuospatial domain have been suggested since the oculomotor hypothesis (Baddeley, 1986), which has proposed that eye movements provide an active rehearsal mechanism for the maintenance of visuospatial information. Later, Logie (1995) introduced the concept of the inner scribe which has proposed the active rehearsal mechanism based on any movement. Accordingly, it has been proposed that execution of any concurrent movement would recruit the resources which are also required for the rehearsal of visuospatial information, and thus result in the interference with visuospatial domain (for a review, see Quinn, 2008). Such movement interference has been shown for eye movements (e.g., Baddeley & Lieberman, 1980; Postle et al., 2006), sequential tapping (e.g., Smyth & Pendleton, 1989), pointing (e.g., Rossi-Arnaud et al., 2012), arm movements (Quinn & Ralston, 1986) and grasping movements (e.g., Spiegel et al., 2013).

Alternatively, spatial attention has been suggested as being involved in the maintenance of visuospatial information (e.g., Awh et al., 2006; Awh & Jonides, 2001). For example, Awh, Jonides and Reuter-Lorenz (1998) have suggested that attention is directed at the to-be-remembered stimulus features during retention interval, and thus enhances the visual processing of those features. Relatedly, concurrent tasks which shift attention away from to-be-remembered stimulus during retention interval disrupt the maintenance of visuospatial information, and thus impair memory performance (e.g., Smyth, 1996; Smyth & Scholey, 1994). Hence, these findings have shown that attention has a functional role in the maintenance of visuospatial information.

Spatial attention has been also shown to be involved in the encoding process of visuospatial domain (for reviews, see Awh, Vogel, & Oh, 2006; Olivers, Peters, Houtkamp, & Roelfsema, 2011). For example, spatial attention behaves as a gateway for visuospatial domain (e.g., Schmidt, Vogel, Woodman, & Luck, 2002; Vogel, McCollough, & Machizawa, 2005; Vogel et al., 2005). That is, directing attention at a particular stimulus feature increases the probability that this feature is transferred and stored into WM (e.g., Schmidt et al., 2002). Relatedly, attention is also involved in the suppression of irrelevant information during encoding, and thus involved in the better transfer of relevant information into WM (e.g., Gazzaley & Nobre, 2012; Gulbinaite et al., 2014; Zanto & Gazzaley, 2009). That is, remembering the relevant information is associated with suppressing interference from the irrelevant information during encoding. Accordingly, visuospatial storage capacity is strongly related to successful attention selection during encoding, i.e., selection of relevant information in the environment (e.g., Vogel et al., 2005). Moreover, attention selection and visuospatial domain have been shown to activate similar cortical regions and generate similar ERPs, supporting the functional role of attention in the encoding of visuospatial information (e.g., Awh et al., 2000; Hönegger et al., 2011; Kuo, Rao, Lepsien, & Nobre, 2009). The attention-based transfer of information into WM is also in line with the WM models which state that attention plays a functional role both in the transfer and storage of information into WM (e.g., embedded process model, Cowan, 1988; TBRS-M, Barrouillet et al., 2004; emergent property view, Postle, 2006).

The close engagement of attention and motor control has been also suggested. For example, the premotor theory of attention has proposed that covert shift of attention is equivalent to movement preparation (Rizzolatti, Riggio, Dascola, & Umiltá, 1987). That is, planning a goal-directed movement is both necessary and sufficient for attending to an object regardless of whether the movement will be overtly executed or not. Differently, the selection for action theory has proposed that attention is directed at the features in the environment that are relevant towards an intended movement (Allport, 1987). That is, goal-directed movements bias attention at those features in the environment.

Accordingly, it has been shown that attention is employed during the planning of grasping movements for selecting the object of interest, extracting the visuospatial parameters such as location or size, and identifying the contact points (e.g., Belardinelli, Stepper, & Butz, 2016; Brouwer, Franz, & Gegenfurtner, 2009; for a review, see Baldauf & Deubel, 2010). Relatedly, it has been shown that perceptual recognition of to-be-grasped features of the object is enhanced due to the attention allocation (e.g., Bekkering & Neggers, 2002; Hannus, Cornelissen, Lindemann, & Bekkering, 2005).

During the execution of grasping movements, attention has been shown to suppress the representation of distracter objects around the object of interest, and thus prevents the effect of distracters on movement kinematics (e.g., Bonfiglioli & Castiello, 1998). Relatedly, dual-task studies have shown that grasping performance is impaired with altered movement kinematics (i.e., delayed adjustment of the grip to object size) when attention resources are shared between a grasping task and perceptual task (e.g., Hesse & Deubel, 2011; Hesse, Schenk, & Deubel, 2012). That is, attention is needed for the effective control of grasping movements both during planning and execution.

Considering the functional interactions between visuospatial domain, attention and motor control, I argue that the neuro-cognitive costs of movement execution for the encoding process of visuospatial domain stem from the common capacity-limited attention resources (for a review, see Herwig, 2015). Such costs are also in line with the previous research showing the movement interference with the encoding process of visuospatial domain (e.g., Dodd & Shumborski, 2009; Hale et al., 1996; Meiser & Klauer, 1999; Quinn & Ralston, 1986). Consequently, based on the literature suggesting that encoding quality is critical for the maintenance and later recall of information (e.g., Bays, Catalao, & Husain, 2009; Cusack, Lehmann, Veldsman, & Mitchell, 2009; Loaiza, McCabe, Youngblood, Rose, & Myerson, 2011), I argue that the interference of movement execution during encoding then resulted in the memory performance decrease for the visuospatial task.

Movement execution costs at the neurophysiological level also fit to the previous ERP research on the manual action control and WM. In the single-task, encoding of visuospatial information generated a posterior slow wave in line with other ERP studies (e.g., Agam & Sekuler, 2007; Löw et al., 1999; Ruchkin et al., 1992). Differently, in the dual-task, encoding of visuospatial information generated also an anterior slow wave. This anterior slow wave is also in line with other ERP studies which have shown that anterior slow waves are generated when the domain-specific resources are not sufficient, and thus additional executive processes are recruited (e.g., Bosch et al., 2001; Hönegger et al., 2011; Löw et al., 1999).

Moreover, previous ERP studies on grasping movements have also shown the posterior slow waves, particularly when the immediate action goal specifies how to execute a movement (e.g., Van Schie & Bekkering, 2007; Westerholz et al., 2013; for a review, see Koester et al., 2016). Accordingly, I argue that the current visuospatial task and manual task activated similar parietal cortical regions most likely due to the common attention resources (for a review, see Theeuwes et al., 2009). Based on the common cortical regions, then, movement execution interfered with the encoding process of visuospatial domain. This argument is also line with the dual-task literature which has suggested that dual-task interference depends on the overlap in the cortical regions required for performing concurrent tasks (e.g., Kinsbourne & Hicks, 1978; Nijboer, Borst, Van Rijn, & Taatgen, 2014; for a review, see Leone et al., 2017). Consequently, in the presence of movement execution, encoding of visuospatial information required additional attention resources, and thus recruited additional cortical activity, which then also supports the generation of the anterior slow wave in the dual-task.

In summary, I propose that the neuro-cognitive resources (e.g., spatial attention and related cortical regions) shared between movement execution and encoding process of visuospatial domain are the reasons of the current movement execution costs.

5.1.2 ERP correlates of re-planning costs for WM

The re-planning of a grasp-and-place movement resulted in domain-general, but process-specific neuro-cognitive costs for the maintenance process of verbal and visuospatial domains. Movement re-planning requires additional cognitive operations which are not required for mere movement execution (or planning). For example, the error that ongoing movement is not satisfying the new desired action outcome must be understood (e.g., Wei & Körding, 2008). Then, ongoing movement must be inhibited by suppressing initial stimulus-response mappings. Subsequently, new plan must be selected, new stimulus-response mappings must be formed, and new movement must be prepared and executed (e.g., Verbruggen et al., 2014). Accordingly, movement re-planning is involved in high-level cognitive control such as decision-making and conflict resolution between the prepared movement and new movement (e.g., Botvinick et al., 2001). In respect to this, it has been shown that movements can be competently re-planned on fly, yet the implementation of a new plan in the presence of a dominant initial plan comes with cognitive costs (e.g., Ullsperger et al., 2014).

In the current studies, both in prepared and re-planned movement conditions, participants had to interpret the meaning of the auditory tone (execute or change the plan) and access the active target representation (pointing direction of the arrow). In the prepared condition, participants executed the movement based on these operations, while in the re-planned condition they had to undergo additional operations for satisfying the new desired action outcome (i.e., new movement direction). For example, participants had to inhibit the initial movement plan prepared based on the initial arrow direction, comprehend the reversed direction of the arrow and accordingly activate the new target representation, select the new target-movement associations, and prepare and execute the new movement (e.g., Hazeltine & Schumacher, 2016).

In line with the additional cognitive operations, previous research has also shown that movement re-planning recruits attention and WM resources, for example, for suppressing stimulus-response mappings (e.g., Mostofsky & Simmonds, 2008), updating action representations (e.g., Trewartha et al., 2013) or selecting, preparing and executing new responses (e.g., Yamanaka & Nozaki, 2013; for reviews, see Gratton, Cooper, Fabiani, Carter, & Karayanidis, 2018; Wessel & Aron, 2017). Accordingly, I argue that movement re-planning recruited cognitive resources which were also required for the maintenance of verbal and visuospatial information, and thus resulted in the re-planning interference with both domains. Since movement re-planning interfered with both domains, it must have engaged in a domain-general resource. I propose that such domain-general resource is the central attention mechanisms.

Domain-general attention mechanisms involved in the maintenance of verbal and visuospatial information have been proposed by different WM models (e.g., MCO-M, Baddeley, 1996; the embedded process model, Cowan, 1988; TBRS-M, Barrouillet et al., 2004; the controlled attention model, Engle, Tuholski, Laughlin, & Conway, 1999; Miyake et al., 2000; the distributed executive control model, Vandierendonck, 2016). For example, Baddeley (1996) proposed the central executive as the domain-general attention controller which is involved in a variety of executive functions such as processing stored information, coordinating domain-specific verbal and visuospatial stores as well as dividing attention between tasks, and thus coordinating dual-task operations. Moreover, it has been shown that when the limits of domain-specific stores are exceeded under high memory load, the central executive is involved in the maintenance of both verbal and visuospatial information (e.g., Allen, Baddeley, & Hitch, 2017; Cowan & Morey, 2007; Doherty & Logie, 2016; Logie, Cocchini, Della-Salla, & Baddeley, 2004; Vandierendonck, Kemps, Fastame, & Szmalec, 2004). Relatedly, the controlled attention model (e.g., Engle et al., 1999) has also proposed that domain-general attention mechanisms are involved in the maintenance under the situations which require high-level cognitive control.

The state WM models have also proposed that domain-general attention mechanisms are involved in both the storage and manipulation of any kind of information (e.g., Barrouillet et al., 2004; Cowan, 1988; Oberauer, 2002). For example, the TBRS-M has proposed that information is maintained in WM through attentional refreshing which requires focusing the general-purpose, capacity-limited attention resources on to-be-remembered information. If any other task is performed concurrently with the maintenance, that task would capture the same general-purpose attention resources. Consequently, the attention focus will be diverted away from refreshing the information stored in WM, which then will disrupt the maintenance. Therefore, any task requiring attention will impair the attention refreshing, and thus the memory performance. Moreover, this impairment depends on the cognitive load of the concurrent task. That is, more difficult the task, longer capturing the attention, and thus larger the impairment for attention refreshing and memory performance.

Accordingly, the current movement re-planning-WM dual-task scenario required WM resources, particularly the central attention capacity, for maintaining the information in the presence of distractive movement re-planning (WM tasks), for changing the prepared movement plan with a new plan (movement re-planning) as well as for coordinating the WM tasks and movement re-planning. Therefore, in the current studies, cognitively demanding movement re-planning acted as a distracter and recruited domain-general attention resources, and thus left fewer resources for the maintenance of information into WM. Consequently, memory performance decreased for both WM tasks, resulting in domain-general, but process-specific neuro-cognitive costs.

The lack of the effect of WM response modality on movement re-planning-WM interactions also supports the argument that movement re-planning and maintenance process share the central attention resources. Accordingly, the current findings are also in line with the dual-task theories which have explained the dual-task interference based on the capacity-limited central cognitive resources (e.g., Kahneman, 1973; Tombu & Jolicoeur, 2003). Moreover, the current findings are also in line with the dual-task literature explaining the dual-task interference based on the common WM resources shared between concurrent tasks (e.g., Hazeltine & Wifall, 2011). However, in contrast to the previous research, in the current studies, domain-general WM resources such as central attention, but not the domain-specific WM resources, explain the interference of movement re-planning with WM.

Movement re-planning costs at the neurophysiological level also fit to the previous ERP research. The maintenance process of verbal and visuospatial domains would have been expected to generate different ERPs, such as the anterior slow waves for verbal domain and posterior slow waves for visuospatial domain (e.g., Ruchkin et al., 1992; Kiss et al., 2007; Löw et al., 1999; Watter et al., 2010). However, there was no difference between the ERPs of verbal and visuospatial domains in the presence of movement re-planning. Previous ERP research has shown that in the presence of high memory load, domain-general slow waves in addition to domain-specific ones are generated during the maintenance both of verbal and visuospatial information (e.g., Kiss et al., 2007; Löw et al., 1999). For example, Kiss and colleagues (2007) showed that anterior negative slow waves were generated for maintaining verbal information, while Löw and colleagues (1999) showed that anterior negative slow waves were generated for maintaining visuospatial information. Accordingly, in the current studies, maintenance of verbal and visuospatial information generated domain-general slow waves, as also in line with the behavioral argument that WM maintenance required the increased attention resources in the presence of movement re-planning.

Moreover, there was a difference between the ERPs of prepared and re-planned movements during the time interval of WM maintenance. Re-planned movements generated a larger P300 compared to prepared movements independent of WM task. In the next section, I will elaborate on the role of P300 in movement re-planning and explain how it is related to the domain-general attention resources and movement re-planning costs.

5.2 Role of P300 in manual action re-planning

The current finding that movement re-planning generated a larger P300 is in line with the previous ERP research on movement re-planning (e.g., Chase et al., 2011; Fleming et al., 2009; Krämer et al., 2011; Randall & Smith, 2011; Trewartha et al., 2013; Vidal et al.,1995). The current thesis further shows that P300 is generated not only for the re-planning of simple movements such as button press, but also for re-planning of complex grasping movements.

The involvement of P300 in movement re-planning can be explained by different theoretical models of P300. According to the context updating hypothesis (Donchin & Coles, 1988), P300 reflects the cognitive processes related to the updating of mental representation of stimulus environment upon the receipt of new information. An attention driven process evaluates whether the new information is matching to the mental representation stored in memory. If there is a match, the current representation is maintained. In contrast, if there is a mismatch, the current representation is updated employing attention and WM processes, which is then associated with a P300.

In the motor control, the context updating hypothesis has been discussed also in relation to response-related processes. To satisfy a desired action outcome, it is important to access the internal action representations and update such representations when necessary. Accordingly, it has been suggested that P300 reflects the updating of internal action representations in the presence of a mismatch between a planned movement and a desired action outcome (e.g., Krigolson & Holroyd, 2008; Trewartha et al., 2013; Ullsperger et al., 2014). Task-switching research has also supported the role of P300 in movement re-planning based on the context updating (e.g., Barceló, Escera, Corral, & Periáñez, 2006; Barceló & Knight, 2007; Barceló, Periáñez, & Nyhus, 2008). For example, Barceló and colleagues (2006) showed that the cue indicating for switching an ongoing task generated a larger P300 compared to the cue indicating for executing the ongoing task. The authors argued that larger P300 was due to the switch preparation such as task-set updating. Moreover, the authors argued that P300 did not reflect solely an unexpected perceptual event, but rather reflected cognitive control for 'changing your mind'. That is, P300 reflects high-level context updating mechanisms, and thus are involved not only in updating the sensory aspects of a stimulus, but also in updating the motor response units (e.g., Barceló & Cooper, 2018).

Verleger and colleagues (2005) have suggested that P300 reflects the cognitive processes related to the perceptual analysis of a stimulus and the initiation of a relevant response. That is, P300 reflects a link between perception and action. Accordingly, previous research has shown that conditions which require the assignment of a specific response to a specific stimulus are associated with P300 generation. For example, P300 is generated when stimulus-response mappings must be selected (e.g., Hsieh & Liu, 2005; Verleger, Grauhan, & Śmigasiewicz, 2016), or a new response is required upon the receipt of a change cue (e.g., Krämer et al., 2011; Randall & Smith, 2011) as well as when a response must be compared with a desired action outcome (e.g., Getzmann et al., 2018). In line with the previous research, the current P300, therefore, may reflect the processes related to the perception-action link between the auditory tone indicating a plan update and the new required movement.

Neuiwenhuis and colleagues (2005) have suggested that P300 reflects the cognitive processes related to the fast decision mechanisms based on the phasic activity of the locus coeruleus-norepinephrine system. This phasic activity is associated with the presentation of a task relevant stimulus and behavioral response initiated by that stimulus. Accordingly, it is reasonable to assume that the current auditory tone (as the change cue in re-planning condition) may activate this system for rapidly deciding about the required changes in ongoing movement such as inhibiting the initial target-response association for selecting a new one (for a computational model which has also supported the idea that P300 reflects cognitive processes related to the decision-making, see O' Connell, Dockree, & Kelly, 2012).

Moreover, generation of a larger P300 for movement re-planning compared to movement execution is also in line with the literature suggesting that P300 reflects the mental effort required for performing the task at hand (e.g., Kok, 2001; Polich, 2007). That is, difficult tasks compared to easy tasks require more mental effort, and thus generate larger P300 (e.g., Kok, 1997; Sirevaag et al., 1989).

Neural sources of P300 as the parietal cortical regions also support the generation of P300 in response to movement re-planning (e.g., Bledowski, Prvulovic, Goebel, Zanella, &

Linden, 2004; for a recent review, see Huang, Chen, & Zhang, 2015). The parietal cortical regions are involved in motor control both at the sensorimotor and cognitive levels such as forming stimulus-response mappings or managing action plans (e.g., Buneo & Andersen, 2006). Accordingly, the parietal cortical regions have been shown to coordinate not only the automatic online adjustments (e.g., Desmurget et al., 1999; Gréa et al. 2002; Pisella et al. 2000; Reichenbach et al., 2010), but also the cognitively demanding movement re-planning (e.g., Mars et al., 2007; Mutha, Stapp, Sainburg, & Haaland, 2014; O' Reilly et al., 2013; Rushworth & Taylor, 2006).

Taken together, the current P300 reflects the cognitive operations involved in movement re-planning such as updating of the internal action representation, preparation of the new movement based on the change cue as well as fast decision mechanisms required for changing the initial plan with a new one. Then, these cognitive operations together enable the corrective movement updates by cancelling the prepared, but inappropriate plan, and selecting and implementing a more appropriate alternative plan.

5.3 Future directions

The current thesis investigated the functional role of WM in manual action control by focusing on the neuro-cognitive costs of movement execution and re-planning for WM domains and processes. Behavioral dual-task studies have also shown the interference of WM operations with manual action control (e.g., Guillery et al., 2013; Guillery et al., 2017; Pardhan & Zuidhoek, 2013). For example, Guillery and colleagues (2013) showed that concurrent WM task interfered with planning and execution of grasping movements as demonstrated by the increased duration of initial force scaling during planning and increased application of grip force during execution. Similarly, the neurophysiological correlates of the interference of WM with separate movement phases can also be investigated. For example, with the current cognitive-motor dual-task paradigm, it can be investigated whether maintaining the information into WM would interfere with movement preparation during the period between the directional arrow and target hit. One of the ERP components related to movement phases is the lateralized readiness potential (LRP) which appears over the contralateral side of the effector performing a movement (e.g., Vaughan, Costa, & Ritter, 1968; for a review, see Shibasaki & Hallett, 2006). The LRP has been shown to be sensitive to the extent of the preparation for an upcoming movement such as known direction (e.g., Verleger, Vollmer, Wauschkuhn, Van der Lubbe, & Wascher, 2000; Wauschkuhn, Wascher, & Verleger, 1997) or known effector (e.g., Osman, Moore, & Ulrich, 1995; Wauschkuhn, et al., 1997). Accordingly, it can be investigated whether the concurrent WM maintenance would interfere with prepared and re-planned movements to the same extent by comparing the LRPs of each movement type.

The neurophysiological correlates of separate cognitive operations involved in movement re-planning, and their interactions with WM can also be investigated. For example, it has been shown that movement re-planning engages in error monitoring (e.g., Holroyd & Coles, 2002; Rodríguez-Fornells et al., 2002) or motor inhibition (e.g., Kok et al., 2004; Swann et al., 2009). ERPs with their high temporal resolution and ability to separate each process in time and spatial domain can allow for the investigation of the functional interactions of each operation with WM separately. Hereby, the shared neuro-cognitive resources between movement re-planning and WM can be clarified further.

In the current studies, participants engaged in a power grip for grasping a fixed-sized sphere with a familiar round shape. In natural environments, people grasp objects with a variety of sizes and shapes as well as perform different grip types such as precision grips (e.g., Feix et al., 2016). Besides the physical object properties, the conceptual object knowledge including affordances also influence the way people grasp objects (e.g., Herbort et al., 2017; Rounis et al., 2018). Therefore, extending the current target object (i.e., sphere) to different object groups such as objects requiring precision grips, unfamiliar objects or tools can provide generalizability of the current findings. Moreover, besides grasping movements, non-prehensile manual actions such as gestures are also commonly performed in natural environments (e.g., Fragaszy & Crast, 2016). Hence, the functional role of WM in different manual actions can also be investigated. Accordingly, such investigations can further the understanding of how the human brain produces the huge variety of skilled manual actions by integrating the motor and cognitive systems.

The current thesis investigated the manual action-WM interactions with healthy, young university students. However, the same paradigm can also be applied to different populations such as the elderly or the experts in sport. Hence, it can be investigated how different groups coordinate motor and cognitive tasks, and how they benefit from WM resources while performing manual actions.

For the elderly, it has been shown that manual dexterity as well as action flexibility decline with age (e.g., Trewartha, Penhune, & Li, 2011; Vasylenko, Gorecka, & Rodríguez-Aranda, 2018). Moreover, like other skilled motor actions, manual actions become more dependent on cognitive processes (for a review, see Li, Bherer, Mirelman, Maidan, & Hausdorff, 2018). However, cognitive abilities including WM capacity also decline (e.g., Reuter-Lorenz & Park, 2010). Accordingly, the functional interactions between manual action control and WM among the elderly would be different from the interactions among young university students. Therefore, investigating the manual action-WM interactions among the elderly can provide insights into the neuro-cognitive mechanisms underlying manual action control for this particular group. Understanding the manual action-cognition interactions, then, can be integrated into the assistive technology for the elderly such as tool usage in intelligent apartments.

For the experts in sport, the better WM capacity has been shown compared to the novices (e.g., Moreau, Morrison, & Conway, 2015; for a review, see Moreau, 2015). Moreover, within the framework of the CAA-A (Schack, 2004), it has been shown that experts have better organized knowledge structures stored in LTM, which then also affect the ability to efficiently use WM capacity. Considering that most of the sports require manual object manipulation, it is important to understand how and what extent the sport experts require WM resources while performing manual actions. Therefore, investigating the neuro-cognitive mechanisms of manual action control by separating movement phases as well as WM domains and processes can clarify the WM resources the the experts benefit while performing manual actions. Such an investigation, then, can be applied to other motor actions as well as used for developing efficient motor training programs. Moreover, such an investigation can also contribute to the detailed examination of the WM structures in the cognitive architecture of complex movements in the framework of the CAA-A.

The current findings can also be applied to different fields outside the human research such as cognitive robotics or medical rehabilitation including prosthetic devices (e.g., Andersen, Hwang, & Mulliken, 2010; Schack & Ritter, 2013). Humans perform manual actions in natural environments with a variety of movement types as well as with an ability to rapidly adapt ongoing movements to the changing action demands. Therefore, for an efficient human-robot interaction, it is critical to develop the robots which can perform manual actions comparable to human actions in terms of variability and flexibility. Such developments can enable robots behave competently in natural environments. Hereby, robots can interact with humans more efficiently by meeting the changing demands of environments as well as specific needs of different populations. For example, assistant robots for the elderly or disabled can become more responsive to the individual needs. Therefore, the cognitive robotics should make use of the human research and integrate that knowledge into the robotics for providing rapid, precise and flexible robot actions.

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*** The reference list for the General Discussion section includes only the references which are in addition to the General Introduction section.**

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6 CONCLUSIONS

CHAPTER 6

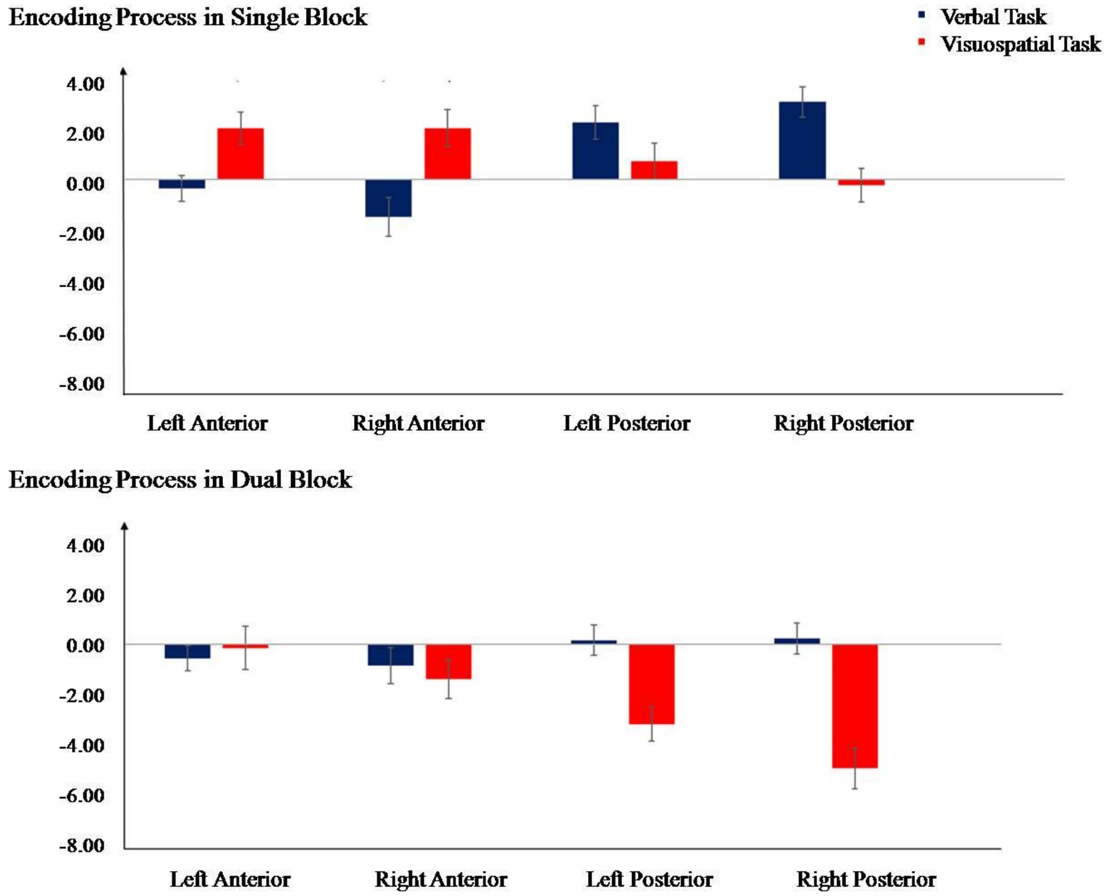
Motor control is important in every aspects of life from daily life activities to complex sport settings. The current thesis investigated a specific group of motor actions, manual actions, which we perform with precision and flexibility for performing almost any activities during a day such as grasping a coffee cup in the morning, communicating with other people by gestures or written text, hitting a ball during a sport, playing a musical instrument, or even performing seemingly pure cognitive tasks such as writing a thesis. Accordingly, it is important to get deeper understanding of how the human brain performs a variety of competent actions. Such an understanding can also serve to meet the needs of specific populations such as the elderly requiring care or the sport experts requiring motor skill learning as well as to develop technological systems which can interact with humans competently in natural environments.

The current thesis, to the best of my knowledge, for the first time investigated how and what extent manual actions are functionally correlated to WM and what the underlying neurophysiological correlates are. The current findings have shown that the neurophysiological interactions between manual actions, in terms of grasp-and-place movement, and WM are complex and dependent on many factors such as movement phase, WM domains and processes. Accordingly, these findings have shown the importance of the systematic investigations of the variables shaping the interactions with a reliable, precise measure such as ERPs.

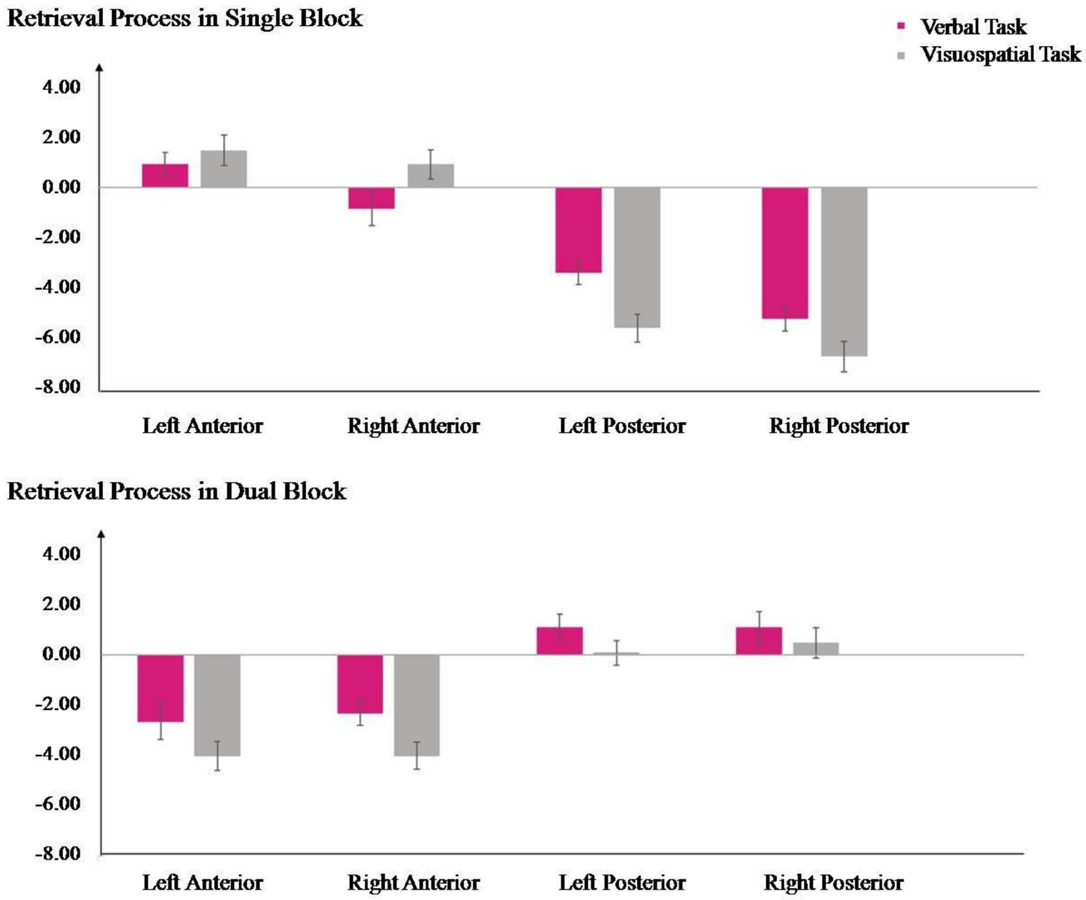
The current findings pointing out the domain interactions between manual action control and WM fit to the WM theories which suggest a functional role of WM in motor control. Moreover, these domain interactions also fit to the motor control theories which focus on the cognitive control of motor actions. Accordingly, the current findings relate to the neuro-cognitive mechanisms underlying manual action control and the role these mechanisms play in the performance of specific movement phases. Importantly, the current findings also contribute to the understanding of movement re-planning, which has been frequently suggested to be the hallmark of cognition, by providing a systematic investigation of the neurophysiological correlates of movement re-planning in relation to cognition.

Taken together, the current thesis promotes the in-depth knowledge about how the human brain plans, executes and adapts rapid, precise and flexible manual actions in complex, dynamic natural environments. Accordingly, the current thesis provides the input for the manual intelligence primarily in the field of human cognitive neuroscience, and also in the other related fields such as cognitive robotics.

SUPPLEMENTARY MATERIAL



Supplementary Figure 1. Bar chart for the encoding process in single and dual blocks. This bar chart represents the mean ERP values from 6 recording electrodes between 200-400 ms for each ROI. The blue bars represent the mean values for the verbal task and red bars represent the mean values for the visuospatial task. These mean values were entered in the four-way repeated measures of ANOVA with the factors *task block*, *WM task*, *hemisphere*, *AP*, which revealed a significant four-way interaction.



Supplementary Figure 2. Bar chart for the retrieval process in single and dual blocks. This bar chart represents the mean ERP values from 6 recording electrodes between 250-650 ms for each ROI. The pink bars represent the mean values for the verbal task and grey bars represent the mean values for the visuospatial task. These mean values were entered in the four-way repeated measures of ANOVA with the factors *task block, WM task, hemisphere, AP*, which revealed a significant three-way interaction (*task block, WM task, AP*).